ABSTRACT

Title of Dissertation: NOVEL APPROACHES TO STUDYING BIODIVERSITY
                         IN REMOTE AREAS: DISTRIBUTION OF LICHENS
                         AND PENGUINS ACROSS THE ANTARCTIC
                         PENINSULA.

                         Paula Victoria Casanovas, Doctor of Philosophy 2013

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Biodiversity inventories are a critical resource, providing baseline information for assessing environmental changes over time. In many cases, the underlying datasets are generated by "opportunistic" sampling efforts or they are consolidated from diverse datasets collected for different purposes. These datasets are typically patchy and incomplete, requiring the use of sophisticated statistical analyses. The Antarctic Peninsula (AP) is one of those areas where direct observation of species distribution is difficult; it is also an area that in recent decades has been experiencing important environmental changes, which influence population and ecosystem dynamics. I addressed biogeographical questions in the AP archipelago, using remote sensing and opportunistic

data sets for two very different groups of organisms: lichens and penguins. Although taxonomically different, both groups are key components of the AP terrestrial ecosystem, and share the need to couple biodiversity surveys with modeling to understand species distribution and abundance patterns in large areas of remote wilderness.

The results of this dissertation work are interesting to polar biologists, because evidence suggests that the input of nutrients by seabirds can significantly impact floral diversity and abundance in nutrient-poor polar communities. The datasets and protocols for data collection and analyses generated in this project are valuable in themselves for the scientific community. They could be used as the basis for a valuable and practicable monitoring program and procedures for the evaluation of the data derived from it. In the Antarctic Peninsula in particular, this information will aid in the delineation and management of protected areas, as well as in the evaluation of the impacts of climate change and human visitation to the most traveled locations.

Furthermore, this research provided an example of how an approach that integrates the use of existing remote-sensing products with independent ongoing field sampling efforts, "citizen scientist" data collection, and historical datasets can yield low-cost, high-benefit studies that can be useful both to understand how species respond to their environment, and to help environmental managers to predict and cope with imminent changes due to global warming.

NOVEL APPROACHES TO STUDYING BIODIVERSITY IN REMOTE AREAS: DISTRIBUTION OF LICHENS AND PENGUINS ACROSS THE ANTARCTIC PENINSULA.

By

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2013

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Preface

Antarctica: the windiest, coldest, driest, wildest continent on earth.

Antarctica is immense in all possible dimensions. the silence is immense, everything seems suspended in time by layers of ancient snow. the noise is immense, glaciers calving, penguin calling each other in organized cacophony. the smell is immense, guano and elephant seals. the sky is immense, deep blue or orange or red, it extents infinite above as it does the sea below.

Antarctica is powerful in all possible dimensions. from peace to torment in hours or minutes. Proud mountains stand stoically againts the fuiry of the wind. the wind has no mercy and nor does the ice. it expands crashing rocks and covering the ocean with its thick and cold skin. life and death are subject to this power.

Antarctica is beautiful in all possible dimensions. beautiful because it is immense and because is powerful. beautiful because is full of mysteries and contradictions. beautiful because is simple but is complex. as with all beautiful things it is painful to think that she could be subdue by the hands of my kind.

Dedication

A Eduardo Zattara,

compañero de aventuras

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Chapter 1: Introduction

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assessing environmental changes over time (Mittermeier et al. 1998; Myers et al.

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sampling efforts (i.e. sampling done at sites and times that are not planned or chosen

in advance) or they are consolidated from diverse datasets collected for different

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requiring the use of sophisticated statistical analyses to make sense of them. The

Antarctic Peninsula (AP) is one of those areas where direct observation of species

distribution is difficult; it is also an area that in recent decades has been experiencing

important environmental changes, which influence population and ecosystem

dynamics (Smith & Stammerjohn 2001; Clarke et al. 2007). I addressed

biogeographical questions in the AP archipelago, using remote sensing and

opportunistic data sets for two very different groups of organisms: lichens and

penguins. Although taxonomically different, both groups are key components of the

AP terrestrial ecosystem, and share the need to couple biodiversity surveys with

modeling to understand species distribution and diversity patterns in large areas of

remote wilderness.

Antarctic Peninsula: climate change, tourism and biodiversity conservation

      The marine environment of the Antarctic Peninsula (AP) is characterized by a

highly variable seasonal sea ice zone, and both ice-free and glacier covered islands and coastal areas (Smith et al. 1999). AP ecosystems have been facing rapid changes in the last century. First, this region has experienced significant increases in air temperature (King 1994; Smith & Stammerjohn 2001; Vaughan et al. 2003; Clarke et al. 2007), accompanied with increases in precipitation (Turner et al. 2005), the loss of winter sea ice (Clarke et al. 2007; Murphy et al. 1995), and subsequent exposure of new terrestrial habitats (Clarke et al. 2007). The mean rate of warming for AP climate stations is 3.7 ± 1.6 ∘C (century^{-1}) (Vaughan 2006), several times the rate of global warming (0.6 ± 0.2 ∘C during the 20th century) (Houghton 2001) and differs from the rate of other continental stations that have not experienced such rapid climate warming. This change in temperature might have a deep impact on the fauna and flora present in the AP. Second, tourism has increased exponentially since the late 1980s. It is clear that in the last two decades, neither the harsh weather nor the geographic isolation deterred tourists from choosing the AP as a vacation destination (Stewart et al. 2005). For example, from 1989/90 to 1998/99 the number of zodiac landings increased by 423% (Naveen et al. 2001). Environmental impact is now one of the most important issues surrounding tourism in Antarctica (Stewart et al. 2005). Both tourists and wildlife are concentrated in the relatively tiny

fraction of Antarctica that is coastal and free of ice in the summer, and this activity leads to concern over similar concentration of environmental impact (Stewart et al. 2005). Furthermore, tourism is concentrated during the austral summer, coinciding with the reproductive period of Antarctic flora and fauna. Research has also highlighted the AP's vulnerability to human-mediated introduction of both

native and alien species (Convey et al. 2000; Smith 1996), spread of human-associated pathogens (Bonnedahl et al. 2005), and transportation accidents (Lynch et al. 2010). However, even though tourists represent a major threat, they could also offer a huge resource for scientific monitoring of wildlife.

While most studies in the AP have focused on specific locations, large scale biological surveys done by experts and non-specialists, historical datasets, and remote sensing data can be combined to identify key habitats important for a variety of broad-distributed species. Lichens and penguins are key components of the AP coastal areas. Given the spatial extent and remoteness of the AP, sampling efforts undertaken by non-specialists, combined with independent ongoing field sampling efforts for other organisms (including penguins), are a powerful tool to study AP terrestrial ecosystems. Furthermore, large scale biological surveys and remote sensing data can be used to identify key habitats important for a variety of species distributed over large areas. For this dissertation, I combined existing valuable data and novel sampling and analysis techniques in a low-cost, high- benefit approach that increase the understanding on how species respond to changes in their environment, and also to help environmental conservation.

Lichens

Lichens are exceptional organisms to address biogeography questions in the Antarctic Peninsula. First, lichens are the dominant macrophytes in the terrestrial Antarctic ecosystem (Øvstedal & Smith 2001). Favorable habitats in the maritime Antarctic host cryptogamic communities comprising carpet- and turf-forming mosses

and lichens; extensive vegetation communities are limited to a narrow elevational range in selected coastal regions (Convey et al. 2008). Lichens are capable of tolerating extreme conditions, such as low and rapidly fluctuating temperatures and low tissue water contents (Convey et al. 2000). Second, Antarctic lichens are long-lived organisms with a high habitat specificity, which means that they can be used to estimate species diversity at all times of the year. Thirdly, literature on lichens as biomonitors in other parts of the world is enormous and can be drawn upon as a resource (Nimis, Scheidegger, & Wolseley 2002). Lichen communities have proven to be useful indicators in a range of different terrestrial ecosystems because they are notably sensitive to environmental stress (McGeoch & Chown 1998). One potential response to environmental change is a change in lichen biodiversity. Climate change can influence lichen growth and ecology, either directly by interfering with major physiological processes (Schroeter et al. 1997; Schroeter & Scheidegger 1995), or by altering relationships between species through competitive displacement (Vaughan et al. 2003) and other mechanisms.

Few trained lichen experts are available to do all the monitoring needed to establish biodiversity inventories and baseline data collection in the AP terrestrial ecosystem. The use of historical datasets has been the only means of studying biodiversity patterns along the Antarctic Peninsula. The first chapter of this dissertation is an analysis of these datasets, testing alternative biogeographical hypotheses that would explain the distribution of lichen and moss biodiversity along the AP. The main results from this work demonstrate that patterns of moss and lichen biodiversity are highly scale-dependent and largely unexplained by the biogeographic

variables found important in other terrestrial systems globally. Even though very useful, the datasets gathered from museum collections used for this study are patchy and incomplete. These lead to the following two chapters of this dissertation, where I design a sampling technique to be performed by non-specialists, and then use it to develop a database on lichen diversity for the Antarctic Peninsula.

Monitoring protocols which can be performed by non-specialists are the best choice in the Antarctic Peninsula, where the logistics of field work are very difficult and expensive. In the second chapter of this dissertation, I propose a "citizen scientist" approach to data collection in which lichen photographs are used to identify parataxonomic units (PUs) that act as species surrogates to rapidly build databases on biodiversity. I describe and test a protocol for collecting preliminary information on macrolichen diversity using data collected as part of the Lichen Biomonitoring Project (LBP) at George Mason University for validation. Furthermore, I propose a mechanistic method for the estimation of PU richness, taking advantage of a sampling design that allows us to explicitly model PU detection probability. For all park units, the observed number of PUs did not differ significantly from the observed or estimated number of species. This protocol combining citizen science with parataxonomy allows for rapid assessment of diversity in areas that lack a sufficient number of taxonomic experts.

Once this technique was proved to be appropriate for estimating lichen diversity, I developed a database on Antarctic Peninsula lichens. The third chapter of this dissertation work describes this database, validates the data using photographs of Antarctic lichens from the Smithsonian collections, and shows examples of data

applications. The dataset of lichens of the Antarctic Peninsula developed here is unique for addressing a broad number of ecological questions regarding Antarctic Peninsula lichen flora, as well as providing preliminary information useful for identifying areas for protection and priorities for future research.

The penguin-lichen relationship

Although terrestrial Antarctic ecosystems are nutrient-poor, dense colonies of seabirds produce substantial volumes of guano that provide significant sources of nutrient input (Hutchinson 1950) with substantial effects on plant species richness (Ellis 2005). Penguins constitute the vast majority of avian biomass in the region, and as such their guano is an important component of the maritime Antarctic ecosystem (Tatur, Myrcha, & Niegodzisz 1997). In comparison with flying birds, the nutrient concentration (in particular phosphorus and nitrogen) near penguin colonies is hundreds of times higher than in sites unaffected by penguins, while the concentration near nesting flying birds is between 8 and 11 times higher than sites far from breeding sites (Ryan & Watkins 1989; Leishman & Wild 2001).

The effect of seabirds on vegetation patterns in the AP is widely recognized (Smith 1978; Tatur 2002). Many studies emphasize that, on a local scale, "the species richness of the Antarctic vegetation is probably greatest when intermediate nutrient levels occur" (Smykla et al. 2007). For example, R.I.L. Smith (1995) observed that lichens at Signy Island growing in conditions enriched by nitrogenous compounds derived from populations of seabirds have relatively rapid colonization and growth rates, reaching 40-90 percent cover in 20 years. At King George Island, a series of

vegetation zones are associated with penguin rookeries. Toxic levels of manuring and trampling next to the colonies cause vegetation damage, but a decrease in penguin-derived fertilized input at around 500 meters from the colonies allow nutrients to fall to levels favorable for the growth of many taxa (Smykla et al. 2007). Penguins influence considerable areas of the Antarctic terrestrial ecosystem (Greenfield 1992; Erskine et al. 1998; Tatur 2002; Park et al. 2006), because water runoff and strong winds redistribute fine particles of guano, nutrient laden solutions, and volatilized ammonia over a much greater area than nesting colonies themselves (Smykla et al. 2007).

The relationship between penguin colonies and lichen diversity has been only studied at a local scale, where researchers looked at the direct impact of the nutrient input on the lichen communities. Chapters one and three of this dissertation test the relationship between penguin colonies and lichen diversity at a larger scale, looking at different sites all along the Antarctic Peninsula. Using two independent datasets (historical data from herbaria records and photodocumentation data from the citizen science surveys), I demonstrate that the size of penguin colonies is positively correlated with the number of lichen species, for small and medium size colonies. This not only demonstrate that the relationship between lichens and penguins is robust, but also that the photodocumentation technique proposed can be used to analyze ecological relationships among lichens and other organisms.

Penguins

Penguins, adapted to polar and sub-polar environments (Stonehouse 1970), have been found to be good indicators of environmental change because of their nesting and dietary restrictions (Smith et al. 1999; Emslie et al. 2004; Forcada et al. 2006). Penguin populations on the western side of the AP have been changing over the last 50 years, and several studies have highlighted environmental drivers associated with these changes (Smith et al. 1999; Croxall, Trathan, & Murphy 2002). While Adélie penguins (*Pygoscelis adeliae*) and Chinstrap penguins (*P. antarctica*) are declining in many sites, Gentoo penguins (*P. papua*) are increasing in abundance and expanding their range southward (Lynch, Naveen, & Fagan 2008). Data from paleontological and modern censuses suggest that penguin distributions are undergoing a fundamental reorganization due to climatic factors that influence their long-term recruitment (Smith et al. 1999), highlighting the sensitivity of the Antarctic ecosystem to climate alteration.

The distribution of penguin colonies along the AP has been recorded over the last 15 years for 128 sites by the Antarctic Site Inventory (ASI), which is a long term monitoring program of AP breeding birds undertaken by Oceanites, Inc, a nonprofit, science and educational foundation. The ASI is unique among penguin research programs in that it encompasses the entire Peninsula and is thus an excellent platform for the study of Antarctic biogeography (Lynch et al. 2008). The broad nature of this dataset is ideal to explore what factors drive penguin distributions and how penguins relate to other organisms in the Antarctic terrestrial ecosystem.

For the fourth and last chapter of this dissertation I study the relationship

between the distribution along the Antarctic Peninsula of three species of penguins (*Pygoscelis adeliae, P. antarctica, P. papua*), and environmental factors that are most effectively measured at broad scales with remote sensing products (sea surface temperature, chlorophyll-a concentration, snow cover and sea-ice extent, using Aqua and Terra MODIS and SeaWiFS data) and the characteristics of the bathymetry near the portion of the coastline harboring breeding colonies. I test how these variables influence the distribution of breeding penguin populations.

As glacial retreat opens up new areas suitable for colonization by penguins, lichens and mosses, it might be expected that the expansion, reorganization, or colonization by breeding penguins at some sites may accelerate the establishment of lichens relative to newly created ice-free areas that lack breeding penguins. Intensive and regular floristic surveys at sites that have recently become ice-free will help identify the extent to which penguins may impact the dynamics of lichen establishment.

Chapter 2: Multi-scale patterns of moss and lichen richness on the Antarctic Peninsula

Abstract

Mosses and lichens are the dominant macrophytes of the Antarctic terrestrial ecosystem. Using occurrence data from existing databases and additional published records, I analyzed patterns of moss and lichen species diversity on the Antarctic Peninsula at both a regional scale (1° latitudinal bands) and a local scale (52 individual snow- and ice-free coastal areas for mosses and 56 for lichens) to test hypothesized relationships between species diversity and environmental factors, and to identify locations whose diversity may be particularly poorly represented by existing collections and online databases. I found significant heterogeneity in sampling frequency, number of records collected, and number of species found among analysis units at the two spatial scales, and estimated species richness using projected species accumulation curves to account for potential biases stemming from sample heterogeneity. The estimates of moss and lichen richness for the entire Antarctic Peninsula region were within 20% of the total number of known species. Area, latitude, spatial isolation, mean summer temperature, and penguin colony size were considered as potential covariates of estimated species richness. Moss richness was correlated with isolation and latitude at the local scale, while lichen richness was correlated with summer mean temperature and, for 17 sites where penguins where present with less than 20,000 breeding pairs, penguin colony size. At the regional

scale, moss richness was correlated with temperature and latitude. Lichen richness, by contrast, was not significantly correlated with any of the variables considered at the regional scale. With the exception of temperature, which explained 91% of the variation in regional moss diversity, explained variance was very low. The results show that patterns of moss and lichen biodiversity are highly scale-dependent and largely unexplained by the biogeographic variables found important in other systems.

Introduction

Mosses and lichens are the dominant macrophytes in the terrestrial Antarctic ecosystem (Smith 1984). In some areas of the AP, moss peats have been recently exposed after burial under permanent or semi-permanent snow patches (Fenton 1982). Favorable habitats in the maritime Antarctic host cryptogamic communities comprising carpet, turf and cushion forming mosses, and crustose, fruticose and foliose lichens, but extensive moss and lichen dominated communities are restricted to a small altitudinal range (to c. 150 m above sea level) along coastal regions (Convey et al. 2008), and rarely extend more than a kilometer inland. Only 5 % of bryophytes known from the Antarctic are endemic (Ochyra, Bednarek-Ochyra, & Smith 2008), consistent with a hypothesis of extinction through glaciation followed by recent recolonization after glacial retreat (Convey et al. 2008). In contrast, Antarctic lichens, about 50% of which are endemic (Øvstedal & Smith 2001; Convey et al. 2009), may have an ancient vicariant distribution (Peat, Clarke, & Convey 2007; Rogers 2007).

Antarctic Peninsula biogeography is unique due to its geographical isolation

and pronounced latitudinal gradients, accompanied by temperature extremes, aridity, seasonal day length, freeze-thaw cycles, katabatic winds, and soil cryoturbation (Kennedy 1999). The AP is climatically less extreme than the rest of the Antarctic continent, and shares more characteristics with subpolar glacial systems (e.g., coastal Patagonia and sub-Antarctic South Georgia) than with the cold ice sheets covering the rest of the Antarctic continent (Vaughan 2006). The South Sandwich, South Orkney and South Shetland Islands form part of the Scotia Ridge, an intermittent arc of islands linking Tierra del Fuego and South Georgia with the AP (Oliver, Jago, & James 1983). The eastern and western portions of the AP also display major climatic and biological differences. The marine environment of the western AP exhibits a much more variable seasonal sea ice zone, and there is far more ice-free land on the western than in the eastern coasts (Smith 1996; Smith et al. 1999).

The ice-free coastal areas of the AP are an excellent system for the study of biodiversity patterns resulting from recent deglaciation. The region contains approximately 2700 islands and rock islets with at least a small area free of snow and ice in an island archipelago stretching 1500 km and 8 degrees of latitude. Previous research has applied the equilibrium theory of island biogeography proposed by MacArthur & Wilson (1963) to some Sub-Antarctic and Southern Ocean islands (without focusing on the AP) in search for determinants of biogeography (Chown, Gremmen, & Gaston 1998). These authors have found that island area partially explains the patterns of plant biodiversity in this island system, but that temperature also plays a role in determining plant richness. Another widely accepted biogeographical pattern is that of a marked decline in biodiversity with increasing

latitude and climatic severity (Convey 2001; Peat et al. 2007).

A major biotic factor that influences floristic biodiversity in the AP islands is allochthonous input of nutrients by seabirds and seals at sites where they breed, moult or rest (Smith 1988; Ryan & Watkins 1989; Leishman & Wild 2001; Smykla, Wołek, & Barcikowski 2007). Penguins, in particular, account for up to 70-80% of avian biomass in the Antarctic (Tatur, Myrcha, & Niegodzisz 1997; Shirihai 2008) and nest in large colonies that, through their accumulated excreta, contribute significantly to the local nutrient status of the substratum (Myrcha, Pietr, & Tatur 1985; Smith 1985; Tatur 2002).

Many authors have recognized the important role of spatial scale in the resolution of geographical patterns (Hutchinson 1953; Ricklefs 1987; Wiens 1989; Levin 1992; Crawley & Harral 2001). Species richness patterns are a function of the scale at which they are observed because the mechanisms affecting species richness are scale-sensitive (Lyons & Willig 1999; Rahbek 2005). The study of Antarctic biogeography of any terrestrial organism is complicated by highly heterogeneous but generally sparse sampling. Even when an area has been visited by scientists, many species will remain undetected because of the differential abundance and likelihood of detection of different types of organisms, and the highly variable expertise of the collectors. Because the data available for the study of Antarctic biogeography are strongly dependent of sampling effort (Chown & Convey 2007), it is critical to address heterogeneous sampling before making inference on empirical patterns of richness. In this analysis, I test various biogeographical determinants of the richness of mosses and lichens at two spatial scales: 1° latitudinal bands (regional scale), and

individual snow- and ice-free coastal areas (local scale). I also identify research priorities that address the challenge of assessing patterns of biodiversity in the Antarctic.

Several analyses have examined the biodiversity of particular islands in the AP. Some examples of these include Ochyra (1998) and Kim et al. (2007) at King George Island, Convey et al. (2000) at Charcot Island, Marshall & Convey (1997) and Smith (1972) at Signy Island, and Smith (1982, 2005) at Anvers Island, Signy Island and Deception Island. Peat et al. (2007) examined the relationship between ice-free ground and lichen and mosses species richness in one degree latitude and longitude boxes, and latitudinal gradients of species richness for the entire Antarctic continent. However, no previous study has examined the broad-scale species richness patterns on the AP from information on individual snow- and ice-free coastal areas, nor the relationship between spatial scale and species richness in the Antarctic.

Materials and Methods

Study Area

I considered moss and lichen records for the Antarctic Peninsula between 60°S and 68°S. At the local scale, the number of sites used in this study (52 sites for mosses and 56 for lichens, all with at least 7 specimens each) provide a broad cross-section of variation in the predictor variables analyzed (Figure 2.1). All sites are separated from each other by water or permanent ice (see Appendix 2.1). At a regional scale, six latitudinal bands between 67°S and 60°S were used for this study

(the band [61°S, 62°S] was not considered because it had less than 50 specimens).

Database

I assembled a database containing records from collected specimens and field studies of mosses and lichens undertaken on the Antarctic Peninsula since 1843. I did not include data on liverworts in this work. Data from historical collections and observations of Antarctic lichens and mosses can be found in the Antarctic Plant Database (APD: http://www.antarctica.ac.uk/Resources/BSD/PlantDatabase/ index.html), and the Australian Antarctic Data Centre (Australian Antarctic Division's herbarium database: http://data.aad.gov.au/), both of which are compiled under the Evolution and Biodiversity of the Antarctic website (EBA: http://www.eba.aq/).

I also conducted a broad literature search for records not included in the above databases, querying electronic resources for studies at the Peninsula-scale, or site-specific studies at each site included either in the Antarctic Site Compendium (Naveen & Lynch 2011) or each site with at least one record in the APD and Australian databases (see Appendix 2.2). I used current nomenclature and the currently accepted species name where synonymy occurred. Using (Øvstedal & Smith 2001, 2009; Ochyra et al. 2008) as references, I amended the nomenclature of every record as needed. I only included specimens that were determined to the species level. I did not include lichen specimens determined by C. W. Dodge or any checklists written by Dodge in this study because many of the species described by Dodge are no longer accepted as valid (Castello & Nimis 1995), unless these specimens had been redetermined. Potential correlates of lichen and moss diversity included

geographic factors (ice-free area, latitude, isolation, and mean temperature), as well as abundance of breeding penguins at the site. Table 2.1 details the rationale for the use of these variables in the analysis, the variable estimation procedure, and the data sources. The Antarctic Digital Database (BAS, SPRI, & WCMC 1993) provided the geographic component of our database.

Analyses

Estimation of species richness

Occurrence data are strongly influenced by sampling effort and sampler expertise, as many species may remain undetected due to their low abundance, small size, poor visual prominence, occupancy of cryptic habitats, etc. For example, some coastal communities of brightly colored lichens such as *Caloplaca spp.* and *Xanthoria spp.* can be seen from afar, while other lichens are more difficult to find, such as those occurring in the fissures of rocks. Also, the expertise of the collector is an important issue when considering sampling effort. To address this problem, I estimated the number of species for each sampling unit (snow- and ice-free patches, latitudinal bands, and the whole Peninsula) using an approach based on species accumulation curves (Soberón & Llorente 1993). As sampling effort, defined by the total number of specimens collected, increases at a given sampling unit, the number of species represented should saturate toward the true species richness. To generate a smoothed species accumulation curve for a sampling unit, I first calculated an individual-based rarefaction curve. I did this by randomly ordering the specimens of a given sampling unit, and then calculating the cumulative number of species represented following the

addition of each new specimen. I used all the specimens that are described at the databases and papers used for this study. I repeated this procedure 100 times for each sampling unit and took the mean of the 100 curves. To calculate asymptotic species richness I fit a Michaelis-Menten curve (Soberón & Llorente 1993; Colwell & Coddington 1994) to the smoothed species accumulation curves of each sampling unit. Even though the Michaelis-Menten model is known to have some pitfalls, it has been shown to perform well for a number of communities and taxa (Keating & Quinn 1998), particularly for systems, like ours, with many rare species (Soberón & Llorente 1993).

Species richness - biogeographic variables relationships

To analyze the relationship between biogeographic variables and lichen and moss species richness, I plotted estimated species richness as a linear function of each predictor variable. To account for variable uncertainty in estimated species richness across sampling units, I used weighted regressions with weights proportional to inverse variance of the species richness estimate on the $\log_{10}$ scale.

I $\log_{10}$-transformed all variables; this approach is widely used in biogeographical studies, including (Peat et al. 2007), and allows for direct comparison with these previous studies. Sites were considered outliers, and removed from the regression analysis, if their Cook's distances (a normalized measurement of the influence of each point on the predicted mean values) was larger than 1 (Cook & Weisberg 1982). For the regressions with penguin colony size, I used only the sites where information about penguin population was available (19 sites for lichen and

moss). I used the statistical package R for the analyses (R Development Core Team 2010).

Research priorities identification

Sites predicted to have many more species than are currently known, or that had been surveyed only once are identify as priorities for future research. Sites that are part of the Antarctic Peninsula Compendium (Naveen & Lynch 2011), sites that have Antarctic Treaty Site Guidelines for visitors, sites that are Antarctic Specially Protected Areas (ASPA) or Antarctic Specially Managed Areas (ASMA), but do not have any information on lichen or moss flora were also identified as requiring particular focus for future floristic surveys.

Results

I estimated a total of 90 moss species and 329 lichen species for the Antarctic Peninsula (68°-60° South). Table 2.2 summarizes all sites with their number of collections, number of specimens, observed number of species, estimated richness (from the Michaelis-Menten analysis) and their corresponding environmental variables. Estimated species richness was correlated with different variables depending on the taxa considered (moss vs. lichen) and the spatial scale of analysis (regional vs. local) (Table 2.3).

Latitude and isolation (as defined by the ice-free area around the sites) were correlated with moss richness at the local scale, but explained only 6% and 12% of the variance respectively. At this site level, lichen species richness was positively

correlated with penguin colony size for those smaller than 20,000 breeding pairs. Hope Bay with a larger (>100,000 breeding pairs) penguin colony, had reduced lichen species richness than expected by the relationship shown for the smaller colonies. The site composed by Baily Head and Whalers Bay at Deception Island (grouped together because there is no glacial separation of these sites) also had had reduced lichen species richness than expected. However, these are two distinct sites; while Baily Head holds one of the largest colonies of chinstrap penguins in the area in the outside of the caldera, there is no penguin colony at Whaler's Bay within the caldera. Summer mean sea surface temperature around the sites was also correlated with lichen species richness, but only explained 10% of the variance in the data. At the regional scale, moss richness was significantly correlated with summer mean sea surface temperature and latitude, whereas lichen species richness was not correlated with any of the variables considered. Because multiple comparisons make it difficult to estimate the family-wise Type I error rate and thus determine the appropriate threshold for statistical significance, I report in Table 1.3 all p-values obtained by our analysis as suggested by Moran (2003). For the purposes of discussion, I consider all correlations with $p < 0.05$ significant while recognizing the potential for spuriously significant correlations.

Of the 27 sites that have guidelines for visitors under the Antarctic Treaty System, only 7 have lichen and moss data available that can be used for biogeographic analyses. Similarly, only 14 of the 30 sites with ASPAs have data available. Of the 142 sites listed in the Antarctic Peninsula Compendium, 18 have lichen and moss data available to use on biogeographic assessments. I only

highlighted in this paper those sites that have been surveyed at least once. Sites that have not been surveyed before but are either frequently visited by tourists or are of special scientific interest could then be found either in the Antarctic Treaty Secretariat documentation (http://www.ats.aq) or in the Antarctic Peninsula Compendium (Naveen and Lynch 2011). Sites that are predicted to have many more species than are currently known are shown in bold in Table 1.2.

Discussion

The human impact in Antarctica has increased substantially in the last 50 years with an expansion of scientific research and their logistical infrastructure since the 1957/58 International Geophysical Year (Nicolet 1984), and an exponential increase in tourism since the late 1980s (Lynch et al. 2010). Both research and tourism activity are concentrated in the relatively tiny and widely dispersed areas of Antarctica that are ice-free in summer and which also support large concentrations of the continent's moss and lichen diversity (Øvstedal & Smith 2001). Human activity has been responsible for a number of changes in terrestrial communities including the introduction of non-native species (Frenot et al. 2005; Smith & Richardson 2011) and the trampling of moss beds (Tin et al. 2009). Understanding the biogeographic patterns of Antarctic mosses and lichens is essential for identifying areas of unusually high species diversity or sensitivity that may warrant special protection within the Antarctic Treaty System.

There are approximately 386 species of lichen (Øvstedal and Smith 2001), and 111 species of moss (Ochyra et al. 2008) known from the AP. Our species richness

estimators provided remarkably close estimates of Peninsula-wide diversity despite the unavoidably limited number of areas with sampling sufficient to be included in our study.

Our results support the hypothesis that different factors affect floristic richness at different spatial scales. However, our results also indicate that traditional biogeographical variables explain little of the variance in lichen and moss richness in the AP at the local scale. Lichen and moss richness patterns at these sites do not seem to support the basic MacArthur and Wilson (1963) model of island biogeography. The MacArthur and Wilson model is based on the assumption that colonization and extinction dynamics are in equilibrium, which might not be true in a dynamically-changing environment like the AP. Also, the existence of regional refuges from the last glacial maximum or centers of endemism might be a confounding factor when looking at patterns of richness with respect to distances from a source mainland.

Latitude and isolation both correlate with moss richness at the local scale but explained little variation among sites ($R^2 = 0.06$ and 0.12 respectively, Table 2.3). One source of unexplained variance could be habitat characteristics for which I have no site-specific data, such as the characteristics of substrata and abundance of water in each site (Smith 2005). Unusual species are often found in particular habitats, such as the alkaline marbles and amphibolite at Signy Island or the alkaline lava and fine ash at Deception Island (Smith 2005). This makes extrapolation between sites difficult, and argues in favor of extreme caution when considering human activities at a site that may appear species poor. While the impact of bird and seal colonies on mosses has been documented for other areas of Antarctica, especially in the Dronning

Maud Land area (Richter 1995; Kanda, Ohtani, & Imura 2002), I did not find a relationship between moss richness and penguin colony sizes in the AP.

Lichen richness at a local scale was related to summer mean temperature, but this variable also explained little of the variance among sites (R^2=0.10, table 2.3). In contrast to the results for moss, the correlation between penguin colony size and local-scale lichen richness implies that penguins can strongly influence lichen diversity at sites where they are present. Sites harboring large (>100,000 nest) penguin colonies appear to have reduced species richness, though more data on sites with large and intermediate colony size would be necessary to confirm this pattern. The effect of seabirds on vegetation patterns in the AP is widely recognized (Smith 1978; Tatur 2002). Many studies emphasize that, on a local scale, "the species richness of the Antarctic vegetation is probably greatest when intermediate nutrient levels occur" (Smykla et al. 2007). For example, Smith (1995) observed that lichens on Signy Island growing in conditions enriched by seabird-derived nitrogenous compounds have relatively rapid colonization and growth rates, reaching 40 to 90 percent cover in 20 years. In a study at King George Island, a series of vegetation zones were identified at varying distance from the island's penguin rookeries (Smykla et al. 2007). Toxic levels of manuring and trampling near to the colonies cause vegetation damage, but a decrease in penguin-derived nitrogenous input at around 500 meters from the colony allows nutrients to fall to levels favorable for the growth of many taxa (Smykla et al. 2007). Penguins influence considerable areas of the Antarctic terrestrial ecosystem (Greenfield 1992; Erskine et al. 1998; Tatur 2002; Park et al. 2006) because water runoff and strong winds redistribute fine particles of

guano, nutrient-laden solutions, and volatilized ammonia over a much greater area than the breeding colonies themselves (Smykla et al. 2007). Penguin populations on the western side of the Antarctic Peninsula have changed much over the last 50 years and are undergoing a fundamental reorganization due to climatic factors that influence their long term recruitment (Smith et al. 1999; Forcada et al. 2006; Lynch, Fagan, & Naveen 2010). As glacial retreat opens up new areas suitable for penguins, lichens and mosses colonization, it might be expected that the expansion, reorganization, or colonization by breeding penguins at some sites may accelerate the establishment of lichens relative to newly created ice-free areas without breeding penguins. Intensive and regular floristic surveys at sites that have recently become ice-free will help identify the extent to which penguins may impact the dynamics of lichen establishment. The effects of other birds and seal colonies on lichen and moss richness patterns (Allen, Grimshaw, & Holdgate 1967; Favero-Longo et al. 2011) also need further investigation, although they are likely to be a significant source of nutrients only were penguins are absent. For example, snow petrel breeding areas can affect local lichen diversity and community composition at remote continental inland sites (Ryan et al. 1989; Ryan & Watkins 1989; Øvstedal & Smith 2001).

At the regional scale 91% in the variability in moss richness was explained by summer mean sea surface temperature. However, lichen richness was not correlated with any of the variables analyzed in this paper. Lichens are extremophiles and very tolerant of a wide range of physical conditions; they are much more influenced by certain chemicals attributes, notably nitrogen and calcium (R.I.S. Smith per. comm.). Also, the differences between moss and lichen richness patterns at the regional scale

might reflect different colonization histories. From their patterns of endemicity, it has been proposed that bryophytes have recently recolonized the AP after extinction through glaciation (Ochyra et al. 2008), and our results agree with the hypothesis of recent moss dispersal from South America. On the other hand, lichen flora may have an ancient vicariant distribution (Peat et al. 2007; Rogers 2007), and therefore these lichen communities could be the results of a long history of colonization and extinction when environmental conditions differed from present day.

Spatial scale considerations are integral to the proper utilization and understanding of biodiversity data, because scale can influence the perception of biodiversity patterns and also can affect the processes that drive them (Rahbek 2005). Heterogeneous sampling presents a major hurdle to collecting accurate observations in the Antarctic Peninsula region, and our analyses have revealed the potential for this problem to confuse inference regarding the importance of various biogeographic factors. However, our analysis of lichen and moss richness patterns at different spatial scales offers a unique perspective and complements existing data from specific sites within the AP region.

Significant heterogeneity exists among sites regarding the number of surveys each received, the number of specimens that have been collected, and the number of species identified. Only a few specimens were collected at the latitudinal band between 61°S and 62°S. This might be because this coastal sector is rather inaccessible, has few potentially interesting vegetation sites, or is off the track for most ships traveling between the South Shetland Islands and the northern AP. A more detailed study of this stretch of coastline might be the target for future research. Also,

as observed by Peat et al. (2007), the lack of information on floral biodiversity on particular islands necessitates floristic surveys in certain areas. Our analysis identifies several sites with disproportionate disparities between predicted and estimated species richness. These results are specially pertinent for lichens, where even in a thorough survey, crustose lichen species are easily overlooked (R.I.S. Smith per. comm.). These sites should be priorities for future floral surveys, along with sites that are visited by tourist operators or are of importance for the Antarctic Treaty System, but have no information on floral richness. This results are relevant to the current efforts to increase Antarctic conservation in the current Antarctic Treaty protected area management system. Biodiversity inventories are a critical resource, providing baseline information for assessing environmental changes over time. This is particularly important in the Antarctic Peninsula region, where rapid climate change is already taken place (Vaughan et al. 2003; Vaughan 2006; Turner et al. 2009).

Table 2.1. Description of the geographic and biological variables used for the analyses.

Variable	Rationale	Source of information	Variable estimation
Ice-free area	Ice-free area measures the capacity of the sites to support species (MacArthur and Wilson 1963).	Antarctic Digital Database (BAS, SPRI, and WCMC 1993, last accessed April 2011).	Sum of all ice-free area available in each site in the austral summer.
Latitude	Strong trend toward decreasing richness as latitude and progression into the Antarctic increases (Convey 2001).	Antarctic Digital Database (BAS, SPRI, and WCMC 1993, last accessed April 2011).	Latitude at the center of the site.
Isolation	The potential for colonization will be determined by the proximity of vegetated sites (MacArthur and Wilson 1963).	Antarctic Digital Database (BAS, SPRI, and WCMC 1993, last accessed April 2011).	Sum of all ice-free area available in a buffer of 10 kilometers around each site, in the austral summer.
Temperature	Species must be tolerant of low temperatures (Kennedy 1999). Satellite data provide the only information on temperature at the sites studied here, because of the scarcity of Antarctic stations. Surface Temperatures (ST) at skin depth, derived from remote sensing infrared data, are a good indicator of	Summer mean sea surface temperature MODIS (Moderate resolution Imaging Spectroradiometer) product (http://oceancolor.gsfc.nasa.gov/, last accessed May 2011). The dataset used has a spatial resolution of	Average of the mean summer temperature in a buffer of 5 kilometers around each site, through 2002-2010 summers.

	near surface air temperatures. In the Antarctic, Comiso (2000) showed that ST data correlate with station temperature data (including in the analysis six stations in the AP). This is not intended to be a measurement of microhabitat temperature.	1 Km^2, and covers mostly ocean surface around the sites.	
Penguin colony-size	Penguin colonies are an important component of the maritime Antarctic ecosystem; they account for ca. 70-80% of the Antarctic avian biomass (Tatur et al. 1997, Shirihai 2008). Penguin colonies vary in size from one site to another, from a few nests to more than 100,000 nests. Penguin and other seabird colonies contribute a significant input of nutrients at the local scale and this has a major influence on floristic richness (see text).	Antarctic Site Inventory database (Lynch et al. 2008), and several papers (Appendix 2.2).	Average nest count of three penguin species together (*Pygoscelis antarctica*, *P. papua* and *P. adeliae*), throughout all visits to a given site. Only 19 of the sites used for this study had data available on penguin population sizes. The penguin colonies are located at the same snow- and ice-free coastal areas delimited for this study.

Table 2.2. Information about the sites used in this study.

Sites in bold are predicted to have many more species than are currently known. ASIC = Antarctic Site Inventory Compendium site, ASPA = Antarctic Specially Protected Area, ATSG = Antarctic Treaty site guidelines for visitors, SMT = summer mean temperature. Note that ASIC cover some (but not all) of ASPAs and ATSG. * Average nest count of three penguin species together, throughout all visits to a given site.

Site Name	Visitation guidelines		
	ASIC	ASPA	ATSG
Almirante Brown Station Vicinity	√		
Andree Island			
Arctowski Station Vicinity	√	√	
Ardley Island		√	
Barton Peninsula (King George Island)			
Barnard Point (Livingston Island)			
Blaiklock Island	√		
Byers Peninsula (Livingston Island)		√	
Claude Point (Brabant Island)			
Cockburn Island	√		
Cormorant Island			
Cuverville Island	√		√
Dorian Bay/Damoy Point	√		
Deception Island site 1	√	√	
Deception Island site 2	√	√	√
Deception Island site 3	√	√	
False Island Point (Vega Island)	√		
Ferraz Station Vicinity (King George Island)	√		
Fildes Peninsula (King George Island)		√	
Fredriksen Island			
Gamma Island			
Cape Geddes (Laurie Island)			
Gibbs Island	√		
Green Island		√	
Half Moon Island	√		√
Cape Hansen (Coronation Island)			
Hope Bay	√	√	

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Site Name			
Horseshoe Island	√		√
Jenny Island			
Jubany Station (King George Island)	√	√	
Cape Lachman (James Ross Island)			
Lagoon Island			
Lagotellerie Island		√	
Léonie Island			
Port Lockroy	√		√
Lynch Island		√	
Metchnikoff Point (Brabant Island)			
Moe Island		√	
Neko Harbor	√		√
Olivine Point (Coronation Island)			
Omega Island			
Penguin Island	√		√
Petermann Island	√		√
Rasmussen Island			
Rothera Point (Adelaide Island)		√	
Shingle Cove (Coronation Island)	√		√
Signy Island site 1			
Signy Island site 2			
Stinker Point (Elephant Island)			
Cape Tuxen			
Uruguay Island			
Vernadsky Station Vicinity	√		
Walker Point (Elephant Island)			

Table 2.2 (continued)

Site Name	Lichen Estimated richness	Observed richness	Collections	Specimens	Moss Estimated richness	Observed richness	Collections	Specimens
Almirante Brown Station Vicinity	9.93	5	2	9	22.05	13	7	29
Andree Island	103.26	14	1	16	41.21	17	1	28
Arctowski Station Vicinity	104.22	21	6	27	26	16	4	42
Ardley Island	53.05	32	10	77	42.73	16	9	30
Barton Peninsula (King George Island)	35.02	11	1	15	50.57	14	2	19
Barnard Point (Livingston Island)	21.31	11	1	21	25.01	11	1	20

Blaiklock Island	54.38	16	2	22	26.85	13	6	25
Byers Peninsula (Livingston Island)	84.82	57	3	181	44.06	39	4	314
Claude Point (Brabant Island)	39.02	10	2	13	18.17	9	2	19
Cockburn Island	63.64	33	3	66	10.36	8	3	32
Cormorant Island	17.37	8	2	14	13.49	8	1	18
Cuverville Island	70.75	34	4	62	41.3	32	7	137
Dorian Bay/Damoy Point	7.82	4	2	7				
Deception Island site 1	71.46	49	7	191	52.38	49	9	643
Deception Island site 2	51.89	38	21	157	37.95	33	27	281
Deception Island site 3	36.07	27	8	107	23.17	20	13	150
False Island Point (Vega Island)	177.15	20	2	22				
Ferraz Station Vicinity (King George Island)	251.03	60	2	77				
Fildes Peninsula (King George Island)	186.43	96	12	199	39.55	24	11	59
Fredriksen Island	52.51	10	5	12	13.26	9	5	24
Gamma Island	21.05	12	3	22	38.51	10	1	13
Cape Geddes (Laurie Island)	43.03	9	4	11	9.32	7	3	26
Gibbs Island	29.97	16	3	35	17.03	10	2	21
Green Island	83.3	23	3	32	32.82	15	4	28
Half Moon Island	33.55	13	5	21	31.74	9	3	12
Cape Hansen (Coronation Island)	74.4	23	4	34	38.47	22	5	47
Hope Bay	48.95	36	16	136	16.31	13	11	65
Horseshoe Island	52.89	17	3	24	21.5	12	4	26
Jenny Island	55.56	25	8	47	21.95	17	10	80
Jubany Station (King George Island)	56.26	20	2	29				
Cape Lachman (James Ross Island)	86.98	10	4	11	10.75	5	2	8
Lagoon Island	107.98	27	6	36	24.06	15	5	39
Lagotellerie Island	46.35	23	3	44	27.79	15	4	30
Léonie Island	117.53	55	6	104	39.57	28	8	91
Port Lockroy	21.37	14	9	48	14.25	9	9	25

Lynch Island	142.55	38	6	52	48.75	27	12	58
Metchnikoff Point (Brabant Island)	30.38	18	3	42	17.77	10	2	21
Moe Island	30.04	14	3	25	97.56	24	3	31
Neko Harbor	85.9	10	1	11	22.52	7	2	10
Olivine Point (Coronation Island)	18.1	9	4	17	55.3	23	3	39
Omega Island	21.69	9	5	17	23.14	19	10	104
Penguin Island	27.08	18	5	57	2.31	2	5	7
Petermann Island	67.19	35	9	74	30.26	24	10	118
Rasmussen Island	130.85	27	3	34	20.7	15	4	48
Rothera Point (Adelaide Island)	61.39	37	8	88	23.94	18	9	75
Shingle Cove (Coronation Island)	43.79	19	7	31	52.34	22	5	36
Signy Island site 1	202.16	160	28	853	55.39	51	30	542
Signy Island site 2	227.84	140	23	392	62.04	54	24	401
Stinker Point (Elephant Island)	46.87	15	1	21	16.77	10	1	22
Cape Tuxen	65.52	25	9	40	44.56	31	7	106
Uruguay Island	177.93	25	5	29	29.38	18	6	43
Vernadsky Station Vicinity	61.56	40	7	115	28.43	25	21	242
Walker Point (Elephant Island)	59.72	21	2	31	27.96	12	2	21

Table 2.2 (continued)

| Site Name | Environmental variables | | | | | |
	Area (m^2)	Lat	Long	Isolation (m^2)	SMT (°C)	Penguins*
Almirante Brown Station Vicinity	7.1 x 10^4	-64.9	-62.87	1.1 x 10^7	0.27	40.9
Andree Island	3.2 x 10^5	-64.52	-61.5	1.0 x 10^7	0	NA
Arctowski Station Vicinity	4.7 x 10^6	-62.17	-58.49	2.8 x 10^7	0.84	12127
Ardley Island	1.2 x 10^6	-62.21	-58.93	5.0 x 10^7	0.74	4803.24
Barton Peninsula (King George Island)	7.5 x 10^6	-62.23	-58.75	5.4 x 10^7	0.73	7872
Barnard Point (Livingston Island)	9.0 x 10^6	-62.74	-60.3	2.4 x 10^7	1.05	NA
Blaiklock Island	1.0 x 10^6	-67.55	-67.2	4.3 x 10^7	0.05	NA
Byers Peninsula (Livingston Island)	5.8 x 10^7	-62.63	-61.09	8.9 x 10^7	1.2	NA
Claude Point (Brabant Island)	1.0 x 10^6	-64.12	-62.58	3.8 x 10^6	0.93	3775
Cockburn Island	4.0 x 10^6	-64.2	-56.84	7.8 x 10^7	-0.56	NA
Cormorant Island	6.2 x 10^3	-64.8	-63.99	3.5 x 10^6	0.77	787.11
Cuverville Island	8.3 x 10^4	-64.68	-62.62	1.5 x 10^7	0.58	6915
Dorian Bay/Damoy Point	1.0 x 10^4	-64.81	-63.51	1.6 x 10^8	0.45	2273
Deception Island site 1	3.8 x 10^7	-62.94	-60.68	5.5 x 10^7	1.05	NA
Deception Island site 2	4.2 x 10^6	-62.98	-60.55	8.9 x 10^7	0.97	125000
Deception Island site 3	3.1 x 10^6	-63.01	-60.58	9.0 x 10^7	1.01	1000
False Island Point (Vega Island)	6.1 x 10^6	-63.9	-57.36	8.6 x 10^7	-0.14	NA
Ferraz Station Vicinity (King George Island)	4.5 x 10^6	-62.08	-58.41	2.2 x 10^7	0.63	19200
Fildes Peninsula (King George Island)	3.1 x 10^7	-62.19	-58.96	2.0 x 10^7	0.73	NA
Fredriksen Island	1.5 x 10^6	-60.73	-44.97	1.3 x 10^7	0.39	NA
Gamma Island	7.3 x 10^5	-64.33	-62.99	1.9 x 10^7	1.52	NA
Cape Geddes (Laurie Island)	9.9 x 10^5	-60.69	-44.56	1.4 x 10^7	0.49	NA
Gibbs Island	3.2 x 10^6	-61.48	-55.48	5.8 x 10^6	0.9	6000
Green Island	1.6 x 10^5	-65.32	-64.15	1.1 x 10^7	0.21	NA
Half Moon Island	9.4 x 10^5	-62.59	-59.92	5.4 x 10^6	1.06	6000
Cape Hansen (Coronation Island)	1.7 x 10^6	-60.66	-45.59	1.8 x 10^7	0.39	NA
Hope Bay	5.5 x 10^6	-63.41	-57.01	8.9 x 10^6	-0.46	123850
Horseshoe Island	4.7 x 10^6	-67.82	-67.29	6.2 x 10^7	0.35	NA
Jenny Island	5.5 x 10^6	-67.73	-68.38	1.0 x 10^7	0.66	NA
Jubany Station (King George Island)	2.9 x 10^6	-62.25	-58.66	2.7 x 10^7	0.9	17979
Cape Lachman (James Ross Island)	1.8 x 10^8	-63.89	-57.91	1.4 x 10^8	-0.38	NA
Lagoon Island	2.7 x 10^6	-67.59	-68.24	8.2 x 10^6	0.46	NA
Lagotellerie Island	1.6 x 10^6	-67.89	-67.4	2.1 x 10^7	0.57	NA
Léonie Island	1.2 x 10^6	-67.6	-68.34	1.1 x 10^7	0.42	NA

Port Lockroy	1.2×10^4	-64.83	-63.5	1.6×10^8	0.44	943
Lynch Island	1.4×10^5	-60.65	-45.61	1.9×10^7	0.41	NA
Metchnikoff Point (Brabant Island)	7.6×10^4	-64.05	-62.58	3.6×10^6	0.91	NA
Moe Island	1.2×10^6	-60.74	-45.68	9.4×10^6	0.46	NA
Neko Harbor	2.1×10^6	-64.85	-62.49	3.8×10^7	0.21	1057.5
Olivine Point (Coronation Island)	1.1×10^6	-60.66	-45.47	2.2×10^7	0.4	NA
Omega Island	4.0×10^6	-64.33	-62.94	1.6×10^7	1.56	NA
Penguin Island	1.8×10^6	-62.1	-57.93	1.1×10^6	1.06	8794
Petermann Island	5.3×10^5	-65.17	-64.14	2.2×10^7	0.62	4437
Rasmussen Island	1.2×10^4	-65.25	-64.09	1.6×10^7	0.28	NA
Rothera Point (Adelaide Island)	4.4×10^5	-67.57	-68.12	5.4×10^6	0.55	NA
Shingle Cove (Coronation Island)	9.0×10^5	-60.65	-45.56	2.0×10^7	0.43	3123
Signy Island site 1	2.5×10^6	-60.72	-45.6	1.4×10^7	0.44	NA
Signy Island site 2	1.1×10^7	-60.7	-45.64	7.2×10^6	0.43	NA
Stinker Point (Elephant Island)	2.8×10^6	-61.19	-55.38	1.0×10^7	0.67	NA
Cape Tuxen	1.2×10^6	-65.28	-64.11	1.2×10^7	0.24	NA
Uruguay Island	2.0×10^5	-65.25	-64.24	1.0×10^7	0.72	NA
Vernadsky Station Vicinity	5.6×10^5	-65.25	-64.25	8.9×10^6	0.74	50
Walker Point (Elephant Island)	3.4×10^5	-61.14	-54.7	1.3×10^7	0.79	NA

Table 2.3. Results of the regression analyses between environmental variables and lichen or moss richness.

Values in the table indicate p-values for the regression analyses, and values between parentheses are the R2 values for the analyses. Bold = significant, blank = Not applicable. Outliers: †Dorian Bay/Damoy Point, †† Moe Island and Penguin Island.

Variable	Lichen		Moss	
	Site	Band	Site	Band
Latitude	0.18 (0.01)	0.51 (-0.11)	**0.03 (0.06)**	**0.04 (0.58)**
Area	0.08 (0.03)	0.35 (0.21)	0.52 (-0.01)	0.69 (0.04)
Summer Temperature	**0.010 (0.10)**	0.69 (-0.19)	0.81 (-0.02)	**0.001 (0.91)**
Isolation	0.08 (0.03)		**0.009 (0.12)**[††]	
Penguins	**0.024 (0.23)**[†]		0.91 (-0.07)	
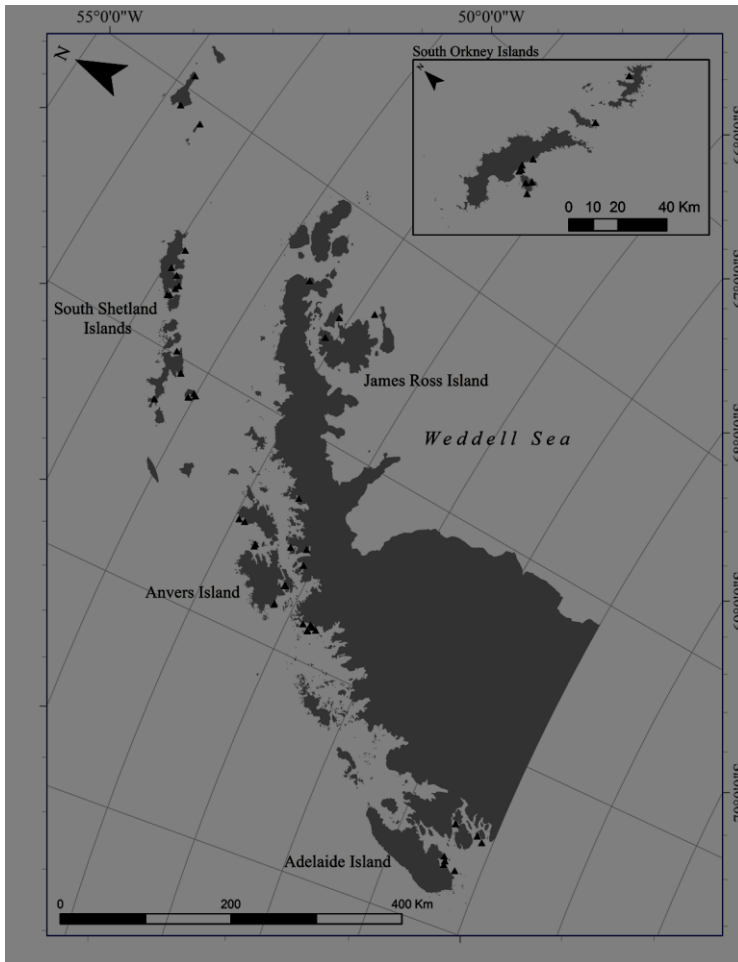
Figure 2.1. Distribution of sites with records used in this study along the Antarctic Peninsula.

Base maps are from the Antarctic Digital Database (BAS, SPRI, and WCMC 1993, last accessed April 2011). The projection used for the map is South Pole Lambert Azimuthal Equal Area, map made using ArcMap 10.0.

Chapter 3: Leveraging citizen science approaches to understanding lichen diversity.

Abstract

Lack of access to experts and the challenges associated with research permits make traditional approaches for the collection and determination of biological specimens impractical in many situations. To accelerate assessments of local biodiversity for conservation and resource management, scientists need cost-effective survey methods and/or surrogate methods for the prediction of species richness. Lichen communities are reliable indicators for the condition of many different terrestrial ecosystems because they are notably sensitive to environmental stress and represent a promising system in which to develop citizen-science based approaches. I propose a "citizen scientist" approach to data collection in which lichen photographs are used to identify parataxonomic units (PUs) which act as species surrogates to rapidly build databases on biodiversity. Each PU is defined as a visually distinguishable unit based on external morphology. Here I describe and test a protocol to collect preliminary information on macrolichen diversity using data collected as part of a Lichen Biomonitoring Project (LBP) at George Mason University for validation. The LBP has surveyed National Park Service units in the Washington, D.C. area for macrolichen diversity since 2002. Lichens from five of these units were photographically surveyed during June-August 2011. The number of specimens and PUs identified depended on photograph and specimen quality, and varied across park

units and plots. To account for variation in sampling effort, I estimated the true

number of PUs and the number of species present in each park unit using the Chao2

metric. I also propose a mechanistic method for the estimation of PU richness, taking

advantage of a sampling design that allows us to explicitly model PU detection

probability. I compared observed and estimated PU and species richness, finding that,

for all park units, the observed number of PUs did not differ significantly from the

observed or estimated number of species. I have developed a protocol combining

citizen science with parataxonomy that allows for rapid assessment of diversity in

areas that lack a sufficient number of botanical experts.

Introduction

The main objective for establishing protected areas is the conservation of

biodiversity (Margules & Pressey 2000; Sarkar et al. 2002, 2006), and the number of

species inhabiting an area is often used as a tool for setting conservation priorities

(Sarkar et al. 2006). For this reason, one of the classic measurements used for

monitoring biodiversity in protected areas is the amount and rate of change in number

of species present over time (Buckland et al. 2012). However, the estimation of

species richness, let alone estimation of change in species richness, remains a

challenge even for relatively small areas. The best method for determining species

richness involves expert collection of specimens in the field and detailed species

determinations. However, this approach is often impractical; in some geographic

areas access of experts to the field is difficult, and the time between the collection of

specimens and their identification by experts is too long to be useful for purposes of

conservation and management (Stevenson, Haber, & Morris 2003; Grantham et al. 2009).

To accelerate assessments of local biodiversity for conservation purposes, cost-effective survey methods and/or surrogate methods for the prediction of species richness are needed. A particular need exists for non-destructive sampling methods that avoid the complications associated with collection and specimen import permits. Examples of such methods can be found in acoustic surveys for birds (Brandes 2008; Depraetere et al. 2012; Tegeler, Morrison, & Szewczak 2012) and amphibians (Bridges, Dorcas, & Montgomery 2000; Acevedo & Villanueva-Rivera 2006) Combining photographic field data collection by non-experts with the use of surrogates for the determination of species richness may allow for efficient collection of preliminary diversity information and the rapid development of databases on biological diversity.

A "citizen scientist" is a non-expert person, usually a volunteer, who helps collect or process data for a scientific project (Cohn 2008). The direct participation of citizen scientists in data collection efforts provides information on spatial and temporal scales that are difficult, if not impossible, to collect using traditional scientific methods (Silvertown 2009; Conrad & Hilchey 2011; Dickinson, Shirk, et al. 2012). In addition to providing numerous scientific benefits, public involvement in biodiversity monitoring builds community support for biological conservation. The participation of lay persons in large-scale regional surveys has been successfully demonstrated in several projects, including the Open Air Laboratories (OPAL) network in England (www.opalexplorenature.org), the Protea Atlas Project (Thuiller

et al. 2004; Gelfand et al. 2005; Midgley et al. 2006), the North America Breeding Bird surveys and Christmas Bird counts (Butcher, Niven, & Society 2007), and the 4th of July butterfly counts (Swengel 1995).

An easy way for people to gather data is by photographing different organisms in their natural environments. Photographic documentation is a noninvasive technique that allows the general public to actively participate in conservation research. As digital camera technology has become cheaper and more ubiquitous, quality digital cameras previously available only to professional photographers are now widely available, and in many cases have been integrated into everyday electronics such as smart phones or tablets. A photograph, just as a physical specimen, provides a record for the scientific community to view and discuss, both in the quest for consensus regarding the organism photographed (Stevenson & Morris 2002), and as a permanent record for any necessary future revision. Purvis et al. (2002) proposed the use of digital photography of lichens not only for monitoring growth and health of specimens, but also to detect changes in assemblage composition over time.

Given that the identification of species from photographs is virtually impossible for many taxa, parataxonomic units (PUs) can be used instead of species. A PU is defined as an artificial classification unit based only on external morphology (Krell 2004). Parataxonomic units have been used for the prediction of species richness in different communities, including aquatic macroinvertebrates (Clarke, Lake, & O'Dowd 2004), colonial reef corals (Budd, Johnson, & Potts 1994), vascular plants (Garrettson et al. 1998), and insects (Oliver & Beattie 1996a; b; Basset et al. 2000).

In this work, I describe and test a protocol for rapid assessment of lichen biodiversity. Lichen communities are useful indicators for the condition of many different terrestrial ecosystems because they are notably sensitive to environmental stress (McGeoch & Chown 1998; Nimis, Scheidegger, & Wolseley 2002). From the mid-1900s to date, many different approaches using lichens as biomonitors of environmental stress have been proposed (Conti & Cecchetti 2001; Asta et al. 2002; Asta et al. 2002; Jeran et al. 2002; Castello & Skert 2005). These approaches have included methods based on different parameters, from species diversity to abundance or cover. Moreover, macrolichens as a group are useful targets for citizen science research. Indeed, working in the southeastern United States and Oregon, trained non-specialists were able to find between 65 and 90 % of the macrolichens species found by a professional lichenologist (McCune et al. 1997). For this study, I propose a survey technique combining photographic documentation by non-scientists with PU identification of lichens from the photographs. I compare the results from the photographic documentation procedure with data from a survey of lichen biodiversity where specimens were identified to the species level by an expert lichenologist. As many species and PUs are always undetected in any kind of survey, I compare not only the observed richness at each location, but also the estimated richness using a phenomenological model for non-detection (the non-parametric estimator Chao2).

Finally, I propose a mechanistic method for the estimation of PU richness, taking advantage of a sampling design that allows us to explicitly model the probability that each PU has been detected in a given survey given that it is present. Because this mechanistic method informs about the source of the failures in

detectability of every PU in the community (Dorazio et al. 2006), this approach gives more information about community composition (for example the relative presence of rare or common PUs), and could be particularly useful for designing future sampling campaigns. This is important not only in the context of PUs, but also when collecting and classifying physical specimens, which suffer from the same errors of omission or expert misidentification.

Materials and Methods

The aims of this study were to test whether or not photographic documentation of corticolous macrolichens by citizen scientists could be used to estimate species richness reliably, and to demonstrate the application of this sampling technique to more complete diversity analyses. This approach has two different challenges to overcome: the use of PUs to predict species richness and the use of data collected by non-specialists.

Reference dataset

Units of the U.S. National Park System near Washington, D.C., were surveyed as part of the Lichen Biomonitoring Project (LBP) at George Mason University during 2004, 2006 and 2009 (dataset on-line at http://mason.gmu.edu/~jlawrey/CUE/). In each park unit, several 20m x 20m quadrat plots were established. Within each plot, presences of all corticolous macrolichen species were recorded by an expert lichenologist. For the LBP, corticolous

macrolichens consisted of all foliose and fruticose lichens growing on tree bark, including those on dead and down trees.

Five of the above National Capital region park units were photographically surveyed during June-August 2011. In each park unit, plots used for the LBP were surveyed with participants instructed to take pictures of corticolous macrolichens, including those on dead and down trees. A variable number of photographers (all lacking previous expertise with lichens) participated in each survey, and different numbers of plots were surveyed at each park unit (Table 2.1).

The photographic protocol consisted of each participant taking pictures of every corticolous macrolichen they saw during a ten minute period in which they walked freely inside the plot. A black and white control scale with rule bars was included in each photograph. At each plot, two or more photographers carried out this protocol simultaneously, starting at different corners of the plot to avoid lack of independence in the observations. This multi-observer protocol controlled and standardized the sampling effort in the field, and allowed for the use of estimators of species richness that account for differences in detectability among organisms.

Before the lichens in the photos were identified to PU, the white balance in each picture was standardized using the black and white control scale for reference. Then, all possible lichens were digitally isolated from the photographs using the imageJ image processing program (Abramoff, Magalhaes, & Ram 2004; Ferreira & Rasband 2010), and given a unique identification name. Each of these isolated lichens

was considered a "digital specimen" (Fig. 3.1). Once all specimens were isolated, four different classifiers independently classified them using lichen species descriptions, photographs and distribution maps in Brodo et al. (2001). The classifiers were non-experts, but they were trained on basic lichen external morphology and taxonomy (Brodo et al. 2001; Nash 2008). The number of specimens and PUs depended on the quality of the photographs and specimens, and varied across park units and plots.

Data analyses

Richness estimations and comparison between the LBP data and the PUs data

Species richness data are always dependent on sampling effort, as many species (or, similarly, PUs) will remain undetected due to the differential abundance and detection probabilities of different type of organisms (Boulinier et al. 1998; MacKenzie et al. 2002). Collector expertise is an additional issue that can influence the success of biodiversity inventories. Species and PU accumulation curves have shown that as the number of plots increases, the number of species and PUs captured also increases. Consequently, I treated the plots in each park as sampling units and then estimated the number of PUs present in each park unit using the Chao2 estimator (Chao 1987). Likewise, I used Chao2 to estimate the number of species in each park unit from the LBP data. The Chao2 estimator estimates the number of species (or PUs) present using the frequency distributions of species (or PUs) from a series of plots at each site. I estimated PU richness for the different classifiers separately. The Chao2 estimator has been widely used for the estimation of species richness for many different organisms, including lichen communities (*e.g.* Peat, Clarke, & Convey 2007;

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Mandl et al. 2010; Spribille et al. 2010; Normann et al. 2010), and showed the least

overall bias in a review of species richness estimators (Walther & Moore 2005).

I compared PU richness with species richness from the LBP, comparing

separately the number of PUs and species observed, and the true number of PUs and

species present as estimated by the Chao2 estimator. I used a randomization method

to assess whether, for each park unit, differences between the two metrics of diversity

(PUs vs. species) were statistically significant. Specifically, I compared the observed

difference between the two metrics of richness against differences obtained from

10000 random permutations of the data between the two techniques. If the observed

difference between the PU-based richness and the species-based richness is just

another value of the distribution of differences derived from permutation, I would not

reject the null hypothesis that these two techniques are equivalent (Efron & Tibshirani

1993; Rossi 2011). I also considered the correlation between the observed richness

values obtained by the two techniques (expert survey of species vs. photographic

survey of PUs), to test whether these two methods showed the same patterns of

species diversity among park units.

I investigated the effect of the number of photographers and the number of

identifiers using a jackknife approach (Miller 1974), where I compared the observed

richness with different combinations of number of photographers and number of

classifiers. I then calculated the difference between the observed species richness

from the LBP project and the observed richness as quantified by PUs from each

combinations of photographers and classifiers.

Introducing a mechanistic method for the estimation of PU richness

To complement the phenomenological approach based on the Chao2 estimator, I developed a mechanistic model that explicitly accounts for the probability of non-detection for each PU in the dataset. To do this, I used a modified version of the hierarchical model proposed by (Dorazio et al. 2006), using multiple classifiers as replicates for each photographer analogous to multiple observers surveying the same visit, and multiple photographers at the same site in lieu of temporal replications. These replications provided the data needed to resolve the ambiguity between PU absence and PU non-detection.

To employ this mechanistic approach, the detection/non-detection data are shaped into a three dimensional array X_{ijk} where the first dimension, i, is the PU; the second dimension, j, is the plot; and the last dimension, k, is the classifier (the array element x_{ijk} is the number of photographers that found PU i in plot j, as identified by classifier k). First, a model of the plot-specific detections of a single PU is developed. This model is then extended to combine information among different PUs in the community for the estimation of PU richness (see Dorazio & Royle 2005; Dorazio et al. 2006 and Appendix 3.1 for a detailed description of model development and parameters estimation). Using this model, I calculated mean PU richness for each park unit, as well as the occupancy and detection estimates for each of the observed PUs.

To understand the effect of the number of photographers and the number of classifiers on the patterns of detection and occupancy, I conducted a series of analyses in which I varied the information input into the model. For example, while retaining

data from four classifiers, I performed the analysis having only one photographer, the combination of any two photographers, and any three photographers. Likewise, I separately retained data from four photographers but having one classifier, the combination of any two classifiers, and any three classifiers. I fit the model using R (R Development Core Team 2010) and WinBugs (Lunn et al. 2000; Sturtz, Ligger, & Gelman 2005).

Results

I processed a total of 2133 photographs, resulting in 2316 digital specimens that were each identified by four classifiers. From these digital specimens, only a mean of 1172 (range = 1023 to 1381 among the four classifiers) were determined to PUs. The total number of photographs and specimens differed among park units (Table 3.1).

Richness estimations and comparison between the LBP data and the PUs data

Estimates of true species richness based on the Chao2 procedure, in general, were not significantly higher than the number of species/PU actually counted, indicating that there were few rare species represented in any of the PU and LBP datasets (Fig. 3.2, Table 3.2). The only exception to this was Rock Creek Park, for which the estimation by Chao2 of species richness (28 species ± 13.2 SE) was almost three times the observed species richness (10 species).

When comparing PU richness with species richness for each park unit, none showed significant differences using the observed richness (number of PUs or species

for each park), and with the exception of Rock Creek Park, none showed significant differences using the Chao2 estimated richness either (Fig. 3.2). There was a strong correlation between the observed number of species from the LBP and the observed number of PUs from the photodocumentation protocol (correlation fitted with no intercept, $R^2 = 0.98$, slope $= 0.88$ and p-value < 0.0001).

The difference between the observed species richness from the LBP project and the observed PU richness from the photodocumentation approached zero as the number of photographers increased and the number of classifiers increased (Fig. 3.2b).

Insights from the mechanistic method for the estimation of PU richness

The hierarchical model developed to account for non-detection produced higher estimates than did the Chao2 estimator as applied to the observed number of PUs (Table 3.2, Figure 3.3c). Frequencies of detection and occurrence for the different PUs showed similar patterns across park units (Fig. 3.3a). There was considerable variation in the observed frequencies of detection (range $=$ 0.1-0.9). However, in general, there were low levels of variation in the observed frequencies of occurrence, which were high for most PUs, suggesting that many PUs are relatively common (Fig. 3.3a-b). These PU-specific probabilities of occurrence and detection suggested that detection failures for many lichen PU were due to low rates of detection, and not to low rate of occurrence (Fig. 3.3a). The changes in these patterns when changing the number of photographers and the number of classifiers used in the analyses are shown in Fig. 3.3d. The pattern of detection and occupancy frequencies

did not change radically as more than two photographers are added to the analysis. Increasing the number of classifiers beyond two did not change detection and occupancy frequencies but did increase the difference between them.

Discussion

I demonstrate a sampling and analysis method for the rapid estimation and comparison of species richness using two datasets of corticolous macrolichens in national park units near Washington, D.C. Our results showed that, with the exception of Rock Creek Park, the observed and estimated richness from both techniques were not statistically significantly different from each other. The significant disparity for Rock Creek Park may reflect an unusually high number of rare species, but more sampling in this park unit may be necessary to clarify whether this represents a bias in the Chao2 estimator or incomplete detection in field surveys. I also demonstrated that species richness estimation by photodocumentation shows the same patterns of differences among parks as traditional sampling by taxonomic experts and that estimates deriving from this approach converge to those from traditional expert surveys as the number of photographers and classifiers increases. For corticolous macrolichens, it appears that at least two photographers in the field and four classifiers is sufficient to reach results en par with more traditional surveys.

The utility of parataxonomic data for biodiversity studies has been reviewed by Krell (2004), who recognized that even though this technique has limitations, it is often the only way to get information about biodiversity of different areas. The use of

parataxonomic data has been found useful in other studies, mostly on invertebrates (Basset et al. 2000, 2004; Barratt et al. 2003; Ward & Stanley 2004; Derraik et al. 2010), but also on mosses (Oliver & Beattie 2002) and ferns (Oldekop et al. 2011) PU richness should only be used for taxonomic groups for which it has been assessed as acceptable surrogates for species richness (Derraik et al. 2010) In such cases, the use of PUs significantly increases the number of observations for each area and decreases the time spent on each classification (Basset et al. 2000).

All biological surveys, whether of species or PUs, must account for the possibility of non-detection, and statistical approaches to differentiate between non-detection and true absence are critical for obtaining unbiased richness estimates. Here I develop a mechanistic statistical approach for the analyses of the data obtained by means of the photodocumentation technique by citizen scientists. By explicitly modeling non-detection probabilities, this model also provides information on the detectability and occurrence of the different PUs in each park. This distinction between detectability and occurrence is useful for designing future sampling campaigns, as well as informing us as to the source of the failures in detectability of PUs in the communities. From our analysis, I can identify PUs that are present in every plot in a given park and relatively easy to find and classify (e.g., *Punctelia subrudecta*, see Fig. 3b), as well as PUs that are common but morphologically cryptic (e.g., *Flavoparmelia caperata* and *Myelochroa aurulenta* which showed the same pattern of occupancy and detection in all the park units studied).

Even though the geographical patterns of richness sometimes match geographical patterns of rarity (Kerr 1997), there are exceptions to this observation

(Prendergast et al. 1993). Therefore, the use of species richness alone as a guide for conservation priorities could lead to leave rare or endemic species unprotected. Distinctiveness is another important characteristic of the biodiversity of an area, and it is usually used in the process of setting conservation priorities (Sarkar et al. 2006). The mechanistic modeling framework for the estimation of PU richness gives insight into the distinctiveness of the communities, as it gives an estimation of the probabilities of detection for each one of the PUs observed. This allows researchers to distinguish communities composed primarily of rare species from communities composed primarily of common species. In this system, I found that the corticolous macrolichen communities in the park units studied consisted of common PUs that varied in their detectability. These results matched those found by the LBP, showing that these macrolichen communities were dominated by pollution-tolerant, nitrophilous common species (e.g. *Physcia millegrana, Punctelia rudecta, Flavoparmelia caperata*), while very few pollution-sensitive rare species were present (e.g. *Tuckermannopsis ciliaris*) (see results at http://mason.gmu.edu/~jlawrey/CUE/). In an opposite situation, low occurrence probabilities for most PUs would indicate a community composed primarily by rare PUs. This result is a clear advantage of this mechanistic model for non-detection over the phenomenological models like Chao2, which is incapable of providing information on the origins of non-detections. Non-parametric estimators, such as Chao2, need a minimum sampling effort to produce reliable estimates (Chao et al. 2009)*,* and they could be used on PUs datasets when it is not possible to have more than one photographer in the field.

Photodocumentation and analysis of PUs allow for the development of biodiversity databases that are immediately available for subsequent taxonomic studies soon after the field work is complete because there is no need to wait for experts to access the field sites and subsequently identify the collected specimens. Citizen scientists could play an invaluable role in the development of these databases, from the collection of data in the field to the identification of PUs from their homes accessing the photographs from a personal computer. Many examples of on-line citizen scientist projects can be found among the Zooniverse projects (www.zooniverse.org). The advantages of using citizen scientists in research projects has been recognized in the scientific community, and with the advance of technology the data collected with this approach has been proved useful for ecological research (Dickinson et al. 2012).

The photodocumentation protocol proposed here is a non-invasive technique that does not require the extraction of organisms from the field (an important characteristic of the method if it would be used for repeated sampling for monitoring purposes). Moreover, for some remote geographic areas, monitoring protocols which can be performed by non-specialists are the only feasible option. This protocol is valuable because it provides a mechanism for rapid assessment of areas being evaluated for conservation and management.

Table 3.1. Sampling effort for each national park unit.

Parks	Number of plots surveyed	Number of photographers	Number of photographs	Number of specimens
Catoctin Mountain	4	4	350	308
Harper's Ferry	5	5	553	718
Manassas	3	3	221	249
Prince William	7	4	695	795
Rock Creek	3	4	313	245

Table 3.2. Species and PU richness for each national park unit.

Parks	Observed species richness – LBP data	Estimated species richness – LBP data (by Chao2, ± SE)	Observed PU richness*	Estimated PU richness (by Chao2, ± SE)	Estimated PU richness (by occupancy method)
Catoctin Mountain	13	15.2 (± 1.6)	Total = 23 Mean = 12	19 (± 4.1)	Mean = 36.1 Median = 35.0
Harper's Ferry	12	12.0 (± 0.0)	Total = 23 Mean = 13	22.2 (± 2.4)	Mean = 37.3 Median = 36.0
Manassas	17	21.9 (± 2.7)	Total = 28 Mean = 15	21.0 (± 1.9)	Mean = 44.0 Median = 43.0
Prince William	20	28.1 (± 3.0)	Total = 31 Mean = 16	21.1 (± 4.1)	Mean = 50.1 Median = 50.0
Rock Creek	10	28.0 (± 13.2)	Total = 13 Mean = 7	10.6 (± 6.1)	Mean = 17.2 Median = 16.0

* Total refers to the combination of PUS from all the determinations, while mean refers to the mean among the determinations. Note that I used the mean PU richness to estimate the Chao2 PU richness.
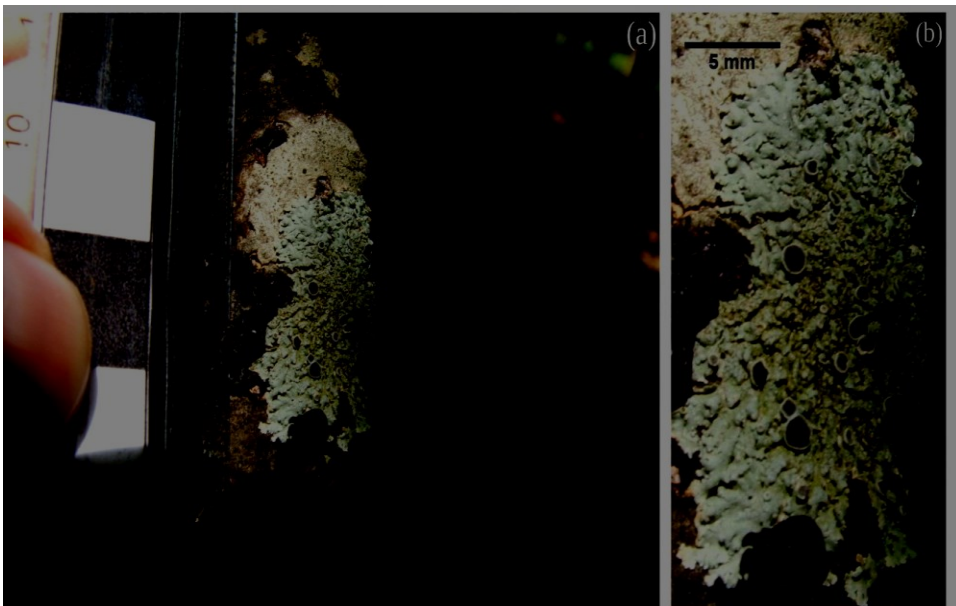
Figure 3.1. Photograph taken in the field.

(a) and associated digital specimen (b). Photograph taken on by P. C. in June 2011 at Prince William

Forest Park, Virginia.
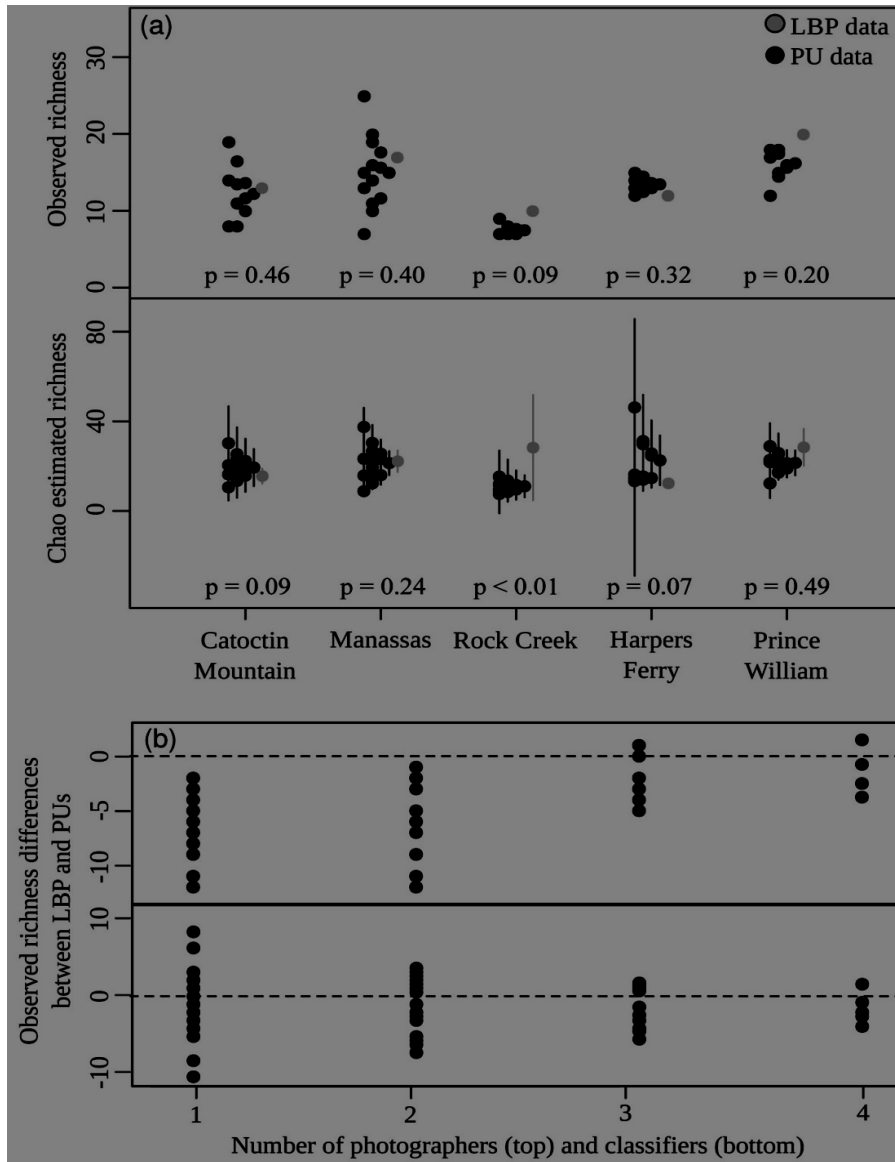
Figure 3.2. Comparison between the Lichen Biomonitoring Project (LBP) species richness and the photodocumentation PU richness.

(a) PU data are shown from left to right, as the data for each determination separately, the mean of any two of the determinations, the mean of any three of the determinations, and the mean of all determinations. P-values corresponding to the difference between the mean richness for the four classifiers and the richness from direct expert survey were derived by randomization as described in the text. (b) Observed richness differences between LBP data and PU data, for different numbers of photographers and different numbers of classifiers.
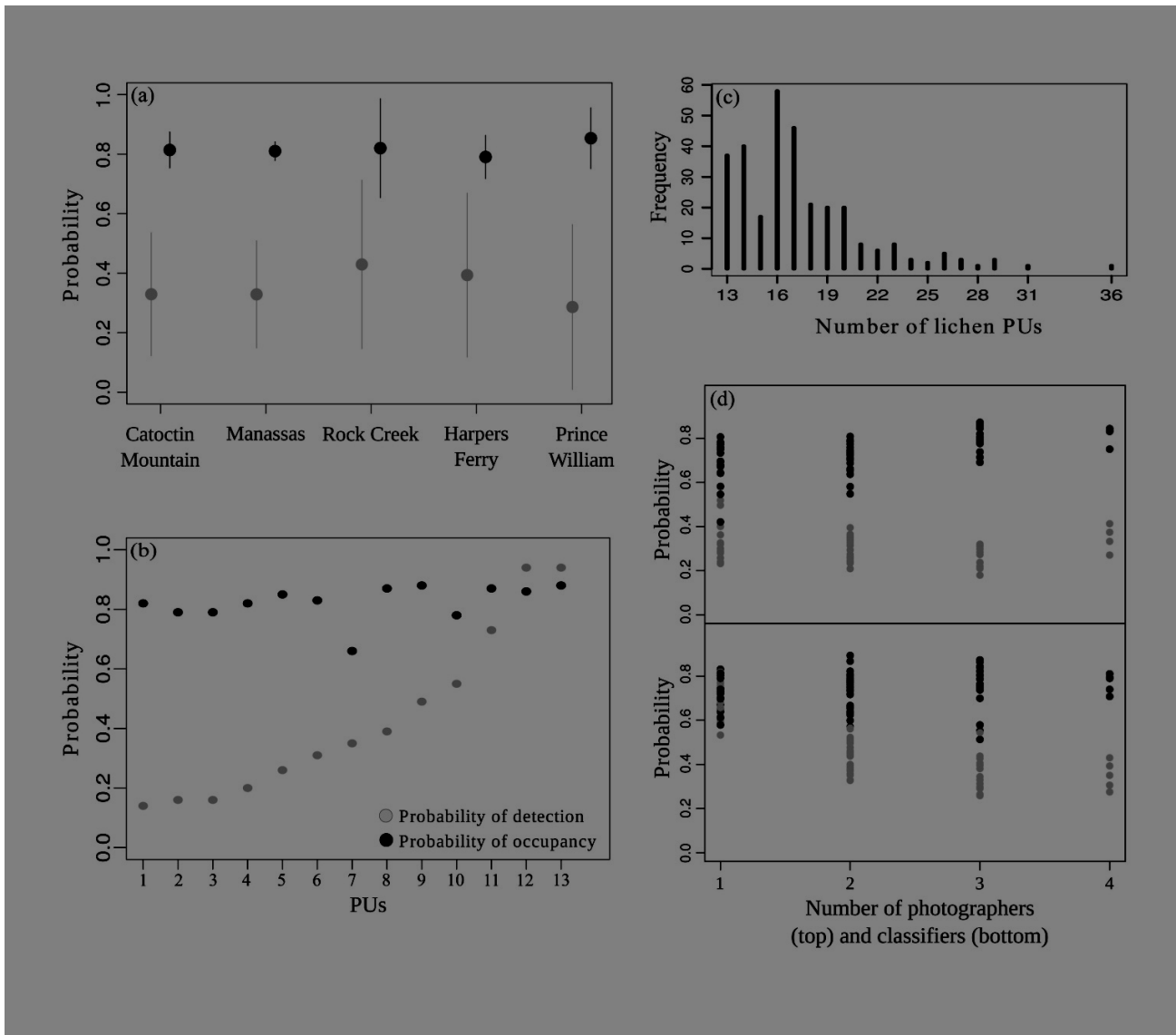
Figure 3.3. Mechanistic statistical method for the estimation of PU richness.

(a) Probabilities of detection and occupancy for each park unit (mean ± SD). (b) PU-specific

probabilities of detection and occupancy for Rock Creek Park (1. *Flavoparmelia caperata*; 2.

Myelochroa aurulenta; 3. *Parmotrema hypotropum*; 4. *Phaeophyscia pusilloides*; 5. *Phaeophyscia*

rubropulchra; 6. *Physcia millegrana*; 7. *Pyxine sorediata*; 8. *Cetrelia chicitae*; 9. *Punctelia rudecta*;

10. *Pyxine caesiopruinosa*; 11. *Candelaria concolor*; 12. *Punctelia subrudecta*; 13. *Umbilicaria*

mammulata). (c) Posterior distribution of lichen PU richness for Rock Creek Park. (d) Probabilities of

detection and occupancy for different numbers of photographers and different numbers of classifiers,

for each park unit separately.

Chapter 4: Understanding lichen diversity on the Antarctic Peninsula using parataxonomic units as a surrogate for species richness

Abstract

Expert collection of specimens in the field and further determination of species is the best method for determining species richness. However, the relative paucity of botanists working in Antarctica makes this approach impractical for broad-scale surveys of Antarctic floral biodiversity. Lichens are the dominant macrophytes of the terrestrial Antarctic ecosystem, and they are a fundamental part of the ice-free terrestrial ecosystem. Many distinct ice-free terrestrial habitats in the Antarctic are not represented in the current network of Antarctic protected areas. However, it is difficult to identify appropriate areas for conservation because comprehensive data on distributional patterns of Antarctic flora are not available, and existing data for most Antarctic lichen species are not compiled. Consequently, cost-effective survey methods and surrogates for the prediction of species richness are needed to accelerate assessments of local biodiversity and help select areas for conservation. A combination of a photographic "citizen scientist" approach for the collection of data, and the use of parataxonomic units (PU) richness as a method for estimating species richness might be an effective means to collect preliminary information and rapidly build databases on the ecosystem's diversity. I have developed a database and

gathered photographic information on lichen occurrences for sites that are frequently visited by tourists. I test the identification capabilities with a reference dataset of Antarctic lichen images from the U.S. National Herbarium, and showed that all species used in this test can be detected, and that for 74% of the images, all classifiers were able to identify the genus of the specimen. Twenty nine sites were photographically surveyed by researchers and tourists between 2009/10 and 2011/12 in the Antarctic Peninsula. I estimated PU richness as a proxy for species richness for each of the 29 sites surveyed, and provide three examples of data applications. These surveys provide preliminary information useful for identifying areas for protection and priorities for future research.

Introduction

The biogeography of the Antarctic Peninsula is unique because of its pronounced latitudinal gradients and its geographical isolation (Fenton 1982). Lichens are the dominant and most diverse macrophytes in the terrestrial Antarctic ecosystem (Smith 1984). Crustose, fruticose and floliose lichens comprise extensive cryptogamic communities, especially along coastal regions (Convey et al. 2008). In a recent study on lichen richness drivers on the Antarctic Peninsula, it was shown that patterns of richness observed using museum records are highly scale-dependent and largely unexplained by the biogeographic variables found important in other systems (Casanovas et al. 2012). However, data available for the study was limited and there are a significant heterogeneity in sampling frequency and sampling effort along the Antarctic Peninsula.

The input of nutrients by sea-birds and seals in the islands where they breed is an important factor that influences lichen diversity (Ryan & Watkins 1989; Leishman & Wild 2001; Smykla et al. 2007; Smith 2008). It has been shown that penguin colonies in particular affect the diversity of lichens at a local scale (richness and composition of the lichen communities change as they approach the edge of a penguin colony, Smykla et al. 2007) and the islands scale (lichen richness is higher in islands with bigger colonies, when colony sizes do not exceed 20,000 breeding pairs, Casanovas et al. 2012).

There are extensive areas of the Antarctic Peninsula where lichen specimens were never collected (e.g. between 61°S and 62°S, Casanovas et al. 2012), and many sites frequently visited by tourists lack any floristic information (Peat et al. 2007; Chown and Covey 2007; Terauds et al. 2012; Casanovas et al. 2012). There are several ice-free terrestrial habitats in the Antarctic that are not represented in the current network of Antarctic protected areas (Terauds et al. 2012). The Antarctic Peninsula climate is changing dramatically (Convey 2011), and biodiversity inventories are a fundamental for establishing baseline conditions against which to judge changes in floral abundance and composition.

Protecting the flora of the Antarctic Peninsula is important to the Antarctic Treaty Parties, and visitor site guidelines explicitly mention the vegetation of some landing sites as a priority for conservation (e.g., Barrientos Island), with trampling and damage of vegetation as one of the potential human impacts at several popular tourist landing areas (Tejedo et al. 2009,2012). However, it is difficult to identify appropriate areas for lichen conservation because comprehensive data on lichens are

not available for most of Antarctica or compiled for most Antarctic lichen species.

Expert collection of specimens in the field and further determination of species is the best method for determining species richness. However, the relative paucity of botanists working in Antarctica makes this approach impractical for broad-scale surveys of Antarctic floral biodiversity. In order to accelerate assessments of local biodiversity and help select areas for conservation, cost-effective survey methods and surrogate methods for the prediction of species richness are needed. A combination of a photographic "citizen scientist" approach for the collection of data, and the use of parataxonomic units (PU; a visually distinguishable unit based only on external morphology, Krell 2004) as a basis for quantifying richness, might be a possible solution to effectively collect preliminary information and rapidly build databases on ecosystems diversity. Parataxonomy has been used successfully for the prediction of species richness in different communities, including aquatic macroinvertebrates (Clarke et al. 2004), colonial reef corals (Budd et al. 1994), vascular plants (Garrettson et al. 1998), and insects (Basset et al. 2000).

A "citizen scientist" is a non-expert person who helps collect or process data with a scientific purpose (Cohn 2008). The direct participation of citizen scientists in data collection efforts provides information on spatial and temporal scales that are impossible to collect using traditional methods (Silvertown 2009; Conrad & Hilchey 2011; Dickinson et al. 2012).

In this paper, I show how such a diversity database can be built using this approach. I combined a photographic survey protocol used by non-scientist visitors to the Antarctic with classification by parataxonomic units to catalogue lichens, the

dominant macrophytes of the terrestrial Antarctic ecosystem, at 29 locations on the Antarctic Peninsula. To test the identification capabilities of the parataxonomic classifications, I developed a photographic dataset using Antarctic lichen collections from the U. S. National Herbarium. I also compared lichen PU richness with species richness for the limited number of sites where historical information was available.

From photographs taken in the three austral summers between 2009/10 and 2011/12, different lichen PUs were isolated in the lab, and cataloged as "specimens". To date I have collected 1804 specimens for identification purposes. I estimated PU richness as a proxy for species and genus richness for each of the 29 sites surveyed. Using these data, I provided three examples of data applications, from basic ecological questions on community composition and relationships between lichens and other taxa, to specific questions directly related to the conservation of the Antarctic Peninsula flora. Additionally, these surveys provide preliminary information useful for identifying areas for protection and priorities for future research.

Materials and Methods

Photographic dataset

To date, 29 sites have been surveyed along the Antarctic Peninsula. Between 1 and 7 (mean 3) non-scientists photographers participated in each survey, and between 1 and 7 (mean=1) separate surveys were completed at each site. The backgrounds of the photographers were variable, but none of them were experts on lichens.

According to the study protocol, each participant took pictures of every

macroscopic lichen seen at a given site, walking freely within the limits of the site in the time available on shore (usually 2-3 hours). Using a black and white control scale included in each photo, I standardized the white balance in each picture and digitally isolated all lichens from the photographs using the ImageJ image processing program (Abramoff et al. 2004, Ferreira and Rasband 2010). Each lichen was given a unique identification name and was considered a "digital specimen" for this paper. Once all specimens were isolated, three different classifiers simultaneously and independently classified them using Øvstedal and Smith (2001, 2009) as a guide. As mentioned for the reference dataset, many lichen species are difficult or impossible to identify without a physical specimen, therefore I consider the determinations to be parataxonomic units (PUs) and not true species. The number of specimens and PU identified among them depended on the number of photographers, the quality of the photographs and specimens, and varied across sites.

Reference dataset

With the objective of testing the identification capabilities of the classifiers (*e.i.* how similar were the determinations of PUs from photographs from the actual species being identified), I developed a reference dataset for which the species photographed were known. Even though, as mention for the photographic dataset, many species cannot be determined only using their external morphology, the classifiers used the photographs and descriptions in Øvstedal and Smith (2001, 2009) as a guide, and I expected that some species (and genera) matched the parataxonomic classifications. The images from this reference dataset were not used to compare them

with the images taken in the field.

In collaboration with the Core Collections Management project at the Smithsonian Department of Botany, I located, imaged and created appropriate metadata for 39 Antarctic physical specimens representing 12 species and 9 genera of lichens. The U. S. National Herbarium hosts lichen collections from multiple trips by Mason Hale to the Antarctic (1980-85), as well as duplicates of Antarctic lichens obtained from other herbaria. For each physical specimen, in the collection, I took photos of the sheet on which the collection is maintained and multiple close-ups. These data (e-records and images) became part of the EMu catalog and are available to lichen researchers worldwide. Three different research assistants (hereafter "classifiers"), acting independently, classified the lichens on the images from the collections using Øvstedal and Smith (2001, 2009) as guides.

Data analyses

PU identifications of the reference dataset, and comparison with species identifications

All images from the reference dataset were identified to PU independently by three classifiers. A total of 12 species and 7 genera were represented in the original dataset, and the PU results showed a mean of 18 PU species and 8 PU genera (using Øvstedal and Smith 2001, 2009 as guides).

Estimation of PU richness for different sites

Estimates of species richness are always dependent on sampling effort (Boulinier et al. 1998), and many PU will remain undetected due to the differential abundance and detection probability of different types of organisms (MacKenzie et al. 2002). Because of this, I estimated true species richness using the non-parametric estimator Chao2 (Chao et al. 2005).

Comparison with historic datasets

Seven sites surveyed with the photodocumentation protocol had been surveyed before, and estimations of species richness were made by Casanovas et al. (2012). I compared the observed and estimated number of species PUs with the observed and estimated number species in each of these sites.

Examples of data applications

Mechanistic model for estimating species richness and probabilities of detection and presence

Using the photodocumentation protocol and analysis of PUs, I used a mechanistic model to estimate of PU richness. This approach calculates the probability that different PUs have of being detected in a given survey by a photographer and a classifier. I used a modified version of the hierarchical model proposed by Dorazio et al. (2006), using multiple classifiers as replicates for each photographer analogous to multiple observers surveying the same visit, and multiple photographers at the same site in lieu of temporal replications. I calculated the mean

species richness, as well as the occupancy and detection estimates for each of the observed PU genera. I did this procedure with two sites that had been visited the most times (Whalers Bay and Jougla Point, seven visits each). I fit the model using R (R Development Core Team 2010) and WinBugs software (Lunn et al. 2000; Sturtz et al. 2005).

Penguin-lichen relationships

In the Antarctic Peninsula, penguins nest in colonies, and through their accumulated excreta, these penguins contribute significantly to the local nutrient status of the substratum (Myrcha et al. 1985, Smith 1985, Tatur et al. 1997). Penguin colonies vary in size from one site to another, from a few nests to >100,000 nests. At a local scale, the input of nutrients by colonies of penguins and other sea-birds has a major influence on floristic richness (Smith 1978, Smykla et al. 2007, Tatur 2002).

Here I correlated lichen PU richness with penguin colony size for the sites where information was available (22 of the 29 sites with lichen data). To calculate penguin colony size at a site, I sum the per-visit abundances of three co-occurring penguin species (*Pygoscelis antarctica, P. papua and P. adeliae*) and then average those abundance across visits. Average penguin colony sizes at the 22 sites ranged from 271 to 6,260 nests. All the colonies are located at the same snow- and ice-free coastal areas delimited in this study. The information on penguin colony sizes comes from the Antarctic Site Inventory database (Naveen & Lynch 2011).

Tourism-lichen relationships

Tourism in the Antarctic Peninsula has been increasing since the late 1980s. Environmental impact in now one of the most important issues surrounding tourism in Antarctica (Stewart et al. 2005). Both tourists and wildlife are concentrated in the relatively tiny fraction of Antarctica that is coastal and free of ice in the summer, and this activity leads to concern over similar concentration of environmental impact (Stewart et al. 2005). Trampling and damage of vegetation have been investigated by Tejedo et al. (2009, 2012) as one of the potential human impacts at tourist landing areas. Research has also highlighted the Antarctic Peninsula's vulnerability to human-mediated introduction of both native and alien species (Smith 1996).

Here, I looked at correlations between lichen PU richness and the number of tourist visiting 20 sites (of 29) where sufficient information was available. The information on tourist visitation comes from the International Association of Antarctica Tour Operators (IAATO). Only the activities of IAATO members are included in this analysis, which account for approximately 95% of all the commercial cruise ships operating and 90% of all the known visitors to the Peninsula. The number of tourist visiting each site was calculated as the mean of the total number of visitors at each site every season, from the 2003-04 to the 2007-08 seasons (IAATO 2006, 2007, 2008).

Results

The complete metadata and the location of the dataset for the all photographic data on lichens of the Antarctic Peninsula can be found in Appendix 4.1.

PU identifications of the reference dataset, and comparison with species identifications

A total of 12 species and 7 genera were represented in the original dataset, and the PU results showed a mean of 18 PU species and 8 PU genera (using Øvstedal and Smith 2001, 2009 as a guides). For 74 percent of the images, all three classifiers identified the genus of the specimen correctly, and for 89 percent of the images at least one classifier identified the genus correctly. All three classifiers identified the species correctly in only 13 percent of the images, but at least one classifier identified the species correctly for 69 percent of the images. All twelve species present in the dataset were detected.

Estimation of PU richness for different sites

The estimations of lichen PU species and genera richness are listed in Table 4.1, and this list is part of the overall database described here.

Comparison with historic datasets

Table 4.2 shows the observed number of species and PUs for each of these sites, as well as the number of physical specimens and digital specimens collected. Except for two cases (Half Moon Island and Petermann Island), the number of species

from historical records and the number of PUs are very similar.

Examples of data applications

Mechanistic model for estimating species richness and probabilities of detection and presence

For the two different sites, PUs occupancy and detection probabilities showed different patterns of detection and occupancy, and for the same PUs these probabilities were different in the two sites in most cases (Figure 4.1). However, there were some PUs that showed similar probabilities of detection and occupancy on both sites (*e.g. Acarospora* and *Turgidoscolum*). The mean PU genera richness for Whalers Bay was 45.5 (± 10.4) PUs and the mean PU richness for Jougla Point was 50.9 (± 11.5).

Penguin-lichen relationships

I found a significant correlation between the observed number of PUs present (using observed or estimated PU genera or PU species) and the size of the penguin colonies (Table 4.3). These results concurred with results on Casanovas *et al.* (2012) which found a significant correlation between lichen species richness derived from historical records and penguin colony sizes.

Tourism-lichen relationships

I found a significant correlation between the observed number of PUs present (using genera PUs: p-value = 0.03; or species PUs: p-value = 0.02) and the number of

visitors to a given site. These are expected results because without correcting for

sampling effort, the most popular sites are also the sites that have more sampling

events in this database. However, I did not find a correlation between the estimated

number of PUs (using genera PUs: p-value = 0.57; or species PUs: p-value = 0.08)

and the number of visitors to the sites studied.

Discussion

Using the reference dataset from the Smithsonian collection, I showed that the determination of genera by non-specialist with minimal training on lichen morphology and taxonomy is very accurate, using the taxonomic resources available. The ability of accurately identify genera from the photographs allow us to use the data collected for answering ecological and conservation questions that would be very hard or impossible if the data were dependent on field collections by experts, specially in the Antarctic Peninsula, where logistics of field work are complicated and expensive. Furthermore, this technique allows for the identification of areas where certain genera are present, and then target surveys for the taxa of interest without having to spend resources on surveying areas that have been photographically surveyed but those genera have not been found.

The estimations of species and genera PU richness for the sites surveyed in this study are the only estimations available for most places. This information is useful to compare diversity among sites, and set up protocols and measurements for the protection of flora in the Antarctic Peninsula.

Comparison with historical datasets showed that for five sites, the richness estimations were very similar to the estimations from the photographic dataset. Petermann Island would need more photographic surveys to understand if the difference with historical datasets is due to sampling issues or if the diversity of lichens on the island had changed over the years. There were very few specimens collected from Half Moon Island in the historical records, and that might be the cause of the difference between the richness estimations between the historical datasets and

the photographic documentation.

The data provided here are a unique resource to address questions regarding the ecology and biogeography of the lichen flora in the Antarctic Peninsula. I provided two examples of data applications, the first one demonstrating the quality of the data for detailed analyses of the richness and composition of the communities in each site, and the second one showing the relationship between penguin colonies and diversity of lichens.

The mechanistic statistical model for the estimation of species richness and the detection probabilities allows for a more comprehensive analysis of the lichen communities that the simple estimation of richness using non parametric estimators like the Chao2. For instance, I can show at the two sites studied for this example, that there are many rare PUs in these lichen communities (and difficult to identify and find on the field). Also, I can identified which PUs are easier to identify and find. This is not only useful when comparing among different sites, or using the data for answering other ecological questions, but for planning future surveys in the same area.

The correlation between penguin colony sizes and lichen richness concurred with results on Casanovas *et al.* (2012) which found the same significant correlation using data derived from historical records and penguin colony sizes. Beyond the importance of showing this relationship between two of the most abundant organisms on the Antarctic Peninsula, this demonstrate how the data presented on this paper can be used for ecological studies that benefit from broad-scale data collections. The correlation between tourism and lichen richness, and the values of richness for each

site themselves, could be use directly to delineate guidelines for visitors to these sites, in terms of the protection of the lichen flora.

In summary, the dataset of lichens parataxonomic units of the Antarctic Peninsula developed here will be useful for addressing a broad number of ecological questions regarding Antarctic Peninsula lichen flora, as well as providing preliminary information useful for identifying areas for protection and priorities for future research.

Table 4.1. Estimation of PU species and genera richness.

Sites	Observed genera PU	Estimated genera PU	Observed species PU	Estimated species PU	Number of photographers
Barrientos Island (Aitcho Islands)	14	17.6	21	28.5	4
Brown station vicinity	8	17.0	8	8	2
Baily Head (Deception Island)	8	10.6	9	12.1	3
Beneden Head	14	NA	20	NA	1
Booth Island	13	53.5	18	67.0	6
Brown Bluff	11	15.0	17	29.1	5
Cuverville Island	15	19.5	33	117.5	4
Damoy Point	6	18.5	7	25.0	2
Danco Island	9	NA	12	NA	1
Detaile Island	4	NA	4	NA	1
Devil Island	13	16.1	14	20.4	3
Entrance Point (Deception Island)	8	14.2	9	21.2	3
Georges Point	19	103.5	32	59.5	4
Half Moon Island	17	18.5	28	48.2	4
Hanna Point	14	18.9	20	44.5	5
Horseshoe Island	10	NA	12	NA	1
Jougla Point	10	10.0	18	24.7	6
Mikkensen Harbor	14	18.9	20	44.7	5
Petermann Island	10	34.5	9	33.5	3
Pleneau Island	10	NA	13	NA	1
Pour qua pa Island	13	NA	20	NA	1
Red Ridge Rocks	6	6.5	11	21.6	2
Spiegot Peak	5	5.6	6	10.0	3
Tayh Head	12	14.2	28	58.0	3
Torgensen Island	12	14.2	3	5	2
Useful Island	4	8.5	4	8.5	2
Waterboat Point	14	18.9	29	62.3	4
Whalers Bay	28	42.0	46	72.1	7

Table 4.2. Comparison between PUs data and historical data.

Site (listed from north to south)	Observed PUs numbers using species (mean among three classifiers)	Observed species numbers	Number of physical specimens (historical data)	Number of digital specimens (PUs data)
Half Moon Island	33	13	21	273
Whalers Bay	42.6	49	107	652
Cuverville Island	31.6	34	62	307
Damoy Point	6.3	4	7	56
Brown station	8.6	5	9	33
Petermann Island	10	35	74	59
Horseshoe Island	13	17	24	93

Table 4.3. Results from the correlation between PUs lichen richness an penguin colony sizes

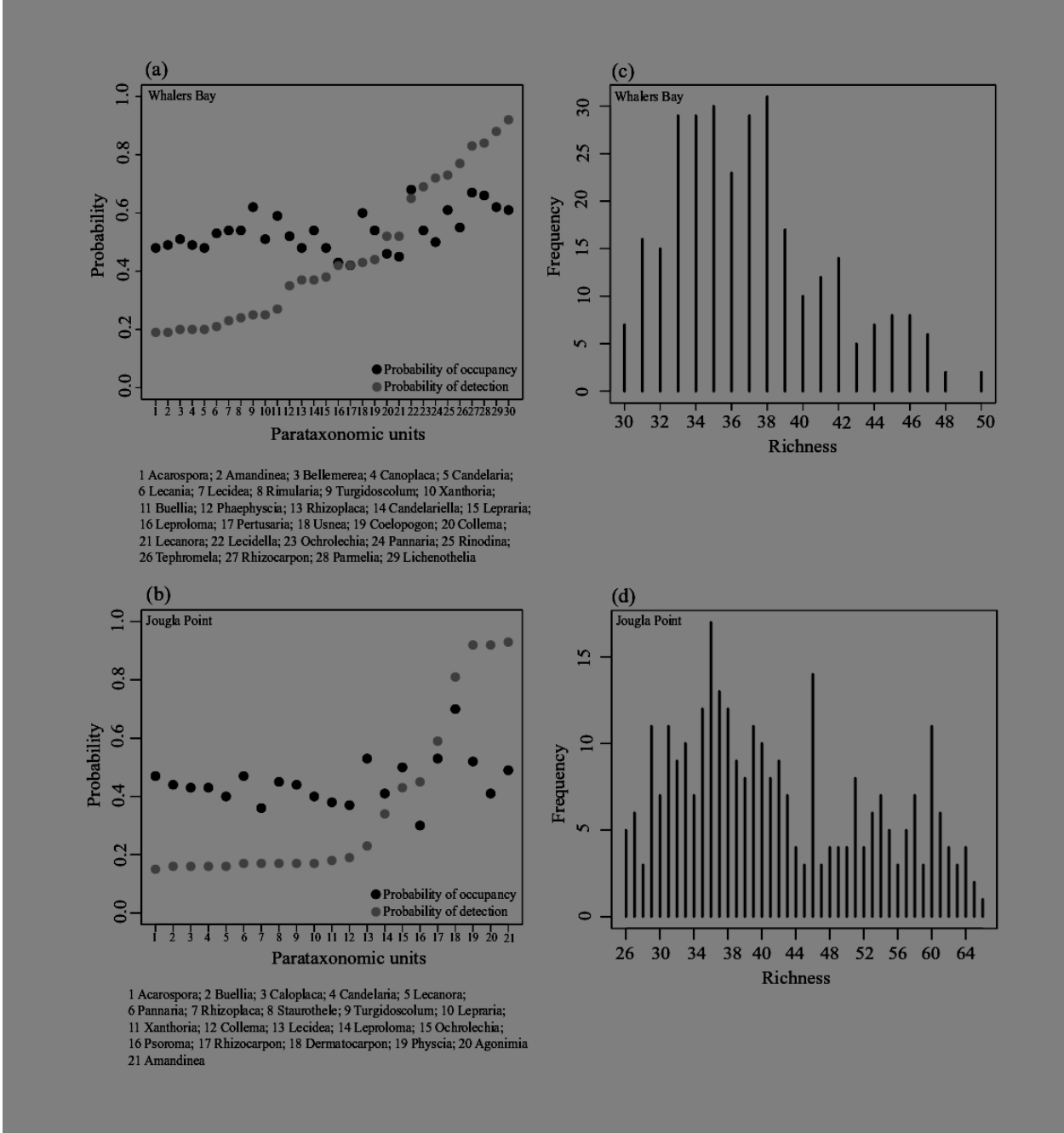| PUs richness	Adjusted R^2	p	Outliers?
Observed number of PU genera	0.23	0.01	none
Chao2 estimated number of PU genera	0.09	0.09	Georges Point
Observed number of PU species	0.26	0.006	none
Chao2 estimated number of PU species	0.27	0.006	none

Figure 4.1. Mechanistic statistical method for the estimation of PU richness.

(a) and (b) PU specific probabilities of detection and occupancy for Whalers Bay and Jougla Point. (c) and (d) Posterior distribution of lichen PU richness for Whalers Bay and Jougla Point.

Chapter 5: Identification and characterization of penguin habitat in the Antarctic Peninsula using remote sensing data.

Abstract

Large scale biological surveys and remote sensing data can be used to identify key marine habitats important for widely distributed marine species. The Antarctic Peninsula and surrounding waters have been experiencing drastic environmental changes in the last decades that influence ecosystem dynamics and habitat distributions. Penguins, important Southern Ocean mesopredators, are considered good indicators of environmental change because of their nesting and dietary restrictions. Recent observations of climate change and penguin distributions suggest a strong link between climate change and trends in penguin populations. I studied the relationship between the distribution of three species of penguins (*Pygoscelis adeliae, P. antarctica, P. papua*) along the Antarctic Peninsula, as recorded for 169 sites over the last 19 years by the Antarctic Site Inventory, and environmental factors that are most effectively measured at broad scales with remote sensing products (sea surface temperature, chlorophyll-a concentration and sea-ice extent, using Aqua and Terra MODIS ad SeaWiFS data). The results suggest that the environmental factors related to the presence or absence of colonies are not always the same as the variables important for determining the abundance of penguins breeding at the site. Also, the variables affecting penguin distribution and abundance are different among the different species of Pygoscelid penguins. These results may be used to help inform decisions and policies by environmental managers.

Introduction

Penguin population abundance on the western side of the Antarctic Peninsula (AP) has been changing over the last 50 years, and several studies have highlighted environmental drivers associated with these changes (Smith et al. 1999; Croxall, Trathan, & Murphy 2002; Lynch et al. 2012). More recently, researchers have begun documenting changes in species spatial distributions as well. One potential driver of change in penguin distributions is the spatio-temporal distribution of ice. Mid-winter amplification of the warming trend can affect the extent, thickness and concentration of seasonal sea ice cover (Smith et al. 1999) and significant changes have been found in the extent and duration of sea ice around Antarctica (Jacobs & Comiso 1997; Comiso 2000). While the so-called "fast-ice" (sea ice that has frozen along the coasts and extends out from land into the ocean) exhibits high inter-annual variability, the duration of sea ice cover has been decreasing (Murphy et al. 1995), likely as a result of regional warming (Smith et al. 1999). Antarctic sea-ice has also been undergoing a long-term decline in spatial extent, particularly in waters near the South Orkney Islands in the north-west Weddell Sea (Murphy et al. 1995). Moreover, the northernmost ice shelves on the western AP have been shrinking over the past 50 years (Vaughan et al. 2003). Some authors have remarked on the importance of sea ice changes on the Antarctic ecosystems (Nicol 2006; Clarke et al. 2007), because the alteration in sea ice dynamics could have a direct impact on the marine fauna through shifts in the timing and extent of habitat for ice-associated biota (Clarke et al. 2007).

Besides ice, the location of penguin breeding colonies and the distribution of regional penguin populations among sites could be determined by primary productivity

and/or sea surface temperature. These drivers are more or less important at different times of the year depending on the breeding phenology of penguins, so the penguin species may be differentially sensitive to change. These variables, however, combine to influence the abundance of Antarctic krill (*Euphausia superba*), widely recognized as a major link between primary producers and many populations of krill-feeding vertebrates, including penguins (Knox 1970).

For this work, I studied the relationship between the distribution of three species of penguins (*Pygoscelis adeliae, P. antarctica, P. papua*) along the western AP and several environmental factors hypothesized to influence penguin distributions. The patterns of distribution and inter-annual changes in the oceanographic variables hypothesized to influence penguin distributions and abundances are different along the AP. Employing zero-inflated Poisson and Binomial regression models for penguin abundance in combination with broad scale remote sensing data, I demonstrate how different species of penguins are influenced by these environmental factors spatially.

Materials and Methods

Datasets

Penguin data

The distribution of penguin colonies along the AP has been recorded over the last 19 years for more than 169 sites by the Antarctic Site Inventory (ASI), a long term monitoring program of AP breeding birds undertaken by Oceanites, Inc, a nonprofit, science and educational foundation. The ASI is unique among penguin research programs

in that it encompasses the entire Peninsula and is thus an excellent platform for the study

of Antarctic biogeography (Naveen & Lynch 2011). The regional-scale nature of this

dataset is ideal for exploring what factors drive penguin distributions and how penguins

relate to other organisms in the Antarctic terrestrial ecosystem. I used presence of

colonies, and the mean nest counts for the different penguin species in each of the sites

where there are colonies present, as the response variables. Unlike most niche models

which use pseudo-absences, here we have known absences which can be used to define

the space of unsuitable habitat; I incorporated these known absences as true zeros for the

analyses of both occupancy and abundance.

Remote sensing and bathymetry data

Five covariates were considered in my penguin distribution models: November

sea-ice conditions, chlorophyll-a concentration as an indicator of krill recruitment, sea

surface temperature, and two aspects of the bathymetry near the coastline (slope and

aspect). I used the November mean for the first three variables, as they showed to have

more influence in previous works (Lynch et al. 2012) and the spring and summer values

for these variables are highly correlated.

Sea-ice spatiotemporal distribution was estimated from NIMBUS-7 Scanning

Multichannel Microwave Radiometer (SMMR) and the Defense Meteorological Satellite

Programs (DMSP) Special Sensor Microwave/Imager (SSM/I) and the Special Sensor

Microwave Imager/Sounder (SSMIS) passive microwave data, with a spatial resolution

of 25 km^2. I used the monthly means for sea-ice concentration, which are generated by

averaging all the available daily files for each individual month, excluding pixels of

missing data. The data were obtained from the National Snow and Ice Data Center in raw binary format, and converted to ASCII format using ESRI ArcGIS10.

Primary marine production was estimated using the merged satellite measurements of ocean chlorophyll data derived from the moderate resolution imaging spectroradiometer (MODIS), in orbit on the Aqua plataform, and the Sea-viewing Wide Field-of-View Sensor (SeaWIFS), in orbit on the OrbView-2. I used the level 3 monthly merged chlorophyll product (concentration of chlorophyll-a in mg/m^3), with a spatial resolution of 9 km^2. The data were obtained from the Ocean Biology Processing Group (OBPG), Global Change Data Center, Earth Sciences Division, Science and Exploration Directorate, Goddard Space Flight Center, NASA (http://oceancolor.gsfc.nasa.gov) in hierarchical data format and converted to ASCII format using ESRI ArcGIS10.

For sea temperature spatiotemporal patterns data I used sea surface temperature (SST) derived from MODIS, from the Aqua platform. SST is derived from the MODIS infrared channels using two channels in either the thermal infrared (11-12 μm) or channels in the mid-infra red region (3.8-4.1 μm). I used level 3 monthly means of SST (in ^{o}C), with a spatial resolution of 4 km^2. The data were obtained from the OBPG, Global Change Data Center, Earth Sciences Division, Science and Exploration Directorate, Goddard Space Flight Center, NASA (http://oceancolor.gsfc.nasa.gov) in hierarchical data format and converted to ASCII format using ESRI ArcGIS10.

The bathymetry data were provided by the Polar Geospatial Center, Department of Earth Sciences, University of Minnesota (in a 50 m^2 resolution). Two characteristics of the bathymetry were used in the analyses, slope and aspect near the coastlines. To estimate the slope, the maximum change in elevation over the distance between a given

cell and its eight neighbors was identified as the steepest downhill descent from the cell. The output raster was calculated in degrees for the angle of this slope. To calculate the aspect for the bathymetry data, a plane to the z-values of a 3 by 3 cell neighborhood around the center cell is fitted. The direction to which the plane faces is the aspect for the given cell. The values of each cell in the output indicate the compass direction that the surface faces at that location (measured clockwise in degrees from 0 to 360, both due north). Both measurements were calculated using the specific tools in ArcGIS10.

All raster data was subset to the Antarctic Peninsula area and re-projected in ArcGIS10 to South Polar Lambert Azimuthal equal area projection.

Habitat characterization

I focused on breeding penguin colonies, which are always found on ice-free land such as occurs on the islands in the west side of the AP. Points every 50 meters on each coastline near ice-free land in the AP mainland and islands were associated with three sets of environmental variables, one set for each penguin species. I traced three circular buffers around each point, with radii equal to the maximum foraging distance offshore for each penguin species respectively. For each marine environmental variable (sea-ice, sea surface temperature and chlorophyll-a concentration), I calculated the mean and standard deviation values in the over water portion of the buffer (Fig. 5.1). Maximum foraging range was described by Trivelpiece, Trivelpiece, & Volkman (1987) for the three species of Pygoscelid penguins at the time in the season when they were feeding 1-2 weeks old chicks, in Point Thomas, King George Island (24 Km for gentoo penguins, 50 Km for Adélie penguins and 33 Km for chinstrap penguins).

For each of the variables tested, maximum and minimum values for the coastal area where penguin colonies are present were calculated. Using these maximum and minimum values, I mapped the availability of habitat in the ice-free coast of the Antarctic Peninsula. I also calculated the frequency distribution for these variables, for each one of the penguin species separately.

Modeling framework

Penguin abundance has a significant number of true zeros (places where it is know that a given species of penguin is truly absent). To take this into account, models for each species were fit using zero-inflated Poisson and negative binomial regressions models. These models are two-component models combining a point mass at zero with the Poisson count distribution or a negative binomial distribution for presence absence data. This modeling framework accommodate for over-dispersion of the data; equation 1 shows the model development from Martin et al. (2005) for the Poisson case.

$$Pr(Y_i = 0 \mid x, z) = 1 - p(x_i) + p(x_i)\exp(-\lambda(z_i))$$

$$Pr(Y_i = r \mid x, z) = p(x_i)\frac{\exp(-\lambda(z_i))\lambda(z_i)^r}{r!}, r = 1,2,\ldots,$$

$$Where$$

$$logit(p(x_i)) = \alpha_0 + \beta_0(x_i)$$

$$\log(p(z_i)) = \alpha_1 + \beta_1(z_i)$$

Equation 1. $p(x_i)$ represents the probability that an observation i is generated through newline the Poisson distribution, irrespective of whether the observation is a zero or non-zero value. $\lambda(z_i)$ represents the mean number of nests at site I and and it can be expressed as a function of the explanatory variables, z through a log transformation. $p(x_i)$ can be expressed as a function of the explanatory variables, x, using a logit transformation. α_0 and α_1 represent constant terms in each regression component and β_0 and β_1 are vectors representing the coefficients estimated for each explanatory variable fitted in the model.

I analyzed presence-absence and abundance separately, because there are more data on the ASI database on presence-absence of colonies than on counts of penguin nests at the colonies. Only data from sites where penguin species are confirmed present or absent where used for the development of the models. Also, I analyzed the bathymetry (slope and aspect) data and the oceanographic data (sea surface temperature, chlorophyll-a and sea ice concentration) separately, because the bathymetry data have data gaps and poor resolution in some areas of the coastline.

The best models among the candidate set of models were found ranking all the models with the deviance information criterion (DIC) (Spiegelhalter et al. 2002). This criterion is use for model comparison in complex hierarchical models, and assesses the models in terms of their fit and complexity. The best models where found through exhaustive screening of all possible models. All analyses were conducted using the statistical package R (R Development Core Team 2010).

Results

Habitat characterization

Maximum and minimum values for the coastal area where penguin colonies are

present are shown in Table 5.1. Figure 5.3 shows the distribution of suitable and

unsuitable habitat using just the maximum and minimum values for the marine variable

for Adélie penguin colonies. The other two penguin species showed a similar pattern.

There were no significant differences among the three species of penguins on the ranges

presented for each variable, and the frequency distributions of the variables showed

similar patterns among species. However, there are small differences for some variables

(Fig. 5.2). Chinstrap colonies are located in areas slightly warmer than Adélie colonies,

even when the inter-annual variability is higher in the warmer areas. Chinstrap and

gentoo colonies are located in areas where the chlorophyll-a concentration is lower than

where Adélie colonies are in general. However, Chinstraps are located in areas where the

inter-annual variability of chlorophyll-a is lower relative to the areas where the other two

species of penguins are located. In relation with the bathymetry of the coast, Adélie

colonies are located in less steep areas than chinstrap colonies.

Habitat models

The results from the habitat models showed that, in general, the presence-absence

of colonies is not explained by the same variables that influenced the number of nests.

The best models are shown in Table 5.2, along with the DIC for each of these models

(only models that have a ΔDIC of less than 3 units are shown in Table 5.2, all models

with their respective DIC and ΔDIC are listed in Appendix 5.1). It is important to note

that not all models that include environmental variables are significantly different from

the null models (a model with only an intercept and no covariates).

For Adélie penguins, bathymetry variables were not shown as important in the

determination of penguin presence-absence or abundances. In contrast, bathymetry was important for the location and abundances of chinstrap penguin colonies, and only the slope of the coastlines appeared important for determining gentoo penguin abundances.

All oceanographic variables appeared important in the determination of Adélie penguin abundances, but only sea-ice and temperature were important for the presence-absence of colonies. For chinstrap penguins, sea-ice appeared as the only variable explaining abundances on this penguin colonies, while sea-ice and chlorophyll-a showed to be related to the presence-absence of colonies along the AP. As for gentoo penguin colonies, all variables appeared important in explaining the abundances and the presence-absence of the colonies.

Discussion

The use of ocean environmental variables to explain the distribution of sea-bird colonies has been extensively tested in many species, as the location of colonial breeding sites is highly non-random and is correlated with the marine habitat (Rolland, Danchin, & Fraipont 1998). Here, I have shown that the oceanographic factors related to the presence or absence of colonies are not always the same as the variables important for determining the abundance of penguins breeding at the site.

Whether or not a penguin colony is present in a certain location might reflect also the conditions at those areas when the penguin colony was originally established, and not necessarily modern conditions. Most penguin colonies in the Antarctic Peninsula could be hundreds of years old (Emslie 2001), with a few exceptions of new gentoo colonies that

had been established in the last 10 years (Lynch et al. 2012). It has been suggested that competition for food during the breeding season, especially during the chick provisioning stage, limit the number of conspecific seabirds in an area (Furness & Birkhead 1984). However, Ainley, Nur, & Woehler (1995) showed that prey depletion by parents feeding chicks does not explain differences in size structuring among Pygoscelid penguins species. They attribute this result to the superabundance of food supply during the breeding season in polar regions. In these areas where resources are not limiting, and the suitable areas are not all colonized, the role of stochastic processes in the establishment of penguin breeding colonies also should be taken into account in future research on the formation and distribution of breeding sites.

The results from this work showed that bathymetry characteristics are important in the characterization of chinstrap and gentoo penguin breeding habitat. However, we found that Adélie colonies are not related to the bathymetry of the coastlines. This result contradicts what was found by Fraser & Trivelpiece (1996),   who found that 5 of the biggest colonies in the AP were associated with deep troughs. Much more work is needed for the understanding of the role of bathymetry in the distribution of penguin colonies, using maps of higher resolution and looking not only at slopes and aspects but also at complexity of the ocean basins around breeding colonies.

For sites occupied by penguins, different species of Pygoscelid showed different preferences for the variables tested in this work. Previous research was focus on how these environmental factors affect penguin population at a very local scale (*e.g.* Trivelpiece et al. 1987; Fraser & Trivelpiece 1996; Croxall et al. 2002), or how these variables are related to changes in number in certain penguin sites where data is available

for many years (Lynch et al. 2012). Here, I showed how these variables are important on determining the geographic distribution of colonies and the abundance patterns for the three Pygoscelid penguin species that inhabit the AP.

For all species of penguins, sea-ice extent appeared as a significant factor determining the number of penguins in the colonies. The preferred habitats of the three species are largely defined by the presence or seasonality of sea ice (Lishman 1985; Trivelpiece et al. 1987; Trathan,et al. 1996; Lynnes, Reid, & Croxall 2004; Forcada et al. 2006; Lynch et al. 2012). Extensive ice cover in late spring and early summer is a physical barrier preventing access to breeding colonies by penguin species that are less ice-tolerant (Lishman 1985; Trathan et al. 1996; Rombolá, Marschoff, & Coria 2003; Forcada et al. 2006). Sea ice also affects the distribution and biomass of phytoplankton required by krill larvae to achieve maximum growth and recruitment (Forcada et al. 2006). Extensive and persistent ice conditions favor krill maturation, because dense winter ice concentrations promote early female gonadal development and spawn (Siegel & Loeb 1995). Slight changes in sea ice extent might amplify the influence of climatic variability on primary production; the southward shift observed in sea ice extent is accompanied by a southward shift in the ocean primary productivity (Smith et al. 1999).

For Adélies and gentoos, chlorophyll-a concentration and variation showed a significant relationship with penguin numbers. Large phytoplankton blooms occur during austral spring and summer, particularly in waters associated with ice edges, islands, and continental shelves (Sullivan et al. 1993; Moore & Abbott 2000; Arrigo & van Dijken 2003). Spring and summer phytoplankton blooms, detected through SeaWiFS (seaviewing wide field-of-view sensor) chlorophyll-a distribution, influence krill

recruitment in the vicinity of the AP; conversely, recruitment may vary along the Peninsula depending on the distribution of blooms (Marrari, Daly, & Hu 2007).

Also for Adélie and gentoo penguins, temperature showed to be significantly correlated with the number of penguins in the colonies. Water temperature appears to have a direct relationship with krill abundance (Fedoulov, Murphy, & Shulgovsky 1996), suggesting an indirect effect on penguin distribution. Sea surface temperature is a good estimator of surface air temperature (Chown, Gremmen, & Gaston 1998), which has a threshold effect on the nature of precipitation (rain vs. snow). Whereas penguins and their chicks are adapted to snow, rain can flood nests and saturate downy chicks, increasing mortality (Boersma 2008); thus, a relatively small change in surface temperature can lead to dramatic changes in breeding success.

Even though the environmental variables tested here were showed to have a significant relationship with penguin breeding numbers, there might be other factors that could affect the numbers of penguins in a given colony, and the geographic pattern of penguin colony distributions. For example, in terms of foraging, there is a number of abiotic variables, like wind and sea surface conditions, that could influence the location of prey (Ashmole & Ashmole 1967; Boersma 1978).

Snow cover plays a direct role in determining the location of penguins breeding on the AP, as all three species require snow-free ground or rocks to lay their eggs. Unusually deep snow and heavy snowfall in the spring is associated with high rates of nest flooding and subsequent nest failure (Boersma 2008). Local topography also can influence the disproportionate impact that changes in snow fall patterns have on different locations, driving spatial redistribution in penguin populations (Fraser & Patterson 1997;

Emslie et al. 2004). Snow cover at the detail relevant for influencing penguin habitat selection is not capture by the resolution of any of the remote sensing datasets, because it is a result of very small-scale local influences.

Microhabitat variables at a smaller spatial scale than the one capture with MODIS data could also influence the distribution and numbers of Pygoscelid penguins. Exposure of birds to different weather conditions according to the microhabitat in the colony could influence breeding success. It was demonstrated that Adélie penguins favored ridges that are more likely to remain free of snow and meltwater (Moczydlowski 1989).

Also, weather conditions and weather events that are not possible to pin point with the temporal resolution offered by MODIS could play an important role in the distribution of penguin colonies. There is considerable variability from year to year in the productivity of a given colony because of inclement weather and extreme weather events. Moreover, repeated rain events in particular can affect survival of chicks considerably as it could cause death due to hypothermia (Boersma 2008; Demongin et al. 2010).

This work is an example of the many advantages of combining opportunistic sampling methods with remote sensing. It is a first step toward understanding the broad-scale distribution patterns of penguins along the Antarctic Peninsula. Further studies should focus on the characterization of microhabitat and local weather events at Pygoscelid colonies, and how these affect the presence-absence distributions and abundance of penguins along the Antarctic Peninsula.

Table 5.1. Minimum and maximum values for the environmental variables near penguin colonies.

	Adélie		Chinstrap		Gentoo	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
SST November mean (ºC)	-1.82	-1.53	-1.73	-1.32	-1.75	-1.04
SST November SD (ºC)	0.21	0.50	0.30	0.46	0.20	0.61
Chlorophyll-a November mean (mg/m^3)	0.13	0.22	0.14	0.24	0.13	0.33
Chlorophyll-a November SD (mg/m^3)	0.01	0.07	0.02	0.04	0.01	0.08
Ice Extent November mean (percent of ocean covered by ice)	0	50.8	0	50.8	0	54.0
Ice Extent November SD (percent of ocean covered by ice)	0	28	0	28	0	36
Slope	1.07	16.02	1.07	15.15	0.18	69.11
Aspect	27	359	58	347	2	359

Table 5.2. Best models for explaining the distribution of penguin colonies.

	Models	AIC weights	DIC	Delta DIC
Abundance				
Marine variables				
Adélie	V1a ~ 1 + V2 + V3 + V4 + V7	0.000	191.93	0.00
Adélie	V1a ~ 1 + V2 + V5 + V6	0.000	192.50	0.58
Adélie	V1a ~ 1 + V3 + V4 + V5 + V6 + V7	0.468	193.68	1.75
Chinstrap	V1a ~ 1 + V7	0.000	-19.73	0.00
Gentoo	V1a ~ 1 + V4 + V5 + V6 + V7	0.000	174.03	0.00
Gentoo	V1a ~ 1 + V3 + V4 + V5	0.000	176.29	2.26
Bathymetry variables				
Adélie	V1a ~ 1 + V10	0.000	214.18	0.00
Adélie	V1a ~ 1	0.000	215.11	0.93
Chinstrap	V1a ~ 1 + V9 + V10	1.000	179.90	0.00
Gentoo	V1a ~ 1 + V9	0.000	300.63	0.00
Occupancy				
Marine variables				
Adélie	V1b ~ 1 + V2 + V3 + V6 + V7	0.010	82.61	0.00
Chinstrap	V1b ~ 1 + V2 + V5 + V6 + V7	0.008	42.68	0.00
Gentoo	V1b ~ 1 + V2 + V4 + V5 + V6	0.002	177.81	0.00
Bathymetry variables				
Adélie	V1b ~ 1 + V9 + V10	0.083	88.16	0.00
Chinstrap	V1b ~ 1 + V9 + V10	0.200	64.09	0.00
Gentoo	V1b ~ 1 + V10	0.191	134.37	0.00

V1a = count of penguin nests; V1b = presence-absence of penguin colonies (0-1)

V2 = SST November mean (ºC); V3 = SST November SD (ºC); V4 = Chlorophyll-a November mean (mg/m^3); V5 = Chlorophyll-a November SD (mg/cm^3); V6 = Ice Extent (November mean); V7 = Ice Extent (November SD); V9 = Slope; V10 = Aspect.
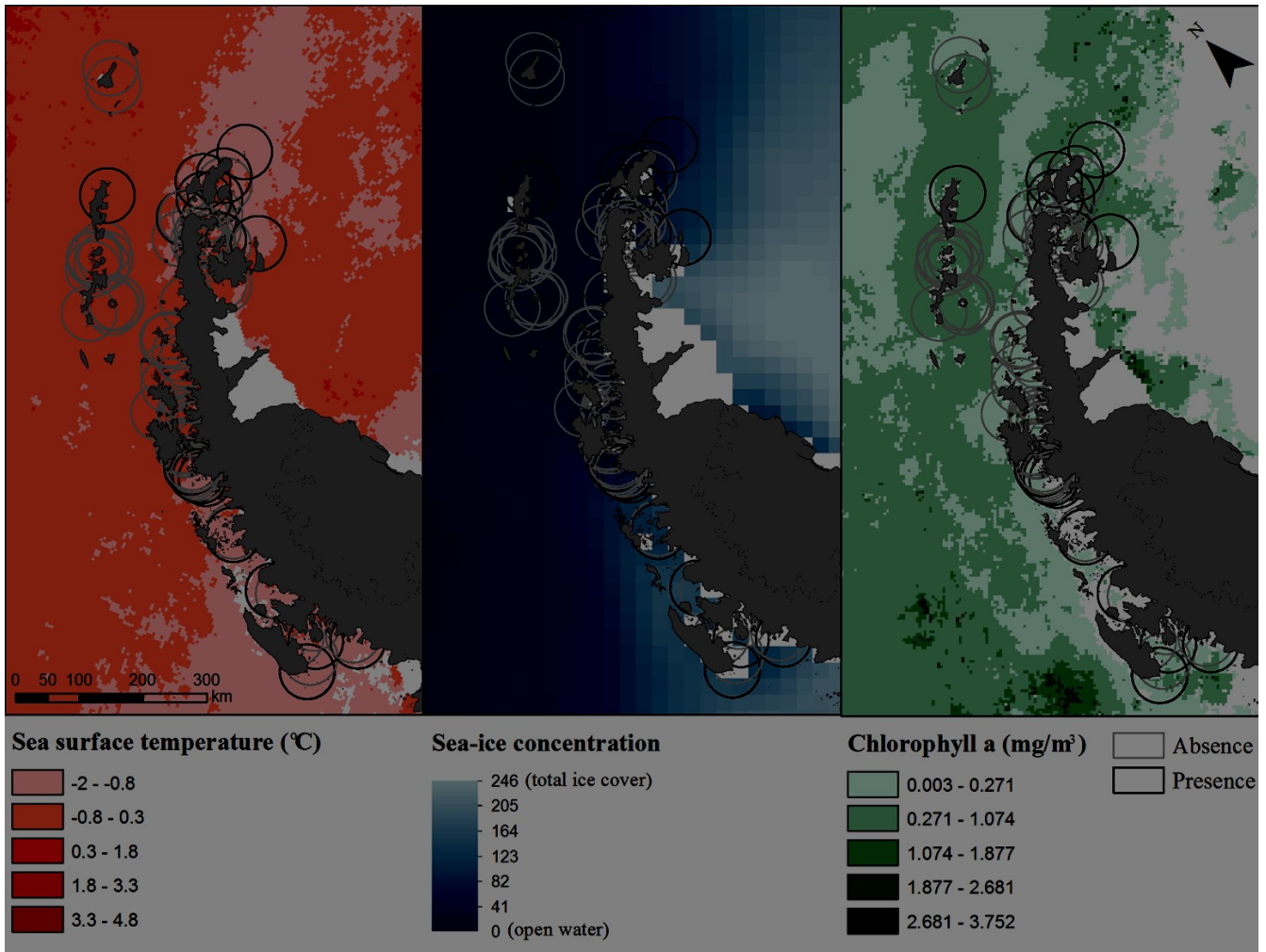
Figure 5.1. Marine variables used for the analyses.

The buffers represent the foraging area around sites where Adélie penguin colonies are known to be present or absent. All images are November means for the variables (from 2002 to 2009).
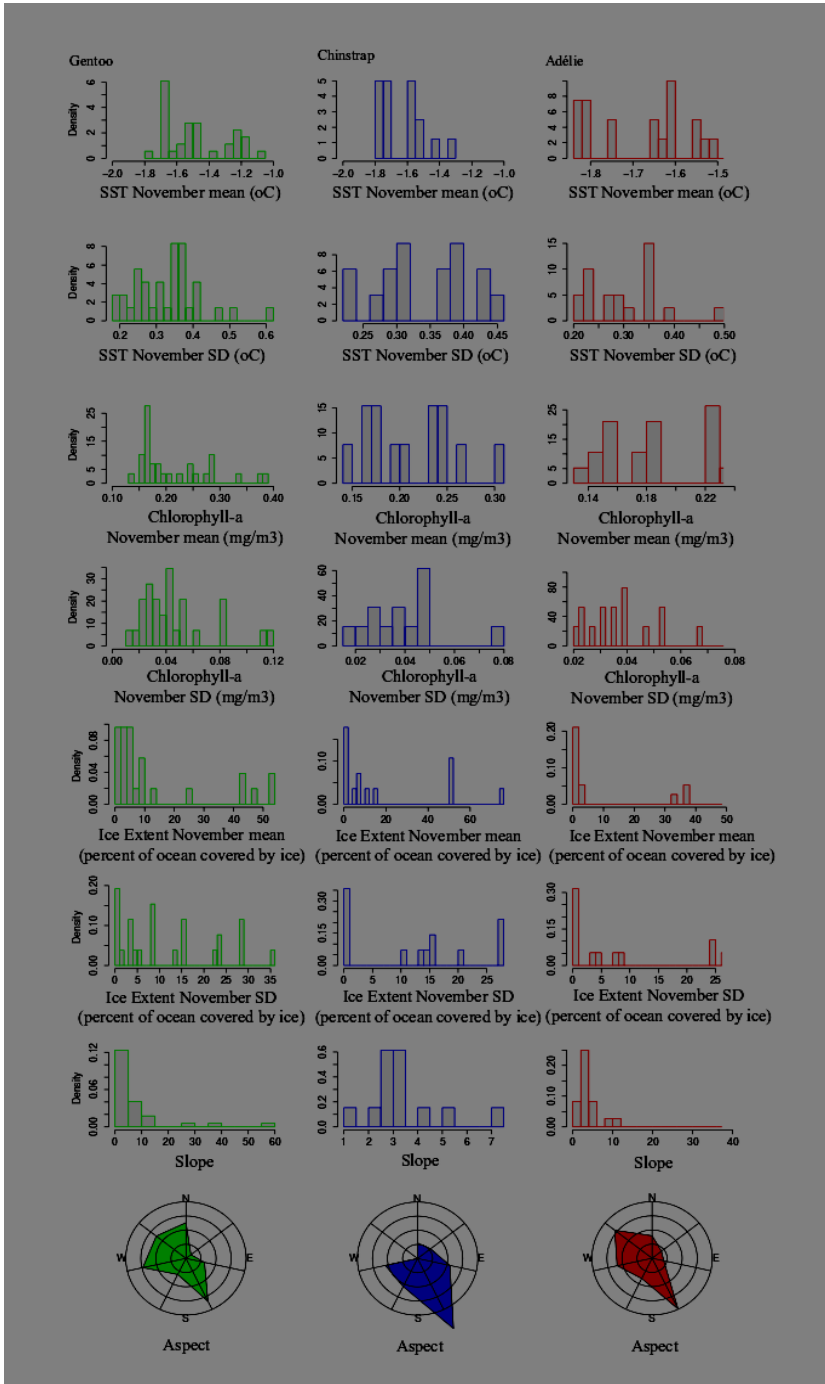
Figure 5.2. Density distribution for all variables studied, at sites with confirmed presence of penguin colonies.
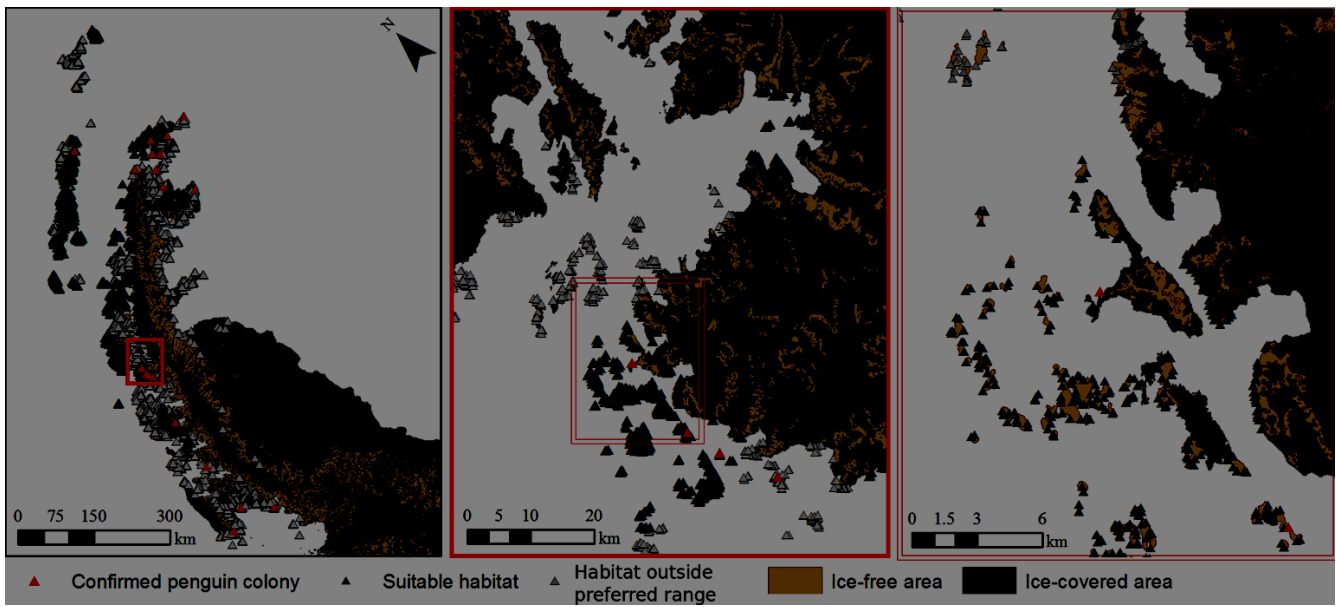
Figure 5.3. Suitable habitat and habitat outside the preferred range for the variables studied for Adélie penguins.
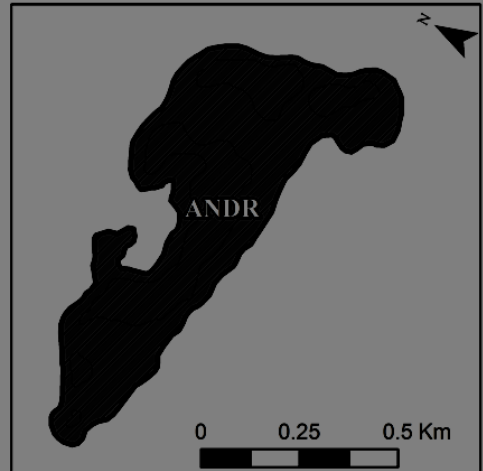
Appendices

Appendix 2.1

Maps showing the sites used in the study. Base maps are from the Antarctic Digital

Database (BAS, SPRI, and WCMC 1993, last accessed April 2011). The projection used

for the maps is South Pole Lambert Azimuthal Equal Area, map made using ArcMap
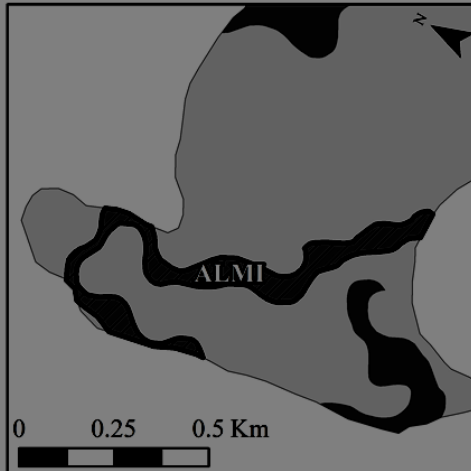
10.0.

ALMI = Almirante Brown Station Vicinity
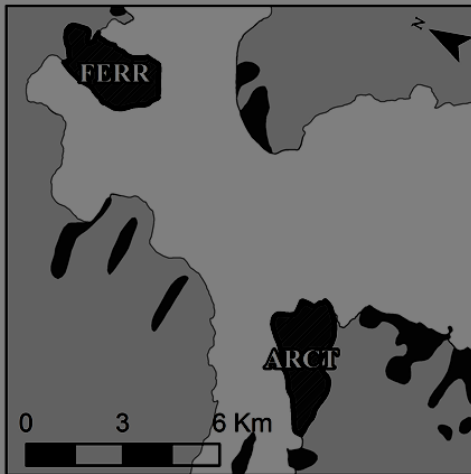
ANDR = Andree Island

King George Island
ARCT = Arctowski Station Vicinity
FERR = Ferraz Station Vicinity

King George Island
BART = Barton Peninsula
JUBA = Jubany Station Vicinity
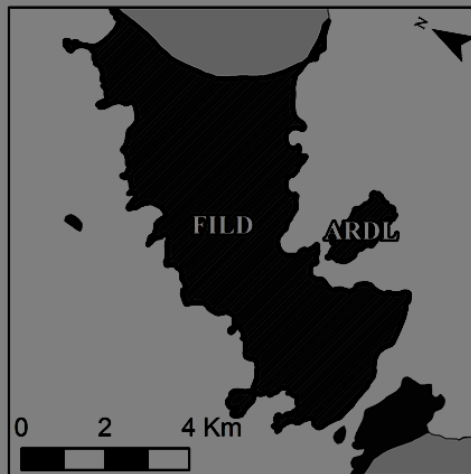
King George Island
ARDL = Ardley Island
FILD = Fildes Peninsula
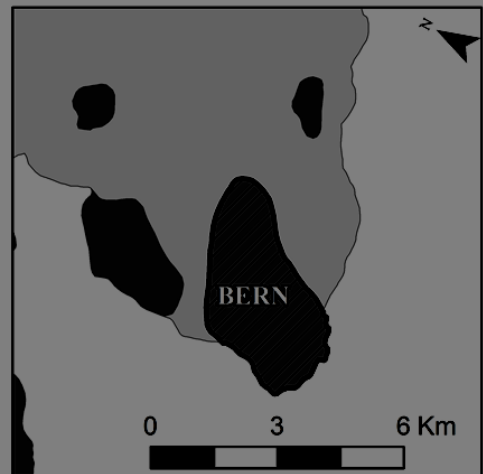
Livingston Island
BERN = Bernard Point

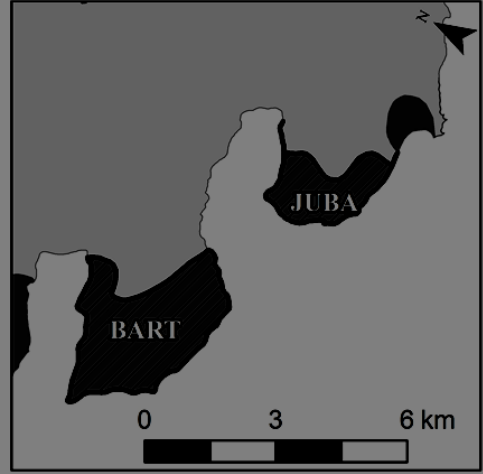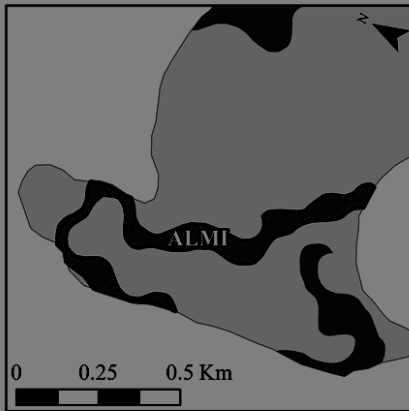ALMI = Almirante Brown Station Vicinity
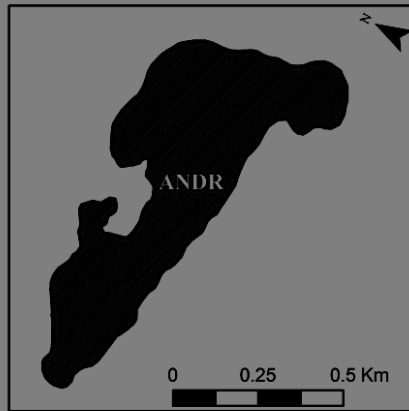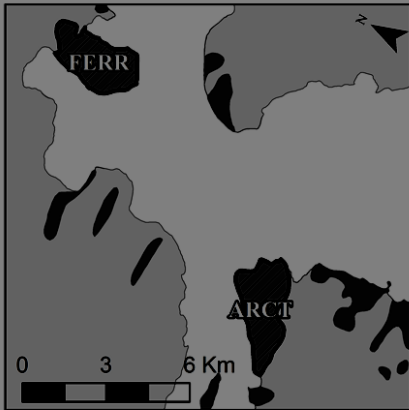
ANDR = Andree Island

King George Island
ARCT = Arctowski Station Vicinity
FERR = Ferraz Station Vicinity
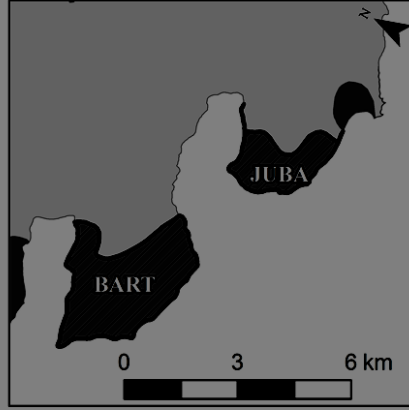
King George Island
BART = Barton Peninsula
JUBA = Jubany Station Vicinity
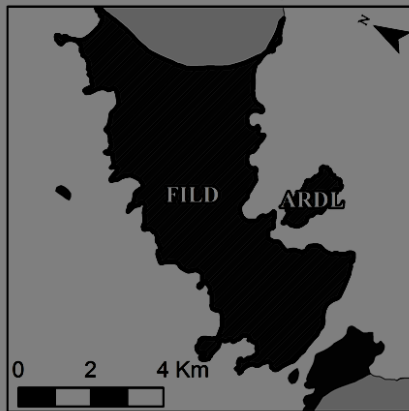
King George Island
ARDL = Ardley Island
FILD = Fildes Peninsula
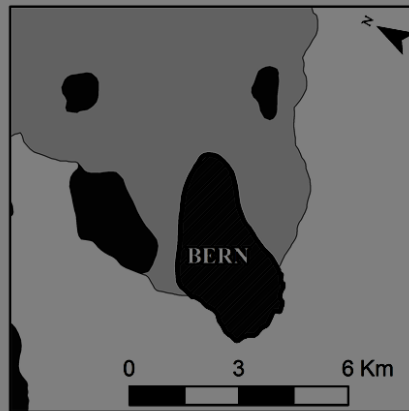
Livingston Island
BERN = Bernard Point
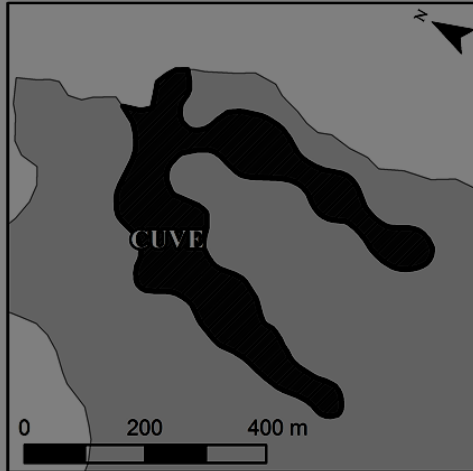
CUVE = Cuverville Island
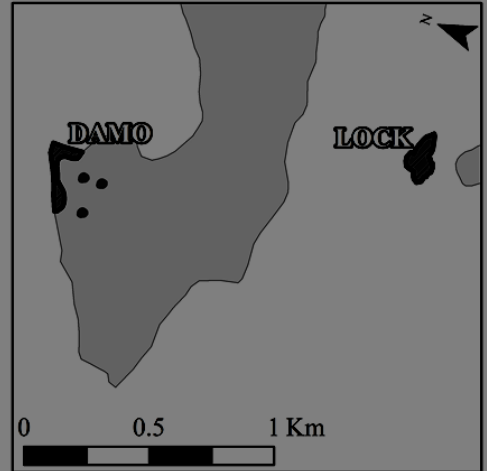
DAMO = Dorian Bay/Damoy Point
LOCK = Port Lockroy
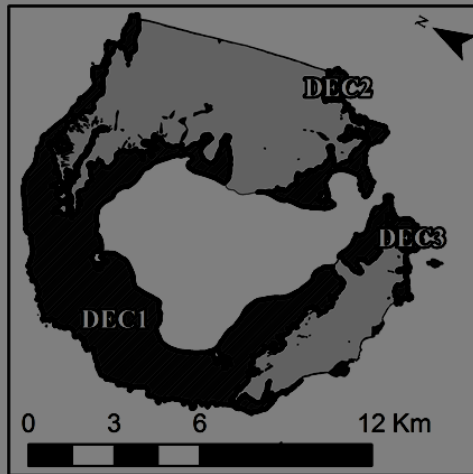
Deception Island
DEC1, DEC2, DEC3 = Sites 1, 2 and 3
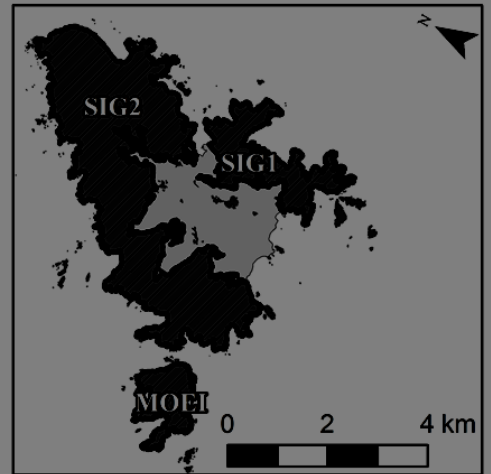
Signy Island
SIG1, SIG2 = Sites 1 and 2
MOEI = Moe Island
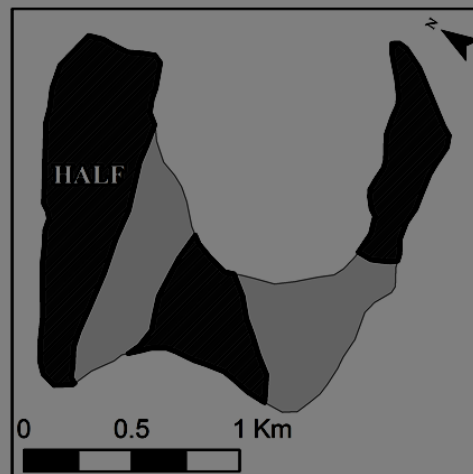
HALF = Half Moon Island
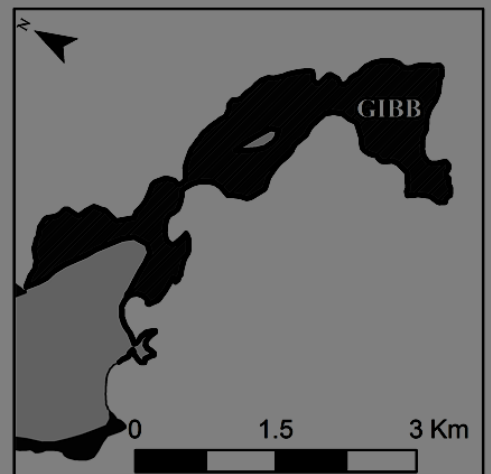
GIBB = Gibbs Island
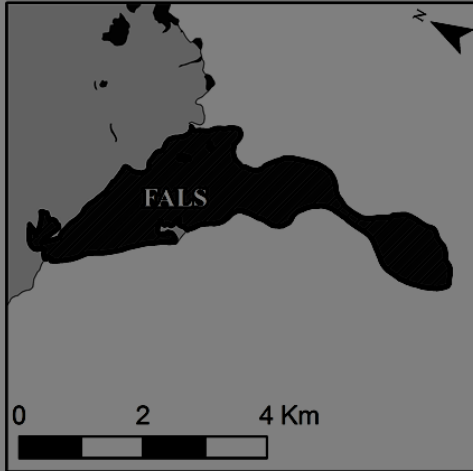
Vega Island
FALS = False Island Point
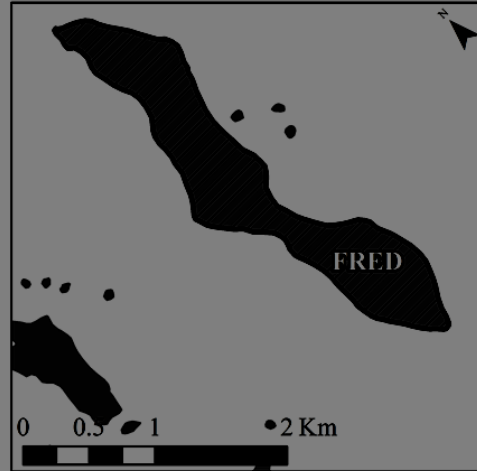
FRED = Fredriksen Island
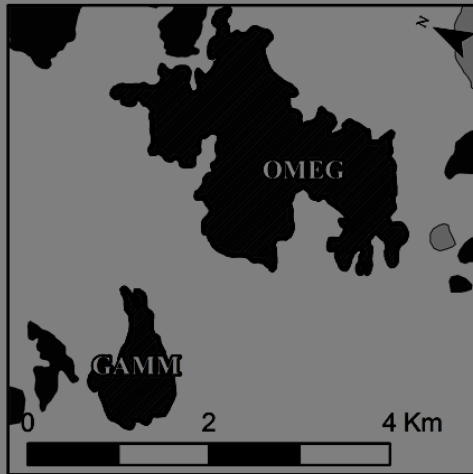
GAMM = Gamma Island
OMEG = Omega Island
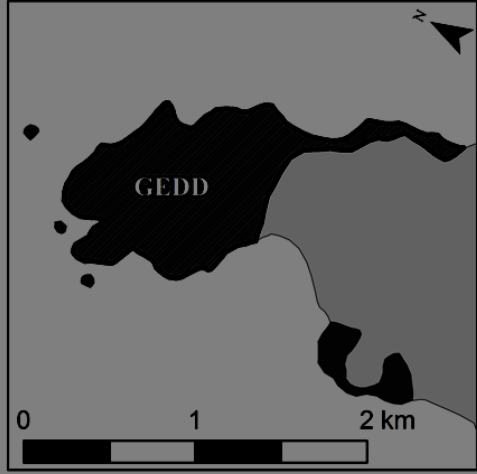
Laurie Island
GEDD = Cape Geddes
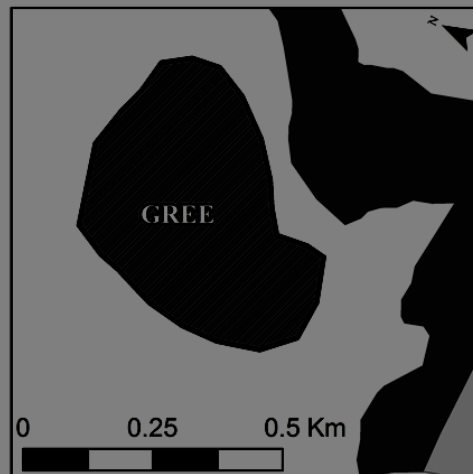
GREE = Green Island
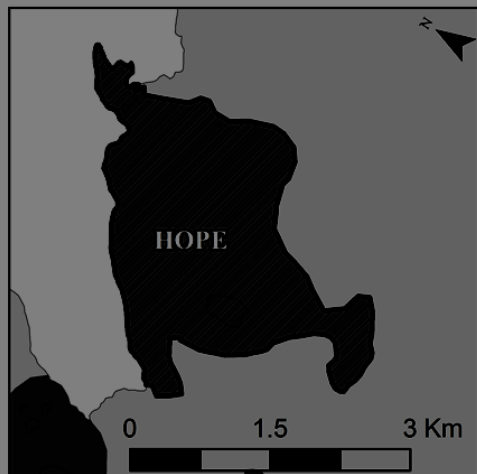
HOPE = Hope Bay
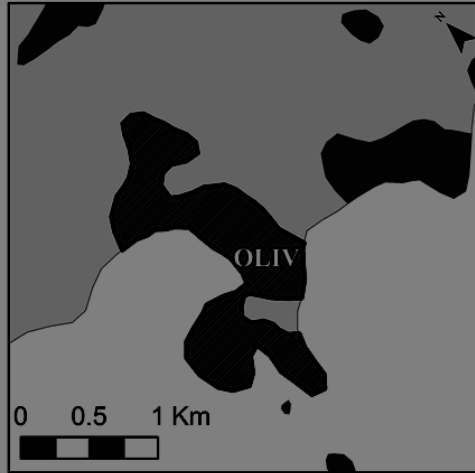
Coronation Island
Olivine Point
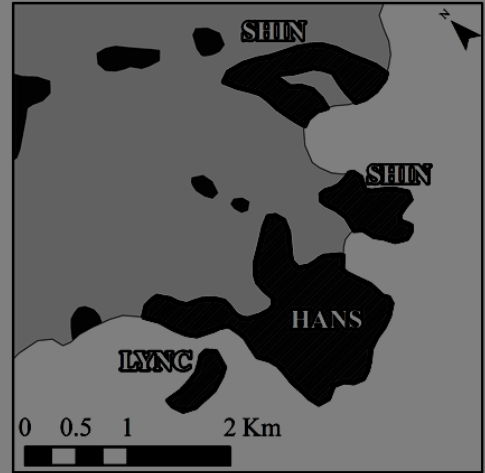
Coronation Island
HANS = Cape Hansen
SHIN = Shingle Cove
LYNC = Lynch Island
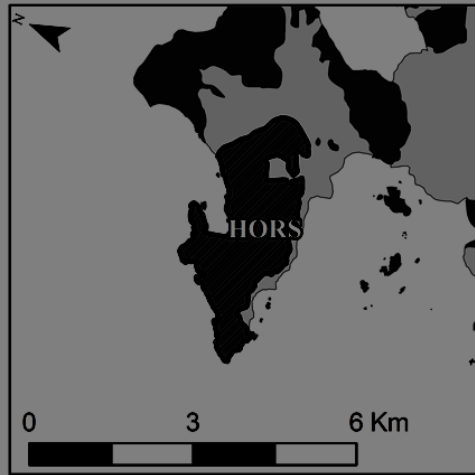
HORS = Horseshoe Island
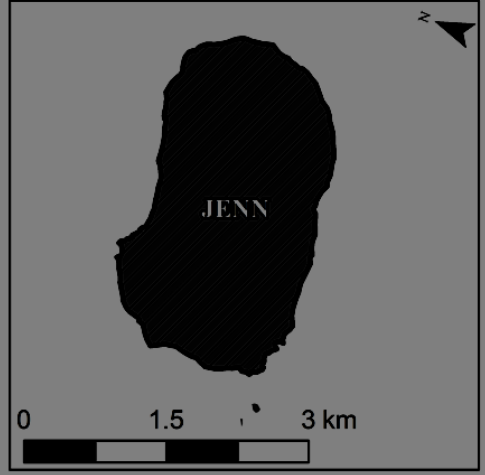
JENN = Jenny Island
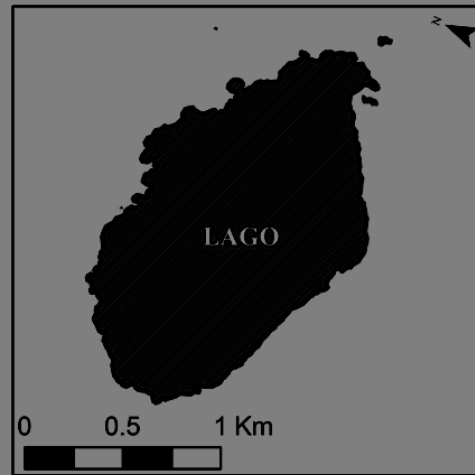
LAGO = Lagotellerie Island
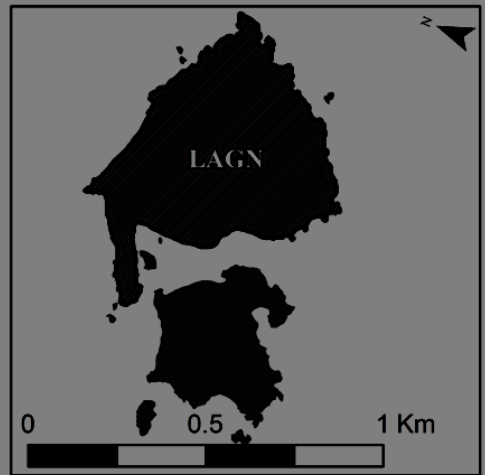
LAGN = Lagoon Island
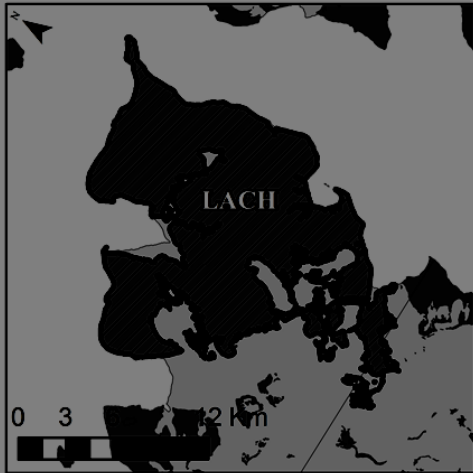
James Ross Island
LACH = Cape Lachman
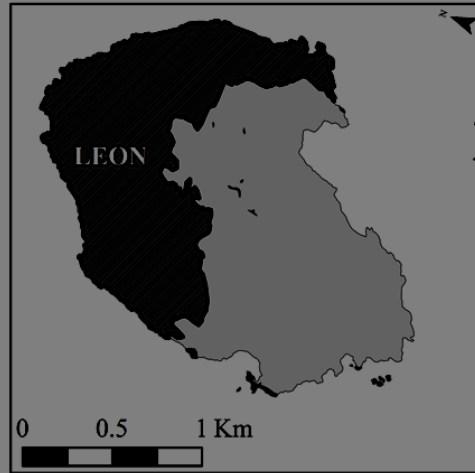
LEON = Léonie Island
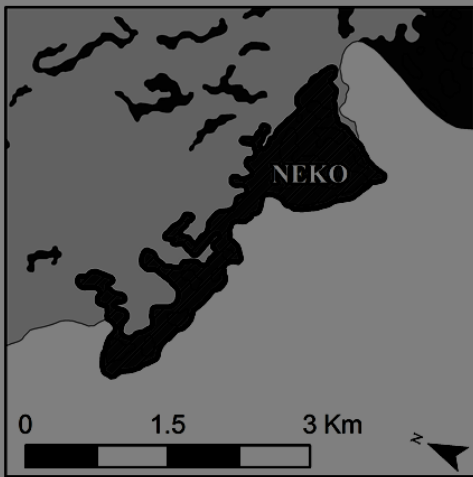
NEKO = Neko Harbor
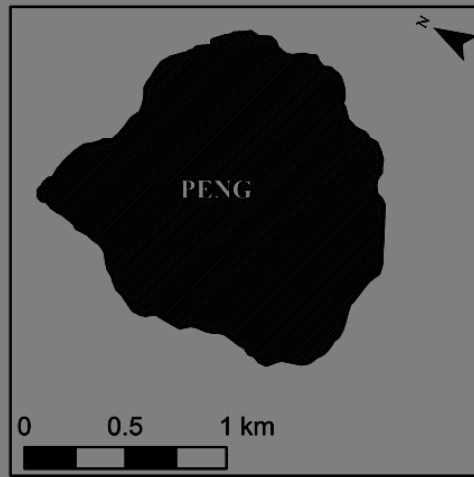
PENG = Penguin Island
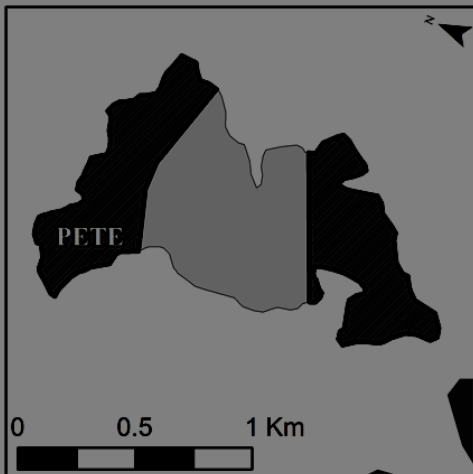
PETE = Petermann Island
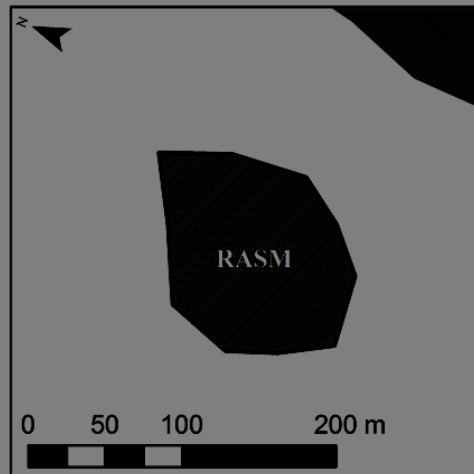
RASM = Rasmussen Island
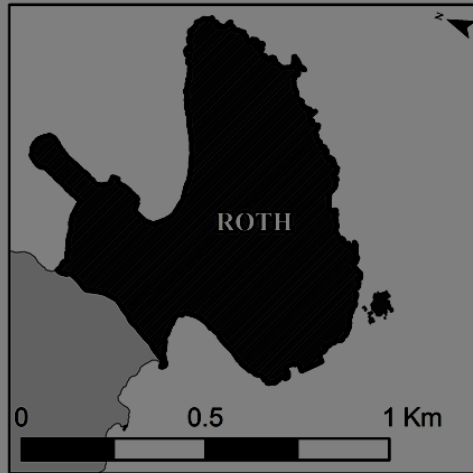
Adelaide Island
ROTH = Rothera Point
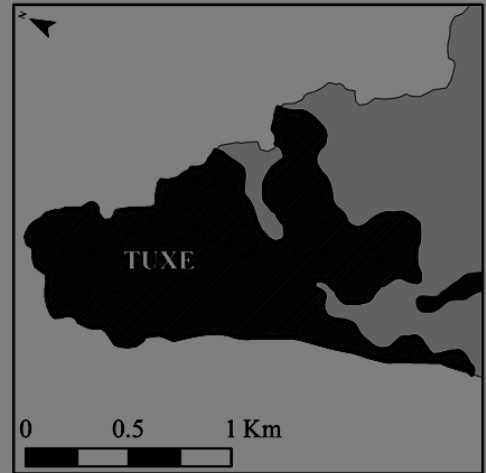
TUXE = Cape Tuxen
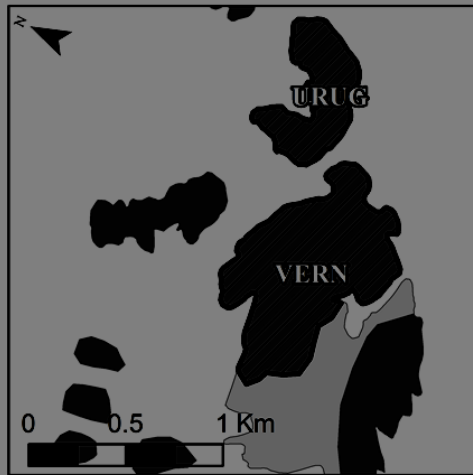
URUG = Uruguay Island
VERN = Vernadsky Station Vicinity
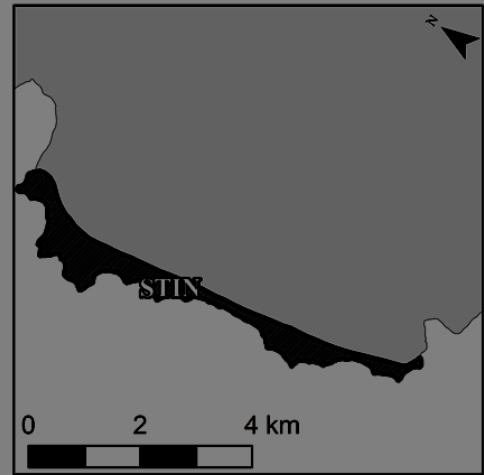
Elephant Island
STIN = Stinker Point
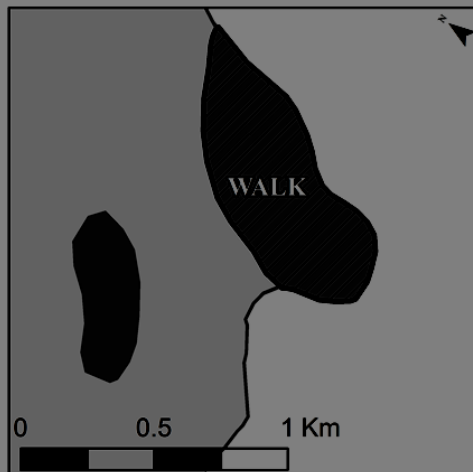
Elephant Island
WALK = Walker Point

Appendix 2.2

Papers with moss and lichen data used for this study:

1. Aptroot, A. & van der Knaap, W.O. (1993) The lichen flora of Deception Island, South Shetland Islands. Nova Hedwigia, 56, 183–192.

2. De Leeuw, C., Aptroot, A. & Van Zanten, B. (1998) The lichen and bryophyte vegetation of Cuverville Island, Antarctica. Nova Hedwigia, 67, 469-480.

3. Martins, M.F.N., Spielmann, A.A., Putzke, J. & Pereira, A.B. (2004) Lichenized fungi on man-made substrata in Deception Island, South Shetland Islands, Antarctica. p. Ciudad Autónoma de Buenos Aires, Argentina.

4. Pereira, A.B., Putzke, M.T.L. & Putzke, J. (2008) Biological Communities Of Keller Peninsula, King George Island-Antarctica* Comunidades Biológicas Da Península Keller, Ilha Rei George–Antártica. Caderno de Pesquisa Sér. Bio., Santa Cruz do Sul, 20, 63–74.

5. Pereira, A.B., Spielmann, A.A., Martins, M.F.N. & Francelino, M.R. (2007) Plant communities from ice-free areas of keller peninsula, king george island, antarctica. Oecologia Brasiliensis, 11, 14.

6. Smykla, J., Wołek, J. & Barcikowski, A. (2007) Zonation of Vegetation Related to Penguin Rookeries on King George Island, Maritime Antarctic. Arctic, Antarctic, and Alpine Research, 39, 143–151.

7. Tatur, A., Myrcha, A. & Niegodzisz, J. (1997) Formation of abandoned penguin rookery ecosystems in the maritime Antarctic. Polar Biology, 17, 405-417.

8. Victoria, F. de C., Costa, D. & Pereira, A.B. (2004) Characterization of plant communities in ice-free areas adjoining the Polish station H. Arctowski, Admiralty Bay,

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King George Island, Antarctica. p. Ciudad Autónoma de Buenos Aires, Argentina.

9. Winkler, J.B. (2000) The role of snowcover on the cryptogamic vegetation in the maritime Antarctic (Potter Peninsula, King George Island). Berichte zur Polarforschung, 371, 151.

Papers with penguin data used in this study:

1. Aguirre, C.A. & Acero, J.M. (1995) Distribution and abundance of birds in the Errera Channel, Antarctic Peninsula, during the 1992/93 breeding season. Marine Ornithology, 23, 129–134.

2. Araya, B. & Arrieta, A. (1971) Las aves de Caleta Potter, Isla Rey Jorge, Antartica Chilena -censo y distribucion. Rev. Biol. mar., 14, 221-228.

3. Chwedorzewska, K.J. & Korczak, M. (2010) Human impact upon the environment in the vicinity of Arctowski Station, King George Island, Antarctica. Pol. Polar Res, 31, 45–60.

4. Cobley, N.D. & Shears, J.R. (1999) Breeding performance of gentoo penguins (Pygoscelis papua) at a colony exposed to high levels of human disturbance. Polar Biology, 21, 355–360.

5. Croxall, J.P. & Davis, L.S. (1999) Penguins: paradoxes and patterns. Marine Ornithology, 27, 1-12.

6. Müller-Schwarze, C. & Müller-Schwarze, D. (1975) A survey of twenty-four rookeries of pygoscelid penguins in the Antarctic Peninsula region. The biology of penguins.

7. Poncet, S. & Poncet, J. (1987) Censuses of penguin populations of the Antarctic Peninsula. 1983-87. British Antarctic Survey Bulletin, 77, 109-129.

8. Shuford, W.D. & Spear, L.B. (1988) Surveys of breeding chinstrap penguins in the South Shetland Islands, Antarctica. British Antarctic Survey Bulletin, 81, 19–30.

9. Trathan, P.N., Forcada, J., Atkinson, R., Downie, R.H. & Shears, J.R. (2008) Population assessments of gentoo penguins (Pygoscelis papua) breeding at an important Antarctic tourist site, Goudier Island, Port Lockroy, Palmer Archipelago, Antarctica. Biological Conservation, 141, 3019-3028.

10. Zale, R. (1994) Changes in size of the Hope Bay Adélie penguin rookery as inferred from Lake Boeckella sediment. Ecography, 17, 297–304.

Description of the mechanistic model used for the estimation of PU richness including model and parameters description, R code for its implementation, and corresponding data.

This modeling approach draws heavily on the model developed in Dorazio and Royle (2005); here we summarize that model in the context of our own application:

The probability that a PU is detected conditional that it is present is given by:

$$p(x_{ij} \mid \Theta_{ij}, \Psi_{ij}) = \Psi_{ij} \binom{K}{x_{ij}} \Theta_{ij}^{x_{ij}} (1 - \Theta_{ij})^{K - x_{ij}} + (1 - \Psi_{ij}) I(x_{ij} = 0)$$

x_{ij} = the number of photographers that found PU i in plot j, as identified by K classifiers
θ_{ij} = probability of detection of PU i given that occurs at plot j
Ψ_{ij} = probability of occurrence of PU i at plot j
K = number of classifiers
I() = indicator function, equals one when its argument is true and is zero otherwise

The effects of the plot-specific and PU-specific differences in rates of occurrence and detection are modeled as:

logit(θ_{ij}) = u_i + α_j
logit(Ψ_{ij}) = v_i + β_j

u_i and v_i denote species-level effects
α_j and β_j denote site-level effects, and it is assumed for this model that they have constant values.

R code for the model and implementation using Prince William Park as an example:

###Code modified from
###http://www.mbr-pwrc.usgs.gov/site/communitymodeling/software-code/

library("reshape")
library("R2WinBUGS")

###################
#Write the model code to a text file (used to run WinBUGS)
cat("
  model{

#Define prior distributions for community-level model parameters
omega ~ dunif(0,1)

```
u.mean ~ dunif(0,1)
mu.u <- log(u.mean) - log(1-u.mean)

v.mean ~ dunif(0,1)
mu.v <- log(v.mean) - log(1-v.mean)

tau.u ~ dgamma(0.1,0.1)
tau.v ~ dgamma(0.1,0.1)

for (i in 1:(n+nzeroes)) {
```

#Create priors for PUs i from the community level prior distributions
```
    w[i] ~ dbern(omega)
    u[i] ~ dnorm(mu.u, tau.u)
    v[i] ~ dnorm(mu.v, tau.v)
```

#Create a loop to estimate the Z matrix (true occurrence for PUs i at point j.
```
  for (j in 1:J) {
      logit(psi[j,i]) <- u[i]

  mu.psi[j,i] <- psi[j,i]*w[i]
  Z[j,i] ~ dbern(mu.psi[j,i])
```

#Create a loop to estimate detection for PUs i at point k during #sampling period k.
```
    for (k in 1:K[j]) {
        logit(p[j,k,i]) <-  v[i]
      mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
        X[j,k,i] ~ dbern(mu.p[j,k,i])
} } }
```

#Sum all PUs observed (n) and unobserved PUs (n0) to find the total estimated richness
```
n0 <- sum(w[(n+1):(n+nzeroes)])
N <- n + n0
```

#Finish writing the text file into a document called basicmodel.txt
```
}",file="basicmodel.txt")


####################
```
##DC lichen data
```
LichenID <- read.csv("DC_lichens_Identifications.csv”)


####################
```
##PRWI = Prince William Park unit
#Select PRWI data from the dataset

```
PRWIPU <- LichenID[LichenID$Taxon_level=="PUs" & LichenID$Protocol=="10M"
& LichenID$site=="PRWI",]
PRWIM <- melt(PRWIPU)
```

#Reshape the tables and select the information needed
#Rep = the classifiers that have identifiers each of the digital specimens
```
PRWIT <- data.frame(cast(PRWIM, plot + Photographer_id + Taxon.name + value ~
Protocol))
PRWIT <-PRWIT[,-5]
names(PRWIT)<- c("Point","Photographer","PUs","Rep")
PRWIdata<-na.omit(PRWIT)
PRWIdata$Occ <- rep(1, dim(PRWIdata)[1])
```

#How many citings for each PU
```
PRWItotal.count = tapply(PRWIdata$Occ, PRWIdata$PUs, sum)
```
#Find the number of unique PUs
```
PRWIuPU = as.character(unique(PRWIdata$PUs))
```
#n is the number of observed PUs
```
PRWIn=length(PRWIuPU)
```
#Find the number of unique plots
```
PRWIupoints = as.character(unique(PRWIdata$Point))
```
#J is the number of plots
```
PRWIJ=length(PRWIupoints)
```

#The detection/non-detection data is reshaped into a three dimensional
#array X where the first dimension, *j*, is the plots; the second
#dimension, *k*, is the rep (classifier); and the last dimension, *i*, is the PU.
 # the array element x$_{ijk}$ is the number of photographers that found PU *i* in plot *j*, as
#identified by classifier *k*

```
PRWIjunk.melt=melt(PRWIdata,id.var=c("PUs", "Point", "Rep"), measure.var="Occ")
PRWIX=cast(PRWIjunk.melt, Point ~ Rep ~ PUs)
```

#Add in the missing lines with NAs
#There are not missing lines in the lichen data (NAs for when a point has not been
sampled)
```
for (i in 1: dim(PRWIX)[3]) {
  b = which(PRWIX[,,i] > 0)
  PRWIX[,,i][b] = 1
  PRWIX[,,i][-b] = 0
}
```

#Create all zero encounter histories to add to the detection array X
#as part of the data augmentation to account for additional
#PUs (beyond the n observed PUs).

#nzeroes is the number of all zero encounter histories to be added
  PRWInzeroes = 50
#X.zero is a matrix of zeroes
  PRWIX.zero = matrix(0, nrow=7, ncol=4)

#Xaug is the augmented version of X. The first n PUs were actually observed
#and the n+1 through nzeroes PUs are all zero encounter histories
  PRWIXaug <- array(0,
dim=c(dim(PRWIX)[1],dim(PRWIX)[2],dim(PRWIX)[3]+PRWInzeroes))
  PRWIXaug[,,(dim(PRWIX)[3]+1):dim(PRWIXaug)[3]] = rep(PRWIX.zero,
PRWInzeroes)
  dimnames(PRWIX)=NULL
  PRWIXaug[,,1:dim(PRWIX)[3]] <- PRWIX

#K is a vector of length J indicating the number of reps at each point j
PRWIKK <- PRWIX.zero
PRWIa=which(PRWIKK==0); PRWIKK[PRWIa] <- 1
PRWIK=apply(PRWIKK,1,sum, na.rm=TRUE)
PRWIK=as.vector(PRWIK)

##################
#Create the necessary arguments to run the bugs() command
#Load all the data
PRWIsp.data = list(n=PRWIn, nzeroes=PRWInzeroes, J=PRWIJ, K=PRWIK,
X=PRWIXaug)

#Specify the parameters to be monitored
PRWIsp.params = list('u', 'v', 'mu.u', 'mu.v', 'tau.u', 'tau.v', 'omega', 'N')

#Specify the initial values
   PRWIsp.inits = function() {
   omegaGuess = runif(1, PRWIn/(PRWIn+PRWInzeroes), 1)
   psi.meanGuess = runif(1, .25,1)
   list(omega=omegaGuess,w=c(rep(1, n), rbinom(PRWInzeroes, size=1,
prob=omegaGuess)),
         u=rnorm(PRWIn+PRWInzeroes), v=rnorm(PRWIn+PRWInzeroes),
         Z = matrix(rbinom((PRWIn+PRWInzeroes)*J, size=1, prob=psi.meanGuess),
    nrow=PRWIJ, ncol=(PRWIn+PRWInzeroes))
)
      }

n<-PRWIn
J<-PRWIJ

#Run the model and call the results ?fit?
PRWIfit = bugs(PRWIsp.data, PRWIsp.inits, PRWIsp.params, "basicmodel.txt",

```
debug=TRUE, n.chains=3, n.iter=1000, n.burnin=500, n.thin=5)
```

#See baseline estimates of PUs-specific occupancy and detection in one of
#the habitat types (PRWI)
```
PRWIPU.occ = PRWIfit$sims.list$u
PRWIPU.det = PRWIfit$sims.list$v
```

#Show occupancy and detection estimates for only the observed PUs (1:n)
```
PRWIpsi = plogis(PRWIPU.occ[,1:n])
PRWIp   = plogis(PRWIPU.det[,1:n])

PRWIocc.matrix <- cbind(apply(PRWIpsi,2,mean),apply(PRWIpsi,2,sd))
colnames(PRWIocc.matrix) = c("mean occupancy", "sd occupancy")
rownames(PRWIocc.matrix) = PRWIuPU

PRWIdet.matrix <- cbind(apply(PRWIp,2,mean),apply(PRWIp,2,sd))
colnames(PRWIdet.matrix) = c("mean detection", "sd detection")
rownames(PRWIdet.matrix) = PRWIuPU

PRWIresults <- data.frame(PRWIuPU,round(PRWIocc.matrix,
digits=2),round(PRWIdet.matrix, digits=2))

PRWIresults$PRWIuPU = with(PRWIresults, factor(PRWIuPU, levels =
PRWIresults$mean.occupancy))

PRWIresults <- PRWIresults[order(PRWIresults$mean.detection) , ]

plot(PRWIresults$mean.occupancy, ylim=c(0,1),pch=19, axes = FALSE, xlab = "", ylab
= "Probability")
points(PRWIresults$mean.detection, ylim=c(0,1),col="red",pch=19)
axis(1, at=c(1:length(PRWIuPU)), lab=F)
text(c(1:length(PRWIuPU)),-0.1, labels=PRWIuPU, xpd=T, srt=40, adj=1,cex=0.5)
axis(side = 2, cex.axis = 1)
box()
```

#See estimates of total richness (N)
```
PRWIN = PRWIfit$sims.list$N
mean(PRWIN)
summary(PRWIN)
table(PRWIN)
plot(table(PRWIN))
```

Example of the data table for "DC_lichens_Identifications.csv" :

Park	Plot	Photographer	Protocol Technique	Growth form	PU name	Classifier
CATO	CATO01	DA	10M Photo	Foliose	Allocetraria oakesiana	1
CATO	CATO01	DA	10M Photo	Foliose	Allocetraria oakesiana	4
CATO	CATO01	EZ	10M Photo	Foliose	Allocetraria oakesiana	1
CATO	CATO01	JS	10M Photo	Foliose	Allocetraria oakesiana	1
CATO	CATO01	JS	10M Photo	Foliose	Allocetraria oakesiana	4
CATO	CATO01	PC	10M Photo	Foliose	Allocetraria oakesiana	1
CATO	CATO01	PC	10M Photo	Foliose	Allocetraria oakesiana	4
CATO	CATO01	PC	10M Photo	Foliose	Allocetraria oakesiana	1
CATO	CATO01	PC	10M Photo	Foliose	Allocetraria oakesiana	4
CATO	CATO01	DA	10M Photo	Foliose	Cetrelia chicitae	3
CATO	CATO01	EZ	10M Photo	Foliose	Cetrelia chicitae	3
CATO	CATO01	JS	10M Photo	Foliose	Cetrelia chicitae	3
CATO	CATO01	PC	10M Photo	Foliose	Cetrelia chicitae	3

Metadata of Antarctic Lichen Photography database

Data set status and accessibility

A. Status

Latest update: 2012

Metadata status: Metadata are complete.

Data verification: The data were checked for consistency. Parataxonomic unit names were thoroughly checked and corrected according to Øvstedal and Smith (2001, 2009).

B. Accessibility

Storage location and medium: The Ecological Society of America's *Ecological Archives*

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D. Copyright restrictions: Any paper using the data should cite this paper.

Data structural descriptors

Description of sampling sites

A. Data Set File

Identity: Sites.csv

Size: 3,823 bytes

Format and storage mode: ASCII text, comma separated

B. Header information

Site_ID: Unique ID for each site

Site_name: Site name according to the U.S. Board on Geographic Names

Latitude: Latitude of the site

Longitude: Longitude of the site

notes: A description of the site, or any other notes of relevance for the site.

Description of visits

A. Data Set File

Identity: Visit.csv

Size: 4,324 bytes

Format and storage mode: ASCII text, comma separated

B. Header information

Visit_ID: Unique number of a site of data collection

Site_ID: ID for each site. For detailed site description see file Sites.txt

Visit_day: Number between 01-31

Visit_month: Number of the month, between 01-12

Visit_year: Year number, using four digits

notes: Any notes relevant to the visit

List of the parataxonomic units on the database

A. Data Set File

Identity: Parataxonomy.csv

Size: 10,519 bytes

Format and storage mode: ASCII text, comma separated

B. Header information

Parataxon_name: Unique name for the parataxonomic unit

Parataxon_level: Indicates if the parataxonomic unit refers to a species or to a genus

Growth_form: Growth form of the lichen parataxonomic unit: crustose, foliose, fruticose

Description of photographs collected in each visit

A. Data Set File

Identity: Photograph.csv

Size: 93,428 bytes

Format and storage mode: ASCII text, comma separated

B. Header information

file_name: Unique name for the photograph

Visit_ID: ID for each visit. For detailed visit description see file Visit.txt

Photographer: ID for the photographer

Copyright_holder: The photographer or the Antarctic Site Inventory

Photo_quality: A qualitative measurement of the picture quality. Poor: the lichens in the image are not possible to distinguish; medium: the lichens in the image can be distinguished, but the resolution is very low, and no small structures are defined; good: the lichens in the image are well defined, but small structures cannot be distinguished; excellent: the lichens in the image are well defined, and small structures on the lichens can be observed.

Notes: Notes about the photograph

Description of specimens isolated from the photographs

A. Data Set File

Identity: Specimens.csv

Size: 145,034 bytes

Format and storage mode: ASCII text, comma separated

B. Header information

catalog_file_name: Unique name for the specimen

file_name: ID for each photograph from where the specimen was isolated. For detailed photograph description see file Photograph.txt

Notes: Notes about the specimen

Identification of specimens by different classifiers

A. Data Set File

Identity: Identification.csv

Size: 509,961 bytes

Format and storage mode: ASCII text, comma separated

B. Header information

identification_ID: Unique number for the identification

catalog_file_name: ID for each specimen. For detailed specimen description see file

Specimens.txt

Parataxon_name: Parataxonomic unit name. For detailed parataxonomic unit name description see file Parataxonomy.txt

Identification_quality: A qualitative measurement of the identification quality (poor, medium, good, excellent)

Determination_day: Number between 01-31

Determination_month: Number of the month, between 01-12

Determination_year: Year number, using four digits

Notes: Notes about the photograph

Description of PU richness by sites

A. Data Set File

Identity: Richness.csv

Size: 1,357 bytes

Format and storage mode: ASCII text, comma separated

B. Header information

Estimation_ID: Unique number for the estimation

Site_ID: ID for the site. For detailed site description see file Sites.txt

Observed_Genus_PU: Number of PUs observed

Estimated_Genus_PU: Estimated number of PUs using Chao2

Observed_Species_PU: Number of PUs observed

Estimated_Species_PU: estimated number of PUs using Chao2

Notes: Notes about the estimations

Appendix 5.1

All models for explaining the distribution of penguin colonies.

V1a = count of penguin nests; V1b = presence-absence of penguin colonies (0-1)

V2 = SST November mean (^{o}C); V3 = SST November SD (^{o}C); V4 = Chlorophyll-a November mean

(mg/m^3); V5 = Chlorophyll-a November SD (mg/cm^3); V6 = Ice Extent (November mean); V7 = Ice Extent

(November SD); V9 = Slope; V10 = Aspect.

		Model	AIC weights	DIC	ΔDIC
Abundance					
Marine variables					
	Adélie	V1a ~ 1 + V2 + V3 + V4 + V7	0.000	191.93	0.00
	Adélie	V1a ~ 1 + V2 + V5 + V6	0.000	192.50	0.58
	Adélie	V1a ~ 1 + V3 + V4 + V5 + V6 + V7	0.468	193.68	1.75
	Adélie	V1a ~ 1 + V2 + V3 + V4 + V5 + V6 + V7	0.532	195.10	3.17
	Adélie	V1a ~ 1 + V2 + V5 + V7	0.000	195.22	3.29
	Adélie	V1a ~ 1 + V2 + V3 + V4 + V5 + V7	0.000	195.51	3.58
	Adélie	V1a ~ 1 + V2 + V4 + V5	0.000	199.28	7.35
	Adélie	V1a ~ 1 + V5 + V6	0.000	199.45	7.52
	Adélie	V1a ~ 1 + V2 + V4 + V5 + V6 + V7	0.000	201.72	9.79
	Adélie	V1a ~ 1 + V2 + V3 + V5 + V6	0.000	202.24	10.31
	Adélie	V1a ~ 1 + V3 + V5 + V7	0.000	203.58	11.65
	Adélie	V1a ~ 1 + V2 + V3 + V6 + V7	0.000	203.88	11.95
	Adélie	V1a ~ 1 + V4 + V5 + V7	0.000	207.26	15.34
	Adélie	V1a ~ 1 + V5 + V6 + V7	0.000	208.03	16.10
	Adélie	V1a ~ 1 + V6 + V7	0.000	208.19	16.26
	Adélie	V1a ~ 1 + V6	0.000	208.91	16.98
	Adélie	V1a ~ 1 + V4 + V5 + V6 + V7	0.000	209.74	17.81
	Adélie	V1a ~ 1 + V3 + V7	0.000	212.19	20.27
	Adélie	V1a ~ 1 + V4 + V5	0.000	215.09	23.17
	Adélie	V1a ~ 1 + V2 + V4	0.000	215.21	23.28
	Adélie	V1a ~ 1 + V2 + V5	0.000	215.72	23.80
	Adélie	V1a ~ 1 + V2 + V4 + V6	0.000	219.80	27.87
	Adélie	V1a ~ 1 + V3 + V4 + V5	0.000	220.97	29.04
	Adélie	V1a ~ 1 + V3 + V5	0.000	221.66	29.73
	Adélie	V1a ~ 1 + V4 + V6	0.000	222.71	30.78
	Adélie	V1a ~ 1 + V4	0.000	222.83	30.90
	Adélie	V1a ~ 1 + V3 + V4 + V6	0.000	222.90	30.98
	Adélie	V1a ~ 1 + V5 + V7	0.000	223.09	31.16
	Adélie	V1a ~ 1 + V3 + V4 + V5 + V7	0.000	223.82	31.90
	Adélie	V1a ~ 1 + V2 + V3 + V6	0.000	224.21	32.28
	Adélie	V1a ~ 1	0.000	225.62	33.69
	Adélie	V1a ~ 1 + V2 + V3 + V4 + V6 + V7	0.000	226.85	34.92
	Adélie	V1a ~ 1 + V4 + V6 + V7	0.000	228.06	36.14
	Adélie	V1a ~ 1 + V2 + V3 + V4 + V6	0.000	228.10	36.18

Adélie	V1a ~ 1 + V2 + V4 + V5 + V7	0.000	228.22	36.29
Adélie	V1a ~ 1 + V2 + V3	0.000	228.62	36.69
Adélie	V1a ~ 1 + V3 + V6 + V7	0.000	228.82	36.89
Adélie	V1a ~ 1 + V2 + V4 + V5 + V6	0.000	229.19	37.26
Adélie	V1a ~ 1 + V4 + V5 + V6	0.000	229.41	37.48
Adélie	V1a ~ 1 + V2 + V3 + V4 + V5 + V6	0.000	231.21	39.28
Adélie	V1a ~ 1 + V2 + V4 + V7	0.000	231.49	39.57
Adélie	V1a ~ 1 + V2 + V4 + V6 + V7	0.000	231.85	39.93
Adélie	V1a ~ 1 + V2 + V3 + V5 + V6 + V7	0.000	231.85	39.93
Adélie	V1a ~ 1 + V5	0.000	232.43	40.50
Adélie	V1a ~ 1 + V3 + V4 + V7	0.000	232.83	40.91
Adélie	V1a ~ 1 + V2 + V6	0.000	233.28	41.36
Adélie	V1a ~ 1 + V3 + V6	0.000	233.37	41.45
Adélie	V1a ~ 1 + V3	0.000	233.73	41.80
Adélie	V1a ~ 1 + V2 + V6 + V7	0.000	235.23	43.30
Adélie	V1a ~ 1 + V4 + V7	0.000	235.46	43.53
Adélie	V1a ~ 1 + V2	0.000	236.75	44.82
Adélie	V1a ~ 1 + V2 + V3 + V4	0.000	236.81	44.88
Adélie	V1a ~ 1 + V2 + V3 + V5 + V7	0.000	237.08	45.15
Adélie	V1a ~ 1 + V3 + V4 + V5 + V6	0.000	237.52	45.59
Adélie	V1a ~ 1 + V7	0.000	238.13	46.21
Adélie	V1a ~ 1 + V3 + V5 + V6	0.000	238.34	46.41
Adélie	V1a ~ 1 + V3 + V4 + V6 + V7	0.000	238.40	46.47
Adélie	V1a ~ 1 + V2 + V3 + V5	0.000	239.94	48.01
Adélie	V1a ~ 1 + V3 + V4	0.000	240.99	49.06
Adélie	V1a ~ 1 + V2 + V7	0.000	242.13	50.20
Adélie	V1a ~ 1 + V2 + V3 + V7	0.000	242.14	50.22
Adélie	V1a ~ 1 + V2 + V5 + V6 + V7	0.000	242.56	50.64
Adélie	V1a ~ 1 + V3 + V5 + V6 + V7	0.000	242.68	50.75
Adélie	V1a ~ 1 + V2 + V3 + V4 + V5	0.000	242.92	50.99
Chinstrap	V1a ~ 1 + V7	0.000	-19.73	0.00
Chinstrap	V1a ~ 1 + V3 + V4 + V6 + V7	0.000	109.79	129.53
Chinstrap	V1a ~ 1 + V2 + V3 + V4 + V6 + V7	0.000	110.08	129.81
Chinstrap	V1a ~ 1 + V3 + V5 + V6	0.000	111.14	130.88
Chinstrap	V1a ~ 1 + V2 + V5 + V7	0.000	113.07	132.81
Chinstrap	V1a ~ 1 + V3 + V4	0.000	114.79	134.52
Chinstrap	V1a ~ 1 + V2 + V3	0.000	115.89	135.62
Chinstrap	V1a ~ 1 + V5	0.000	116.06	135.80
Chinstrap	V1a ~ 1 + V3 + V6	0.000	117.23	136.97
Chinstrap	V1a ~ 1 + V3 + V4 + V5 + V7	0.000	120.72	140.45
Chinstrap	V1a ~ 1 + V2 + V3 + V5 + V6	0.000	123.27	143.01
Chinstrap	V1a ~ 1 + V3 + V4 + V5 + V6	0.000	123.91	143.64
Chinstrap	V1a ~ 1 + V2 + V3 + V4 + V6	0.000	127.80	147.53
Chinstrap	V1a ~ 1 + V2 + V5 + V6 + V7	0.000	130.09	149.82
Chinstrap	V1a ~ 1 + V2 + V3 + V4 + V5	0.000	131.57	151.31
Chinstrap	V1a ~ 1 + V2 + V4 + V5 + V6 + V7	0.000	132.08	151.82
Chinstrap	V1a ~ 1 + V6 + V7	0.000	133.76	153.50
Chinstrap	V1a ~ 1 + V3 + V6 + V7	0.000	134.08	153.82
Chinstrap	V1a ~ 1 + V2 + V7	0.000	134.33	154.06
Chinstrap	V1a ~ 1 + V3 + V5 + V7	0.000	134.63	154.37
Chinstrap	V1a ~ 1 + V3 + V5 + V6 + V7	0.000	135.74	155.47
Chinstrap	V1a ~ 1 + V3 + V4 + V6	0.000	135.89	155.63

Chinstrap	V1a ~ 1 + V2 + V3 + V4 + V5 + V7	0.000	137.37	157.10
Chinstrap	V1a ~ 1 + V2 + V5 + V6	0.000	137.49	157.22
Chinstrap	V1a ~ 1 + V4 + V6	0.000	137.88	157.62
Chinstrap	V1a ~ 1 + V3 + V4 + V5	0.000	139.59	159.33
Chinstrap	V1a ~ 1 + V2 + V3 + V4 + V5 + V6	0.000	140.30	160.03
Chinstrap	V1a ~ 1 + V2 + V3 + V4 + V5 + V6 + V7	1.000	140.75	160.49
Chinstrap	V1a ~ 1 + V2 + V4 + V5 + V7	0.000	141.13	160.86
Chinstrap	V1a ~ 1 + V3 + V4 + V7	0.000	141.60	161.33
Chinstrap	V1a ~ 1 + V4 + V5 + V6 + V7	0.000	142.01	161.74
Chinstrap	V1a ~ 1 + V2 + V3 + V6 + V7	0.000	142.05	161.79
Chinstrap	V1a ~ 1 + V2 + V3 + V5 + V7	0.000	142.98	162.71
Chinstrap	V1a ~ 1 + V2 + V4 + V5 + V6	0.000	142.99	162.73
Chinstrap	V1a ~ 1 + V2 + V3 + V5	0.000	143.14	162.87
Chinstrap	V1a ~ 1 + V2 + V3 + V4 + V7	0.000	143.55	163.28
Chinstrap	V1a ~ 1 + V2 + V4 + V7	0.000	144.02	163.75
Chinstrap	V1a ~ 1 + V4 + V5 + V6	0.000	144.81	164.54
Chinstrap	V1a ~ 1 + V5 + V6 + V7	0.000	147.43	167.16
Chinstrap	V1a ~ 1 + V2 + V4 + V6 + V7	0.000	147.43	167.16
Chinstrap	V1a ~ 1 + V2 + V3 + V6	0.000	148.53	168.27
Chinstrap	V1a ~ 1 + V4 + V7	0.000	148.71	168.44
Chinstrap	V1a ~ 1 + V3 + V4 + V5 + V6 + V7	0.000	150.38	170.12
Chinstrap	V1a ~ 1 + V3	0.000	150.84	170.57
Chinstrap	V1a ~ 1 + V6	0.000	152.56	172.29
Chinstrap	V1a ~ 1 + V3 + V7	0.000	154.32	174.05
Chinstrap	V1a ~ 1 + V2 + V4 + V6	0.000	154.81	174.54
Chinstrap	V1a ~ 1 + V3 + V5	0.000	156.52	176.26
Chinstrap	V1a ~ 1	0.000	157.11	176.84
Chinstrap	V1a ~ 1 + V2 + V6 + V7	0.000	159.89	179.62
Chinstrap	V1a ~ 1 + V4	0.000	166.30	186.04
Chinstrap	V1a ~ 1 + V4 + V5	0.000	167.19	186.92
Chinstrap	V1a ~ 1 + V2 + V3 + V7	0.000	167.59	187.32
Chinstrap	V1a ~ 1 + V4 + V6 + V7	0.000	167.97	187.71
Chinstrap	V1a ~ 1 + V2 + V4	0.000	168.99	188.73
Chinstrap	V1a ~ 1 + V2	0.000	169.58	189.31
Chinstrap	V1a ~ 1 + V2 + V3 + V5 + V6 + V7	0.000	172.39	192.13
Chinstrap	V1a ~ 1 + V2 + V6	0.000	172.46	192.19
Chinstrap	V1a ~ 1 + V2 + V4 + V5	0.000	173.30	193.04
Chinstrap	V1a ~ 1 + V2 + V3 + V4	0.000	173.98	193.71
Chinstrap	V1a ~ 1 + V4 + V5 + V7	0.000	174.52	194.26
Chinstrap	V1a ~ 1 + V5 + V7	0.000	177.34	197.07
Chinstrap	V1a ~ 1 + V5 + V6	0.000	184.61	204.34
Chinstrap	V1a ~ 1 + V2 + V5	0.000	189.14	208.87
Gentoo	V1a ~ 1 + V4 + V5 + V6 + V7	0.000	174.03	0.00
Gentoo	V1a ~ 1 + V3 + V4 + V5	0.000	176.29	2.26
Gentoo	V1a ~ 1 + V4 + V5 + V6	0.000	186.08	12.04
Gentoo	V1a ~ 1 + V2 + V4 + V7	0.000	190.04	16.01
Gentoo	V1a ~ 1 + V2 + V3 + V4 + V5	0.000	195.38	21.34
Gentoo	V1a ~ 1 + V3 + V4 + V6 + V7	0.000	195.96	21.93
Gentoo	V1a ~ 1 + V6 + V7	0.000	199.33	25.30
Gentoo	V1a ~ 1 + V3 + V5 + V6 + V7	0.000	199.43	25.40
Gentoo	V1a ~ 1 + V2 + V3	0.000	201.33	27.30
Gentoo	V1a ~ 1 + V2 + V3 + V4 + V5 + V6 + V7	1.000	201.44	27.41
Gentoo	V1a ~ 1 + V2 + V5 + V7	0.000	208.99	34.95

Gentoo	V1a ~ 1 + V2 + V3 + V4 + V6	0.000	210.57 36.53
Gentoo	V1a ~ 1 + V2 + V3 + V4 + V6 + V7	0.000	211.43 37.40
Gentoo	V1a ~ 1 + V3 + V4 + V5 + V6	0.000	211.54 37.50
Gentoo	V1a ~ 1 + V2 + V7	0.000	211.55 37.51
Gentoo	V1a ~ 1 + V2 + V3 + V4 + V5 + V6	0.000	212.09 38.05
Gentoo	V1a ~ 1 + V2 + V3 + V5 + V7	0.000	212.45 38.42
Gentoo	V1a ~ 1 + V2 + V3 + V7	0.000	213.05 39.02
Gentoo	V1a ~ 1 + V4 + V5	0.000	215.52 41.49
Gentoo	V1a ~ 1 + V5	0.000	215.55 41.52
Gentoo	V1a ~ 1 + V2 + V6	0.000	215.87 41.84
Gentoo	V1a ~ 1 + V2 + V3 + V4 + V5 + V7	0.000	215.98 41.95
Gentoo	V1a ~ 1 + V2 + V4 + V6	0.000	216.34 42.31
Gentoo	V1a ~ 1 + V2 + V4 + V5 + V6 + V7	0.000	216.44 42.40
Gentoo	V1a ~ 1 + V5 + V6 + V7	0.000	216.71 42.68
Gentoo	V1a ~ 1 + V4 + V7	0.000	217.09 43.06
Gentoo	V1a ~ 1 + V2 + V3 + V6	0.000	217.53 43.50
Gentoo	V1a ~ 1 + V2 + V5	0.000	217.72 43.68
Gentoo	V1a ~ 1 + V4	0.000	218.72 44.69
Gentoo	V1a ~ 1 + V3 + V4 + V5 + V7	0.000	219.00 44.97
Gentoo	V1a ~ 1 + V4 + V6	0.000	219.23 45.20
Gentoo	V1a ~ 1 + V2 + V5 + V6	0.000	219.35 45.32
Gentoo	V1a ~ 1	0.000	219.39 45.36
Gentoo	V1a ~ 1 + V3 + V4 + V5 + V6 + V7	0.000	219.79 45.75
Gentoo	V1a ~ 1 + V3 + V5 + V7	0.000	219.86 45.82
Gentoo	V1a ~ 1 + V4 + V5 + V7	0.000	219.92 45.89
Gentoo	V1a ~ 1 + V2 + V3 + V5 + V6	0.000	220.42 46.38
Gentoo	V1a ~ 1 + V2 + V4 + V5 + V7	0.000	221.26 47.22
Gentoo	V1a ~ 1 + V3 + V5 + V6	0.000	221.81 47.77
Gentoo	V1a ~ 1 + V7	0.000	222.02 47.98
Gentoo	V1a ~ 1 + V2 + V3 + V5	0.000	222.22 48.19
Gentoo	V1a ~ 1 + V3 + V6 + V7	0.000	222.28 48.25
Gentoo	V1a ~ 1 + V3 + V7	0.000	222.69 48.65
Gentoo	V1a ~ 1 + V2 + V3 + V4	0.000	222.69 48.66
Gentoo	V1a ~ 1 + V3 + V4 + V7	0.000	222.88 48.85
Gentoo	V1a ~ 1 + V3 + V5	0.000	223.18 49.14
Gentoo	V1a ~ 1 + V2 + V6 + V7	0.000	224.14 50.10
Gentoo	V1a ~ 1 + V2 + V5 + V6 + V7	0.000	224.66 50.63
Gentoo	V1a ~ 1 + V3 + V4 + V6	0.000	225.89 51.85
Gentoo	V1a ~ 1 + V2 + V3 + V4 + V7	0.000	226.04 52.01
Gentoo	V1a ~ 1 + V4 + V6 + V7	0.000	226.40 52.36
Gentoo	V1a ~ 1 + V3 + V4	0.000	226.54 52.50
Gentoo	V1a ~ 1 + V2 + V4 + V5	0.000	227.43 53.40
Gentoo	V1a ~ 1 + V6	0.000	228.15 54.12
Gentoo	V1a ~ 1 + V5 + V6	0.000	228.73 54.70
Gentoo	V1a ~ 1 + V2 + V3 + V6 + V7	0.000	230.27 56.24
Gentoo	V1a ~ 1 + V2 + V4 + V5 + V6	0.000	230.28 56.24
Gentoo	V1a ~ 1 + V5 + V7	0.000	231.10 57.06
Gentoo	V1a ~ 1 + V3	0.000	231.94 57.91
Gentoo	V1a ~ 1 + V2	0.000	232.40 58.36
Gentoo	V1a ~ 1 + V2 + V4 + V6 + V7	0.000	233.25 59.21
Gentoo	V1a ~ 1 + V2 + V4	0.000	235.93 61.89

Gentoo	V1a ~ 1 + V3 + V6	0.000	237.39	63.36	
Gentoo	V1a ~ 1 + V2 + V3 + V5 + V6 + V7	0.000	243.23	69.19	

Bathymetry variables

Adélie	V1a ~ 1 + V10	0.000	214.18	0.00	
Adélie	V1a ~ 1	0.000	215.11	0.93	
Adélie	V1a ~ 1 + V9 + V10	1.000	219.51	5.33	
Adélie	V1a ~ 1 + V9	0.000	220.35	6.17	
Chinstrap	V1a ~ 1 + V9 + V10	1.000	179.90	0.00	
Chinstrap	V1a ~ 1 + V9	0.000	190.50	10.60	
Chinstrap	V1a ~ 1 + V10	0.000	194.02	14.11	
Chinstrap	V1a ~ 1	0.000	200.32	20.42	
Gentoo	V1a ~ 1 + V9	0.000	300.63	0.00	
Gentoo	V1a ~ 1 + V9 + V10	1.000	314.86	14.23	
Gentoo	V1a ~ 1 + V10	0.000	316.78	16.15	
Gentoo	V1a ~ 1	0.000	318.15	17.52	

Occupancy

Marine variables

Adélie	V1b ~ 1 + V2 + V3 + V6 + V7	0.011	82.61	0.00	
Adélie	V1b ~ 1 + V3 + V4 + V7	0.009	88.64	6.02	
Adélie	V1b ~ 1 + V3 + V4 + V5 + V6	0.005	88.99	6.38	
Adélie	V1b ~ 1 + V4 + V7	0.015	89.75	7.14	
Adélie	V1b ~ 1 + V2 + V7	0.015	91.07	8.46	
Adélie	V1b ~ 1 + V2 + V4 + V5	0.007	92.56	9.94	
Adélie	V1b ~ 1 + V3 + V6 + V7	0.030	92.63	10.01	
Adélie	V1b ~ 1 + V5 + V6	0.014	93.51	10.90	
Adélie	V1b ~ 1 + V2 + V4	0.016	93.56	10.94	
Adélie	V1b ~ 1 + V5 + V6 + V7	0.017	94.13	11.52	
Adélie	V1b ~ 1 + V2 + V4 + V5 + V6	0.004	94.50	11.89	
Adélie	V1b ~ 1 + V4 + V6	0.017	95.05	12.44	
Adélie	V1b ~ 1 + V4 + V5 + V6 + V7	0.008	95.07	12.45	
Adélie	V1b ~ 1 + V3 + V5 + V6 + V7	0.018	95.45	12.83	
Adélie	V1b ~ 1 + V2 + V3 + V7	0.008	95.71	13.09	
Adélie	V1b ~ 1 + V3 + V5 + V7	0.009	96.78	14.17	
Adélie	V1b ~ 1 + V2	0.040	96.80	14.19	
Adélie	V1b ~ 1 + V2 + V6 + V7	0.024	96.92	14.31	
Adélie	V1b ~ 1 + V2 + V3 + V5	0.009	97.34	14.72	
Adélie	V1b ~ 1 + V5	0.038	97.38	14.76	
Adélie	V1b ~ 1 + V3 + V4 + V5 + V6 + V7	0.008	97.42	14.80	
Adélie	V1b ~ 1 + V2 + V3 + V6	0.009	97.49	14.88	
Adélie	V1b ~ 1	0.096	97.66	15.05	
Adélie	V1b ~ 1 + V2 + V3 + V4 + V5 + V7	0.001	97.67	15.05	
Adélie	V1b ~ 1 + V4 + V5	0.015	97.78	15.17	
Adélie	V1b ~ 1 + V6	0.038	98.00	15.38	
Adélie	V1b ~ 1 + V2 + V4 + V6 + V7	0.011	98.34	15.73	
Adélie	V1b ~ 1 + V3 + V5	0.024	98.46	15.84	
Adélie	V1b ~ 1 + V3 + V7	0.020	98.61	15.99	
Adélie	V1b ~ 1 + V2 + V5 + V6	0.008	98.67	16.05	
Adélie	V1b ~ 1 + V3	0.053	98.67	16.06	
Adélie	V1b ~ 1 + V2 + V5 + V6 + V7	0.011	98.71	16.10	
Adélie	V1b ~ 1 + V2 + V4 + V7	0.008	98.79	16.17	

Adélie	V1b ~ 1 + V3 + V4	0.021	99.14	16.53
Adélie	V1b ~ 1 + V5 + V7	0.015	99.49	16.88
Adélie	V1b ~ 1 + V7	0.035	99.72	17.11
Adélie	V1b ~ 1 + V2 + V5	0.019	99.74	17.12
Adélie	V1b ~ 1 + V4 + V5 + V6	0.007	100.02	17.41
Adélie	V1b ~ 1 + V2 + V5 + V7	0.007	100.09	17.47
Adélie	V1b ~ 1 + V2 + V3 + V4 + V5	0.003	100.26	17.65
Adélie	V1b ~ 1 + V3 + V5 + V6	0.010	100.42	17.81
Adélie	V1b ~ 1 + V4	0.039	100.44	17.83
Adélie	V1b ~ 1 + V2 + V4 + V6	0.011	100.82	18.21
Adélie	V1b ~ 1 + V3 + V6	0.026	101.06	18.44
Adélie	V1b ~ 1 + V3 + V4 + V6 + V7	0.017	101.44	18.83
Adélie	V1b ~ 1 + V3 + V4 + V5 + V7	0.003	101.45	18.84
Adélie	V1b ~ 1 + V2 + V3 + V5 + V7	0.003	101.73	19.12
Adélie	V1b ~ 1 + V2 + V3 + V4 + V5 + V6	0.002	101.95	19.34
Adélie	V1b ~ 1 + V2 + V3	0.021	102.00	19.38
Adélie	V1b ~ 1 + V2 + V3 + V4 + V7	0.003	102.00	19.38
Adélie	V1b ~ 1 + V2 + V3 + V4 + V6 + V7	0.006	102.07	19.45
Adélie	V1b ~ 1 + V4 + V6 + V7	0.018	102.16	19.55
Adélie	V1b ~ 1 + V2 + V3 + V4 + V6	0.005	102.28	19.66
Adélie	V1b ~ 1 + V3 + V4 + V5	0.009	102.34	19.73
Adélie	V1b ~ 1 + V2 + V3 + V4	0.009	102.90	20.29
Adélie	V1b ~ 1 + V6 + V7	0.034	103.87	21.25
Adélie	V1b ~ 1 + V2 + V3 + V5 + V6 + V7	0.007	104.07	21.46
Adélie	V1b ~ 1 + V2 + V6	0.021	104.16	21.55
Adélie	V1b ~ 1 + V2 + V3 + V5 + V6	0.004	104.69	22.07
Adélie	V1b ~ 1 + V3 + V4 + V6	0.012	104.75	22.14
Adélie	V1b ~ 1 + V2 + V4 + V5 + V6 + V7	0.004	105.07	22.46
Adélie	V1b ~ 1 + V2 + V4 + V5 + V7	0.003	105.70	23.09
Adélie	V1b ~ 1 + V4 + V5 + V7	0.006	108.36	25.75
Adélie	V1b ~ 1 + V2 + V3 + V4 + V5 + V6 + V7	0.003	108.38	25.77
Chinstrap	V1b ~ 1 + V2 + V5 + V6 + V7	0.008	42.68	0.00
Chinstrap	V1b ~ 1 + V4 + V6 + V7	0.012	52.29	9.60
Chinstrap	V1b ~ 1 + V5 + V6 + V7	0.014	53.59	10.91
Chinstrap	V1b ~ 1 + V2 + V3 + V4 + V5 + V7	0.002	57.89	15.21
Chinstrap	V1b ~ 1 + V3 + V4 + V6	0.009	59.12	16.44
Chinstrap	V1b ~ 1 + V3	0.041	59.19	16.51
Chinstrap	V1b ~ 1	0.109	59.48	16.80
Chinstrap	V1b ~ 1 + V5 + V7	0.017	59.98	17.30
Chinstrap	V1b ~ 1 + V2 + V3 + V5 + V7	0.005	60.14	17.46
Chinstrap	V1b ~ 1 + V2 + V4 + V5	0.013	60.74	18.06
Chinstrap	V1b ~ 1 + V3 + V4	0.022	60.77	18.09
Chinstrap	V1b ~ 1 + V3 + V4 + V5 + V6	0.004	61.35	18.67
Chinstrap	V1b ~ 1 + V3 + V7	0.017	61.80	19.12
Chinstrap	V1b ~ 1 + V4 + V7	0.021	62.06	19.38
Chinstrap	V1b ~ 1 + V5 + V6	0.015	63.31	20.63
Chinstrap	V1b ~ 1 + V2 + V3 + V4 + V5 + V6	0.002	65.43	22.75
Chinstrap	V1b ~ 1 + V2 + V3 + V7	0.010	65.70	23.02
Chinstrap	V1b ~ 1 + V2 + V5	0.019	65.75	23.07
Chinstrap	V1b ~ 1 + V3 + V5 + V6 + V7	0.006	65.86	23.18
Chinstrap	V1b ~ 1 + V5	0.040	66.26	23.58
Chinstrap	V1b ~ 1 + V7	0.046	66.44	23.76

Chinstrap	V1b ~ 1 + V3 + V5 + V7	0.007	66.50	23.82
Chinstrap	V1b ~ 1 + V2 + V3 + V5 + V6 + V7	0.003	66.50	23.82
Chinstrap	V1b ~ 1 + V3 + V4 + V5	0.011	66.53	23.85
Chinstrap	V1b ~ 1 + V4	0.058	66.84	24.16
Chinstrap	V1b ~ 1 + V2 + V4 + V5 + V6	0.005	66.88	24.20
Chinstrap	V1b ~ 1 + V2 + V3 + V4 + V6	0.004	67.12	24.44
Chinstrap	V1b ~ 1 + V4 + V5 + V7	0.011	67.20	24.52
Chinstrap	V1b ~ 1 + V2 + V4 + V6 + V7	0.006	67.25	24.57
Chinstrap	V1b ~ 1 + V6	0.040	67.46	24.78
Chinstrap	V1b ~ 1 + V2 + V3 + V5	0.009	67.69	25.01
Chinstrap	V1b ~ 1 + V2 + V4 + V5 + V7	0.005	68.01	25.33
Chinstrap	V1b ~ 1 + V2 + V3 + V4 + V6 + V7	0.002	68.13	25.44
Chinstrap	V1b ~ 1 + V2	0.050	68.20	25.52
Chinstrap	V1b ~ 1 + V3 + V6 + V7	0.013	68.36	25.68
Chinstrap	V1b ~ 1 + V2 + V3 + V4 + V5	0.006	68.52	25.84
Chinstrap	V1b ~ 1 + V2 + V6	0.019	68.57	25.89
Chinstrap	V1b ~ 1 + V2 + V4	0.026	68.83	26.15
Chinstrap	V1b ~ 1 + V2 + V3 + V6	0.008	68.88	26.20
Chinstrap	V1b ~ 1 + V3 + V4 + V5 + V7	0.004	68.90	26.22
Chinstrap	V1b ~ 1 + V3 + V4 + V5 + V6 + V7	0.002	69.11	26.43
Chinstrap	V1b ~ 1 + V2 + V3 + V4 + V5 + V6 + V7	0.001	69.27	26.59
Chinstrap	V1b ~ 1 + V6 + V7	0.033	69.28	26.60
Chinstrap	V1b ~ 1 + V3 + V6	0.015	69.30	26.62
Chinstrap	V1b ~ 1 + V3 + V5 + V6	0.005	69.51	26.83
Chinstrap	V1b ~ 1 + V3 + V5	0.015	69.61	26.93
Chinstrap	V1b ~ 1 + V4 + V5	0.031	69.84	27.16
Chinstrap	V1b ~ 1 + V4 + V5 + V6 + V7	0.006	70.15	27.47
Chinstrap	V1b ~ 1 + V2 + V3	0.022	70.32	27.64
Chinstrap	V1b ~ 1 + V4 + V6	0.023	70.89	28.21
Chinstrap	V1b ~ 1 + V2 + V3 + V4 + V7	0.004	71.12	28.44
Chinstrap	V1b ~ 1 + V2 + V5 + V7	0.010	71.74	29.06
Chinstrap	V1b ~ 1 + V2 + V3 + V6 + V7	0.006	71.88	29.20
Chinstrap	V1b ~ 1 + V2 + V3 + V5 + V6	0.003	72.23	29.55
Chinstrap	V1b ~ 1 + V3 + V4 + V7	0.008	72.54	29.86
Chinstrap	V1b ~ 1 + V4 + V5 + V6	0.012	73.38	30.70
Chinstrap	V1b ~ 1 + V2 + V5 + V6	0.007	73.43	30.75
Chinstrap	V1b ~ 1 + V2 + V4 + V5 + V6 + V7	0.003	74.20	31.52
Chinstrap	V1b ~ 1 + V3 + V4 + V6 + V7	0.005	74.26	31.58
Chinstrap	V1b ~ 1 + V2 + V3 + V4	0.010	74.69	32.01
Chinstrap	V1b ~ 1 + V2 + V7	0.024	75.62	32.94
Chinstrap	V1b ~ 1 + V2 + V4 + V7	0.010	78.31	35.63
Chinstrap	V1b ~ 1 + V2 + V6 + V7	0.016	82.20	39.52
Chinstrap	V1b ~ 1 + V2 + V4 + V6	0.010	88.15	45.47
Gentoo	V1b ~ 1 + V2 + V4 + V5 + V6	0.002	177.81	0.00
Gentoo	V1b ~ 1 + V2 + V3 + V5 + V6 + V7	0.008	183.55	5.74
Gentoo	V1b ~ 1 + V2 + V3 + V5	0.017	193.14	15.33
Gentoo	V1b ~ 1 + V3 + V6	0.011	196.79	18.98
Gentoo	V1b ~ 1 + V3 + V4 + V5 + V6 + V7	0.009	198.33	20.52
Gentoo	V1b ~ 1 + V2 + V3	0.032	200.87	23.06
Gentoo	V1b ~ 1 + V2 + V3 + V6	0.012	203.76	25.96
Gentoo	V1b ~ 1 + V2 + V3 + V4 + V5 + V6 + V7	0.012	205.37	27.56
Gentoo	V1b ~ 1 + V3 + V4	0.045	205.56	27.75
Gentoo	V1b ~ 1 + V3	0.008	206.28	28.47

Gentoo	V1b ~ 1 + V2 + V3 + V4 + V5 + V6	0.025	206.69 28.88
Gentoo	V1b ~ 1 + V3 + V5 + V6 + V7	0.014	206.72 28.91
Gentoo	V1b ~ 1 + V2 + V5 + V6 + V7	0.018	207.85 30.04
Gentoo	V1b ~ 1 + V3 + V4 + V7	0.018	209.05 31.24
Gentoo	V1b ~ 1 + V2 + V3 + V5 + V6	0.006	209.85 32.04
Gentoo	V1b ~ 1 + V4 + V5 + V7	0.002	210.09 32.28
Gentoo	V1b ~ 1 + V2 + V3 + V4 + V5	0.016	210.34 32.53
Gentoo	V1b ~ 1 + V2 + V5 + V7	0.005	212.58 34.77
Gentoo	V1b ~ 1 + V2 + V3 + V4 + V6	0.020	212.69 34.88
Gentoo	V1b ~ 1 + V2 + V3 + V4 + V5 + V7	0.010	216.81 39.00
Gentoo	V1b ~ 1 + V6 + V7	0.103	216.95 39.15
Gentoo	V1b ~ 1 + V4 + V5 + V6	0.006	217.64 39.83
Gentoo	V1b ~ 1 + V3 + V7	0.032	218.02 40.21
Gentoo	V1b ~ 1 + V2 + V3 + V4	0.036	218.56 40.75
Gentoo	V1b ~ 1 + V2 + V4	0.010	218.69 40.89
Gentoo	V1b ~ 1 + V2 + V4 + V6	0.006	218.95 41.14
Gentoo	V1b ~ 1 + V2 + V4 + V6 + V7	0.017	219.04 41.24
Gentoo	V1b ~ 1 + V3 + V4 + V5 + V7	0.007	219.83 42.02
Gentoo	V1b ~ 1 + V2 + V6 + V7	0.045	220.10 42.29
Gentoo	V1b ~ 1 + V2 + V3 + V7	0.017	220.23 42.42
Gentoo	V1b ~ 1 + V2 + V5	0.008	220.88 43.07
Gentoo	V1b ~ 1 + V2 + V3 + V6 + V7	0.020	222.18 44.37
Gentoo	V1b ~ 1 + V4 + V6	0.017	222.60 44.79
Gentoo	V1b ~ 1 + V3 + V5	0.018	222.62 44.81
Gentoo	V1b ~ 1 + V2	0.005	222.79 44.99
Gentoo	V1b ~ 1 + V5 + V6 + V7	0.039	223.07 45.27
Gentoo	V1b ~ 1	0.014	223.31 45.50
Gentoo	V1b ~ 1 + V3 + V4 + V6	0.017	223.50 45.69
Gentoo	V1b ~ 1 + V3 + V4 + V5 + V6	0.007	224.11 46.30
Gentoo	V1b ~ 1 + V2 + V4 + V7	0.004	224.21 46.40
Gentoo	V1b ~ 1 + V2 + V7	0.010	224.31 46.51
Gentoo	V1b ~ 1 + V2 + V5 + V6	0.003	225.30 47.49
Gentoo	V1b ~ 1 + V2 + V3 + V4 + V7	0.015	225.33 47.52
Gentoo	V1b ~ 1 + V4 + V5 + V6 + V7	0.024	225.60 47.79
Gentoo	V1b ~ 1 + V2 + V4 + V5	0.004	226.00 48.20
Gentoo	V1b ~ 1 + V2 + V4 + V5 + V6 + V7	0.013	226.22 48.41
Gentoo	V1b ~ 1 + V2 + V4 + V5 + V7	0.002	226.63 48.82
Gentoo	V1b ~ 1 + V2 + V3 + V5 + V7	0.007	227.56 49.75
Gentoo	V1b ~ 1 + V4 + V5	0.006	228.25 50.44
Gentoo	V1b ~ 1 + V3 + V4 + V5	0.017	228.43 50.62
Gentoo	V1b ~ 1 + V5 + V6	0.007	228.74 50.93
Gentoo	V1b ~ 1 + V3 + V6 + V7	0.038	228.99 51.18
Gentoo	V1b ~ 1 + V2 + V6	0.002	229.11 51.30
Gentoo	V1b ~ 1 + V3 + V5 + V6	0.009	229.21 51.40
Gentoo	V1b ~ 1 + V5 + V7	0.006	229.97 52.16
Gentoo	V1b ~ 1 + V2 + V3 + V4 + V6 + V7	0.009	230.74 52.93
Gentoo	V1b ~ 1 + V4 + V6 + V7	0.040	231.44 53.63
Gentoo	V1b ~ 1 + V3 + V4 + V6 + V7	0.015	231.76 53.95
Gentoo	V1b ~ 1 + V7	0.008	232.88 55.07
Gentoo	V1b ~ 1 + V4 + V7	0.004	233.36 55.56
Gentoo	V1b ~ 1 + V5	0.015	234.18 56.38

	Gentoo	V1b ~ 1 + V4	0.011	235.86	58.06
	Gentoo	V1b ~ 1 + V3 + V5 + V7	0.014	242.00	64.20
	Gentoo	V1b ~ 1 + V6	0.005	243.15	65.34
Bathymetry variables					
	Adélie	V1b ~ 1 + V9 + V10	0.083	88.16	0.00
	Adélie	V1b ~ 1 + V9	0.187	91.91	3.74
	Adélie	V1b ~ 1	0.506	93.56	5.39
	Adélie	V1b ~ 1 + V10	0.224	95.82	7.66
	Chinstrap	V1b ~ 1 + V9 + V10	0.209	64.09	0.00
	Chinstrap	V1b ~ 1 + V9	0.565	71.73	7.64
	Chinstrap	V1b ~ 1 + V10	0.061	72.32	8.23
	Chinstrap	V1b ~ 1	0.164	74.52	10.42
	Gentoo	V1b ~ 1 + V10	0.191	134.37	0.00
	Gentoo	V1b ~ 1	0.357	140.68	6.32
	Gentoo	V1b ~ 1 + V9 + V10	0.172	142.38	8.01
	Gentoo	V1b ~ 1 + V9	0.280	143.78	9.41

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