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**PADRÕES DE DISTRIBUIÇÃO ESPACIAL DE AVES**  
**MARINHAS NO BRASIL**

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***“I now belong to a higher cult of mortals, for I have seen the albatross!”***

***(“Agora eu pertenço a um seletto grupo de mortais, por ter visto os albatrozes!”)***

Robert Cushman Murphy, em carta para sua esposa.

(1912)

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## RESUMO

A distribuição de animais marinhos pode ser regida por fatores oceanográficos, fisiográficos e biológicos. Diferentes espécies relacionam-se com diferentes características ambientais. Deste modo, regiões com características ambientais distintas podem suportar comunidades distintas. Este estudo teve como objetivos descrever a distribuição espacial das aves marinhas no Brasil. Entre os anos de 2009–2018 foram realizadas 2633 contagens ao largo da desembocadura do Rio Amazonas (Norte), no trajeto para as ilhas de Fernando de Noronha, Atol das Rocas, Arquipélago de São Pedro e São Paulo (Nordeste), Ilha da Trindade (Leste), e entre Cabo Frio/Rio de Janeiro e Chuí/Rio Grande do Sul (Sudeste e Sul). Devido à falta de informações prévias na região Norte, optou-se por analisar os dados separadamente. Neste contexto, o Apêndice 1 traz informações inéditas para a região da Foz do Rio Amazonas. Foi observada elevada riqueza, principalmente devido à presença de migrantes de ambos os Hemisférios. As aves concentraram-se em duas regiões com processos oceanográficos distintos, i.e., a zona de formação de anéis (vórtices) gerados pela retroflexão da Corrente Norte do Brasil, e a desembocadura do Rio Amazonas. No segundo trabalho, foi investigada a influência de padrões oceanográficos na distribuição, riqueza e abundância das espécies nas águas ao largo da costa do Brasil. Avaliamos, ainda, padrões latitudinais de riqueza e se as assembleias de aves se adequam à proposta de Ecorregiões Marinhas. Elevadas abundâncias estiveram relacionadas a processos de meso-escala, como frentes oceanográficas na desembocadura do Rio Amazonas, ressurgências de Cabo Frio/RJ e nos montes submarinos da Cadeia Vitória-Trindade, e no extremo Sul na região da Frente Subtropical de Plataforma. As maiores riquezas foram na região Norte, na Foz do Rio Amazonas, ao redor da Ilha da Trindade e nas regiões Sudeste-Sul ao largo da isóbata de 200 m; isso indica que maiores riquezas são relacionadas a sítios de ‘parada/uso’, se comparadas a regiões utilizadas como ‘passagem’ (Nordeste e Leste). As aves marinhas mostraram-se um grupo intrigante para o estudo das variações de riqueza de espécies em relação aos gradientes latitudinais, distinto do padrão terrestre descrito extensamente: observaram-se três picos, um na faixa 0–5°N (Foz do Amazonas), outro em 20°S (Ilha da Trindade), e outro crescente, dos 23°S até o extremo sul (34°S, região Sudeste-Sul). Por sua vez, as Ecorregiões Marinhas não se adequaram às assembleias de aves, e os

resultados indicaram que as delimitações biogeográficas devem ajustar-se melhor em nível de Província. Processos de meso-escala são indicadores fundamentais na distribuição de aves marinhas e, aqui, destacamos a importância dos desagues continentais na agregação desses organismos, bem como a riqueza de espécies sustentadas por elas.

**Palavras-chave:** Biogeografia, Deságue continental, Ecorregiões Marinhas, Gradiente latitudinal, Processos oceanográficos, Riqueza de espécies.



## ABSTRACT

The distribution of marine animals is ruled by oceanographic, physiographic, and biological features. Different species follow distinct environmental characteristics, therefore, different oceanographic features can sustain distinct communities. Here, we aimed to describe the spatial distribution of seabirds off the Brazilian coast. Seabird counts (2633 total counts) were carried out between 2009–2018, off the mouth of Amazon River (North region), on trips to Fernando de Noronha, Atoll das Rocas, São Pedro and São Paulo Rocks (Northeast), Trindade Island (East), and between Cabo Frio/Rio de Janeiro State and Chuí/Rio Grande do Sul State (Southeast and South). Due to the lack of any information about seabirds in North Brazil, we choose to analyse this region separately. In the first Appendix, we introduce new information on seabirds next to the Amazon River mouth, an unexplored area. A species-rich assemblage was recorded, based mainly on migrants from both Hemispheres. Seabirds associated with two distinct mesoscale oceanographic processes, i.e. on a ring-formation zone, and at the mouth of Amazon River. In the second Appendix, we look at oceanographic processes influencing the distribution patterns of species richness and abundance of seabirds in the entire Brazilian coast. In addition, we explored the latitudinal gradient of species richness for seabirds, and test if the Marine Ecoregions of the World concept (Spalding et al. 2007, *BioScience*) fits well for seabirds, which are highly mobile vertebrates. Higher abundances were related to mesoscale features, such as the freshwater front by the Amazon River discharge (North), the wind-driven upwelling from Cabo Frio and topographical-driven upwelling at Vitória-Trindade mountain chain (East), and at the Subtropical Shelf Front in the South. Areas high in species richness were located at Amazon River mouth, Trindade Island and on the 200 m isobath from Southeast to South regions. This suggests that higher richness is related to staging areas for seabirds, as opposed to transit/passage areas (such as the East and Northeast regions). Seabirds showed three distinct peaks in latitudinal gradient of species richness: at 0–5°N (Amazon River discharge), at 20°S (Trindade Island), and upwards from 23°S to 34°S (Southeast and South regions). Seabirds fit better into a province-scale level of marine ecoregions than at a smaller, regional, or larger, global, scales. Mesoscale features were key to

explaining seabird distributions, and we highlighted the importance of freshwater discharges in sustaining species rich assemblages.

**Key-words:** Biogeography, Freshwater discharge, Latitudinal gradient, Marine Ecoregions of the World, Oceanographic processes, Species richness.

## INTRODUÇÃO

Padrões de distribuição dos organismos marinhos refletem suas adaptações, histórias de vida e interações biológicas. A capacidade de locomoção/movimentação do indivíduo possibilita que ele explore diferentes habitats e realize busca ativa dos seus requerimentos. Essas movimentações estão, assim, relacionadas às demandas energéticas e fisiológicas, levando em conta o ambiente de entorno e recursos alimentares necessários para os organismos (Gwinner 1990). Para realizá-las, os animais acessam suas capacidades sensoriais e motoras. Quando reunidas as movimentações individuais, e entre as populações, os padrões de distribuição da espécie são evidenciados. Na dinâmica do ambiente marinho, onde os fluidos estão em constante movimentação e os limites entre habitats não é fixo, ainda não temos a compreensão da distribuição de muitos organismos. Dentre eles, com suas peculiaridades evolutivas e que ocupam o fluido do ar, e não da água salgada, estão as aves marinhas (Schreiber & Burger 2001).

A definição de aves marinhas não é unânime, mas o conceito mais utilizado, e adotado aqui, é de que aves marinhas são aquelas que vivem em áreas costeiras ou oceânicas e se alimentam de recursos marinhos e estuarinos (Furness & Monaghan 1987). A definição agrega grupos taxonômicos não afins, tratando-se de uma definição não natural. Por outro lado, esses grupos convergiram, independentemente, em diversas adaptações morfológicas, fisiológicas e de história de vida (Schreiber & Burger 2001). Dentre as morfológicas, glândulas de sal (excreção) e uropigianas (impermeabilização) bem desenvolvidas, pés palmados para natação, e bicos com serrilhas ou ponta em forma de gancho para captura de presas escorregadias (peixes e lulas). De modo geral, as espécies têm maturação sexual tardia (3–7 anos), baixo tamanho de ninhada (1–3 ovos), e alto cuidado parental com a prole (Furness & Monaghan 1987, Schreiber & Burger 2001). A taxa de sobrevivência dos indivíduos adultos é alta, formando pares reprodutivos duradouros (monogâmicos ou monogâmicos-sociais) e costumam ser longevos. Essas características fazem com que as ameaças às espécies causem grandes impactos populacionais (Furness & Monaghan 1987), e esse grupo é o mais ameaçado de todas as Aves (Croxall et al. 2012).

Dentre essa diversidade, as aves marinhas separam-se, ainda, em costeiras e oceânicas. O limiar entre essa distinção também não é preciso, visto que, existem

exceções dentro dos grupos. Aves costeiras são as que dependem da costa no dia-a-dia, alimentando-se e retornando para o local de descanso, como a maioria dos atobás (Sulidae: Suliformes) e trinta-réis (Sternidae: Charadriiformes). As aves oceânicas são as que se alimentam e repousam no mar, retornando à terra apenas para reprodução, por exemplo, os albatrozes e petréis (Procellariiformes). Ainda, dentro das estratégias de vida, existem espécies não migratórias e espécies migratórias. As migratórias tendem a ter uma área de vida enquanto reproduzem (normalmente, ao redor da colônia) e, no período não reprodutivo, utilizam áreas de invernagem distintas das de reprodução. Diversas espécies são, inclusive, migrantes transequatoriais (e.g., Guilford et al. 2009, Weimerskirch et al. 2015), sendo o trinta-réis-do-Ártico *Sterna paradisaea* o vertebrado de maior migração até hoje conhecida (Fijn et al. 2013). As espécies que não migram utilizam a colônia o ano inteiro como local de reprodução e descanso; de modo geral, são aves tropicais.

A compreensão dos padrões de distribuição e abundância de aves marinhas requer a avaliação de fatores oceanográficos, meteorológicos e biológicos. O ambiente marinho é heterogêneo e, portanto, diferentes escalas de investigação podem resultar em diferentes tipos de respostas quanto aos processos regentes desses padrões (Hunt & Schneider 1987). Por exemplo, em larga- (>1000 km) e meso-escalas (100–1000 km), processos físicos são mais importantes para as aves, enquanto interações biológicas predador-presa são mais importantes em escalas menores (<100 km) (Hunt & Schneider 1987, Weimerskirch 2007, Fauchald 2009). Entre os fatores físicos, os principais são as massas d'água e as suas características físico-químicas (Hunt 1990). As características dessas correntes e processos influenciarão a concentração e disponibilidade de recursos alimentares que, deste modo, suportarão processos e interações biológicas em diferentes escalas (Hunt 1990). A característica biológica regente da distribuição de aves marinhas é a quantidade e disponibilidade das suas presas (Hunt 1990, Weimerskirch 2007), que ainda não é clara, mas que tem a chave para o seu entendimento na escala em que o tópico é investigado (Fauchald 2009). A associação das aves com o ambiente marinho é cada vez mais demonstrada com estudos de rastreamento, em conjunto com as descrições de padrões oceanográficos e níveis tróficos utilizados pelos diferentes grupos (Rayner et al. 2016, Paiva et al. 2017).

O entendimento das relações ecológicas das aves marinhas com o seu ambiente sem a interpretação de dados oceanográficos é incompleto (Ballance et al. 2006). A

associação de parâmetros oceanográficos com a presença de aves marinhas através de observações diretas em embarcações aponta como os principais fatores as massas d'água e a temperatura superficial do mar – TSM (e.g., Ballance et al. 2006, Jungblunt et al. 2017). Locais de alta produtividade primária como frentes oceanográficas e ressurgências, têm, também, elevada abundância de predadores de topo de cadeia trófica, como as aves marinhas (Scales et al. 2014b, Grecian et al. 2016). Talvez, dentre os processos oceanográficos que influenciam a distribuição da megafauna marinha, os mais conhecidos sejam os vórtices e as frentes térmicas. Essas zonas, por si só, devido às forças físicas, acumulam partículas (Olson & Backus 1985). Esses processos, ambos de meso-escala, são documentados amplamente como locais favoráveis ao acúmulo de presas, e com isso, atraem as aves marinhas (Scales et al. 2014b).

As aves agregam-se tanto em vórtices de centro frio quanto de centro quente, ou até mesmo nos processos nas suas margens (Hyrenbach et al. 2006, Tew Kai & Marsac 2010). As frentes oceanográficas são documentadas há décadas como locais de forrageio de aves (Schneider 1982, Hunt 1990). Com o avanço das tecnologias de telemetria e de sensoriamento remoto, hoje é possível identificar essas associações diretamente, cruzando os dados de rastreamento com mapas de TSM (Scales et al. 2014a, Cox et al. 2016). Mistura de massas d'água de diferentes propriedades físico-químicas como, por exemplo, em desagues continentais no ambiente marinho, formam processos de turbulência na coluna d'água, influenciadas tanto pelo aporte de água quanto pelas marés. Adicionalmente, esses desagues continentais trazem consigo um grande aporte de nutrientes, que por sua vez são, também, incorporados nesses processos de mistura. As aves marinhas, de modo geral aquelas com hábito mais costeiro, agregam-se nesses locais, tirando proveito de presas que se acumulam nessas frentes oceanográficas dinâmicas (Urbanski et al. 2017, Phillips et al. 2018). As resoluções de satélite permitem atualmente elucidar as associações das aves com estruturas Lagrangianas em escalas finas (detectadas através dos ‘expoentes de Lyapunov’), as quais demonstram o aprendizado das aves em direcionar seus movimentos a essas zonas de maiores probabilidades de agregação de presas (Grecian et al. 2018).

Essas relações espécies-ambiente moldam os padrões de distribuição e de diversidade dos grupos em larga escala. No ambiente terrestre há um consenso de padrão geral com maior diversidade nos trópicos, diminuindo gradativamente em direção aos

pólos (Gaston 2000). Análises baseadas em organismos fósseis e viventes sugerem que no ambiente marinho existe um padrão bimodal na riqueza de espécies (Powell et al. 2012, Chaudhary et al. 2016). Os picos de riqueza de espécies, nos resultados apresentados, são nos domínios de médias-latitudes (20–30°), em ambos os Hemisférios (Powell et al. 2012, Chaudhary et al. 2016). Análises globais evidenciam padrões diferentes entre regiões costeiras e oceânicas, nas escalas de diversidade, mas com certa consistência de maior diversidade em médias-latitudes (em larga escala) (Tittensor et al. 2010, Edgar et al. 2017). Dentre os trabalhos que incluíram predadores de topo nas análises, padrões contrastantes entre mamíferos marinhos vs. atuns e peixes-de-bico (Worm et al. 2005, Tittensor et al. 2010, Reygondeau et al. 2012). Mamíferos marinhos oceânicos (cetáceos) apresentam padrões de riqueza elevados em médias-latitudes, enquanto os costeiros (pinípedes), demonstraram maiores riquezas nos pólos, seguido das latitudes médias (Tittensor et al. 2010). Atuns e peixes-de-bico apresentam padrões diferentes, com maiores riquezas associadas aos trópicos e às latitudes médias (Worm et al. 2005) e apresentam afinidades com padrões oceanográficos específicos (Reygondeau et al. 2012). Até o presente momento apenas um trabalho aborda o tema, utilizando uma ordem de aves marinhas, e nenhum dos trabalhos investigados sequer usou algum dos grupos de aves nas análises (à exceção de Chown et al. 1998).

O único grupo com padrão de riqueza de espécies analisada foi o dos Procellariiformes (albatrozes e petréis). Essas aves marinhas, tipicamente oceânicas, apresentam riqueza pronunciada entre as latitudes 40–50°S (Chown et al. 1998, Davies et al. 2010). Esse padrão foi abordado em relação a preditores ambientais quanto à tese da energia local reger a diversidade, sendo a temperatura do ar e a velocidade média anual do vento os fatores mais importantes, junto com um componente espacial (Davies et al. 2010). Diretamente, a investigação quanto ao padrão de riqueza de espécies em relação à latitude, não teve outros esforços utilizando aves marinhas como modelos. Esforços de mapear as regionalizações de assembleias de aves marinhas (biogeografia) foram feitas em escalas menores. Por exemplo, no Mar Mediterrâneo, onde a assembleia de aves do Sul e Oeste são do grupo que migram em período não reprodutivo para o Oceano Atlântico, enquanto as do Norte e Leste, não são migratórias e completam o ciclo de vida dentro do Mediterrâneo (Zotier et al. 1999). No Estreito de Bering, entre o Alasca e a Sibéria, guildas de aves piscívoras e zooplantívoras distribuem-se de modo semelhante

no eixo Norte-Sul, principalmente determinado por fatores oceanográficos, mas, no eixo Leste-Oeste, tendem a dividir-se nos diferentes estratos criados por três correntes superficiais que fluem de sul para norte (Piatt & Springer 2003).

O reconhecimento, delimitação e nomeação de ‘bioregiões’ faz parte da disciplina da biogeografia, bem como os processos que os moldam e os mantêm. Gradientes geográficos, fisiográficos e biológicos têm papel importante na estruturação de unidades ecológicas. Esses fatores são importantes na identificação de bioregiões, reconhecidos desde os estudos pioneiros de Alexander von Humboldt (Schrodt et al. 2019). Dentre as bioregionalizações, talvez a mais conhecida do ambiente marinho seja a proposta das ‘Ecorregiões Marinhas do Mundo’ (*Marine Ecoregions of the World – MEOW*) de Spalding et al. (2007). Essa classificação levou em conta características oceanográficas e organismos de baixa capacidade móvel e sésseis; ela foi proposta em escala mundial, e têm como objetivo regionalizar zonas ecológicas até as margens da plataforma continental (~200 m de profundidade) (Spalding et al. 2007). Alguns anos depois, Spalding et al. (2012) propuseram ‘Províncias Pelágicas’ (*Pelagic Provinces*) para os ‘mares abertos’ (*high seas*), em ambientes oceânicos de profundidade maior do que 200 m. Para isso, os autores utilizaram critérios oceanográficos e dos organismos que ocupam os 200 primeiros metros da superfície da coluna d’água (Spalding et al. 2012). Enfatiza-se que, em ambos os estudos, aves marinhas não foram incluídas nas assembleias-base na definição das bioregiões.

Diferentes regimes oceanográficos podem caracterizar diferentes assembleias de aves, dadas as características ambientais preferenciais dos diferentes grupos (Woehler et al. 2010). O Brasil, com sua ampla extensão latitudinal e diferentes regimes e processos oceanográficos, pode sustentar diferentes assembleias de aves marinhas. Por exemplo, a costa do extremo Norte do país é influenciada pela Corrente Norte do Brasil, com Água Tropical, e intrusões da Água Central do Atlântico Sul e Água Intermediária da Antártica, além de aportes substanciais da pluma da foz do Rio Amazonas (Silva et al. 2005). Por sua vez, a porção Leste do Brasil é dominada por processos decorrentes dos meandros da Corrente do Brasil (Silveira et al. 2000). Ao chegar na porção Sudeste do país a Corrente do Brasil encontra com os montes da Cadeia Vitória-Trindade (CVT) e segue o seu fluxo de maneira paralela à costa, com processos de ressurgência em pequena escala na Cadeia, e de média escala em Cabo Frio; ambos propiciam aumentos de biomassa fitoplanctônica

com as águas frias e ricas em nutrientes (Gaeta et al. 1999, Coelho-Souza et al. 2012). A região Sul do Brasil é influenciada tanto pela Corrente do Brasil quanto pela Corrente das Malvinas, estando no limite norte da Convergência Subtropical (Garcia 1998, Matano et al. 2010); semelhante ao extremo Norte do Brasil há, ainda, o aporte de grandes descargas de águas continentais, que formam a pluma do Rio da Prata, e tornam o ambiente dinâmico e altamente produtivo (Ciotti et al. 1995, Garcia et al. 2004). Essas diferenças oceanográficas podem suportar diferentes conjuntos de espécies em cada região.

A comunidade de aves marinhas ao largo da costa do Brasil, em geral, é bem compreendida, apesar da carência de estudos na região Norte e Nordeste do país. Estudos realizados a bordo de navios científicos (Neves et al. 2006), acompanhamento de pesca (Olmos 1997), encalhes nas praias e espécimes em museus (Carlos 2009, Daudt et al. 2017), demonstram bom entendimento acerca da riqueza e dos padrões de ocorrência/sazonalidade das espécies. Por outro lado, padrões espaciais de ocorrência e sua relação com o ambiente ainda são pouco explorados. Apenas dois trabalhos, ambos no Sul do país, avaliaram a influência de parâmetros ambientais na composição da assembleia de aves marinhas, encontrando as massas d'água e TSM como os principais determinantes, e dos quais o efeito da TSM foi inversamente proporcional à riqueza de espécies (Neves et al. 2006, Krüger & Petry 2011). Ambos os trabalhos também destacam a predominância de aves Procellariiformes na região oceânica, porém, não se tem um comparativo com a região Norte e Nordeste do país. O entendimento das relações entre as aves oceânicas e os fatores que influenciam na sua distribuição é importante para a compreensão dos padrões de diversidade, interações ecológicas entre as aves, suas presas e seu ambiente, bem como quanto a possíveis riscos/interações que enfrentam ou podem vir a enfrentar.

Os padrões espaciais de distribuição são fundamentais no entendimento dos possíveis impactos gerados por diversas atividades humanas de exploração do ambiente. Um dos maiores impactos negativos nas populações de aves marinhas é a captura incidental em pescarias de espinhel pelágico (Croxall et al. 2012). No Sul do Brasil, por exemplo, pardelas-de-óculos (*Procellaria conspicillata*) coincidem sua distribuição com zonas de alto esforço pesqueiro (Bugoni et al. 2009). Projeções de mudanças ambientais devido ao aquecimento global indicam que tanto os locais de pescarias, quanto as distribuições de aves marinhas, tendem a mudar e aumentar suas sobreposições (Krüger



et al. 2018), devendo agravar os impactos negativos dessa interação. Outros impactos crescentes no ambiente marinho são nas áreas com potencial de extração de energias renováveis, como parques eólicos em zonas de alta intensidade de ventos e turbinas para geração de energia em locais com fortes correntes marinhas ou flutuações de maré. Essas atividades já mostram-se negativas para as aves em diversos locais, onde existe risco de colisão das aves nas instalações em corredores migratórios ou zonas de transição, assim como locais de alimentação de aves mergulhadoras (Waggitt & Scott 2014, Dierschke et al. 2016). Deste modo, a compreensão da distribuição espacial (inclusive, tridimensional) das aves marinhas é crucial para prever e mitigar essas interações negativas.

Identificar áreas de agregações de indivíduos e suas importâncias ecológicas são a base para implementar zonas de proteção ambiental, como Unidades de Conservação e as ‘Áreas Marinhas Protegidas’ (*Marine Protected Areas – MPA*). O reconhecimento de áreas de uso comum para diversas espécies, com base em animais rastreados com aparelhos remotos, demonstra-se uma técnica promissora nesse contexto (Lascelles et al. 2016). Deste modo, podemos identificar áreas de importância anuais/sazonais, e para diversos táxons. Para as aves marinhas, o Sul do Brasil é reconhecido como uma área importante para diversas espécies (Dias et al. 2017, Krüger et al. 2017). Dados de contagens no mar, junto com animais rastreados podem otimizar a delimitação dessas áreas protegidas (Louzao et al. 2009). As contagens trazem informações importantes quanto a locais de agregações e alimentação, por demonstrarem grandes números de indivíduos interagindo com o ambiente; por outro lado, dados de rastreamento, por serem inerentes de um único indivíduo, auxiliam na compreensão do uso do hábitat em maior escala, identificando fatores ambientais pelos quais àquele indivíduo (espécie) utiliza.

Recentemente, em uma revisão global quanto a esforços de pesquisa para a identificação de padrões de distribuição de aves marinhas, o Brasil é destacado como uma enorme lacuna de amostragem (Mott & Clarke 2018), com apenas um trabalho identificado ao longo de todo território nacional (a saber, Bugoni et al. 2009). Nesse sentido, o objetivo deste trabalho foi de avaliar a distribuição e abundância de aves marinhas em relação a parâmetros oceanográficos e fisiográficos, e identificar padrões biogeográficos das comunidades de aves marinhas no Brasil. Para isso, esta obra está dividida em duas partes, apresentadas nos Apêndice 1 e 2. No Apêndice 1, o leitor encontrará a análise de associação entre dados de abundância e ocorrência da assembleia

de aves marinhas com parâmetros oceanográficos e fisiográficos no extremo Norte do país, no intuito de compreender quais são as variáveis mais relacionadas com as aves e, ainda, como espacialmente as aves estão distribuídas na região. Esse Apêndice traz dados inéditos da região Norte do país, completando uma lacuna de conhecimento para as aves marinhas no Brasil. No Apêndice 2 o leitor irá deparar-se com uma análise em macroescala, tendo o Brasil como referência, a fim de elucidar padrões biogeográficos da assembleia de aves marinhas ao longo da costa do país. Associações de abundância média e riqueza de espécies com padrões oceanográficos de superfície, com foco nos processos de meso-escala, também são discutidas. Para isso, incluímos dados das regiões Norte, Nordeste, Leste, Sudeste e Sul, testando se as aves marinhas, animais altamente móveis, seguem as propostas de bioregionalizações marinhas propostas por Spalding et al. (2007), tanto no nível de ‘Províncias’, quanto no de ‘Ecorregiões’. Ainda, tendo essa amplitude geográfica de abrangência, investigamos os padrões de riqueza de espécies ao largo de 39° de latitude.

## **MATERIAL E MÉTODOS**

### *Área de estudo e descrição oceanográfica*

Os dados para este estudo foram coletados em diferentes faixas latitudinais, sob diferentes regimes oceanográficos (Fig. 1; Tabela 1). Na porção Sul-Sudeste do Brasil, 1434 contagens foram realizadas entre a plataforma continental externa e o talude superior entre o Rio Grande do Sul e o Rio de Janeiro, como parte do Projeto ‘Talude’. Na porção Sudeste-Leste do país, 664 contagens foram realizadas sobre ou adjacente à Cadeia Vitória-Trindade, por meio do Projeto ‘Trindade’; ainda, 143 contagens realizadas no cruzero ‘Chevron’ e 15 contagens em idas ao Arquipélago dos Abrolhos. Cruzeiros feitos para o Atol das Rocas e Arquipélago de São Pedro e São Paulo foram plataformas para 99 contagens na região Nordeste. No Norte do Brasil, entre a foz do Rio Amazonas e o Oiapoque, 118 contagens em navegação e 101 contagens estacionárias foram realizadas ao largo do estado do Amapá.

A plataforma continental é bem variável ao largo da extensão do Brasil. A separação usual de plataforma continental interna (ambiente ‘costeiro’) e externa

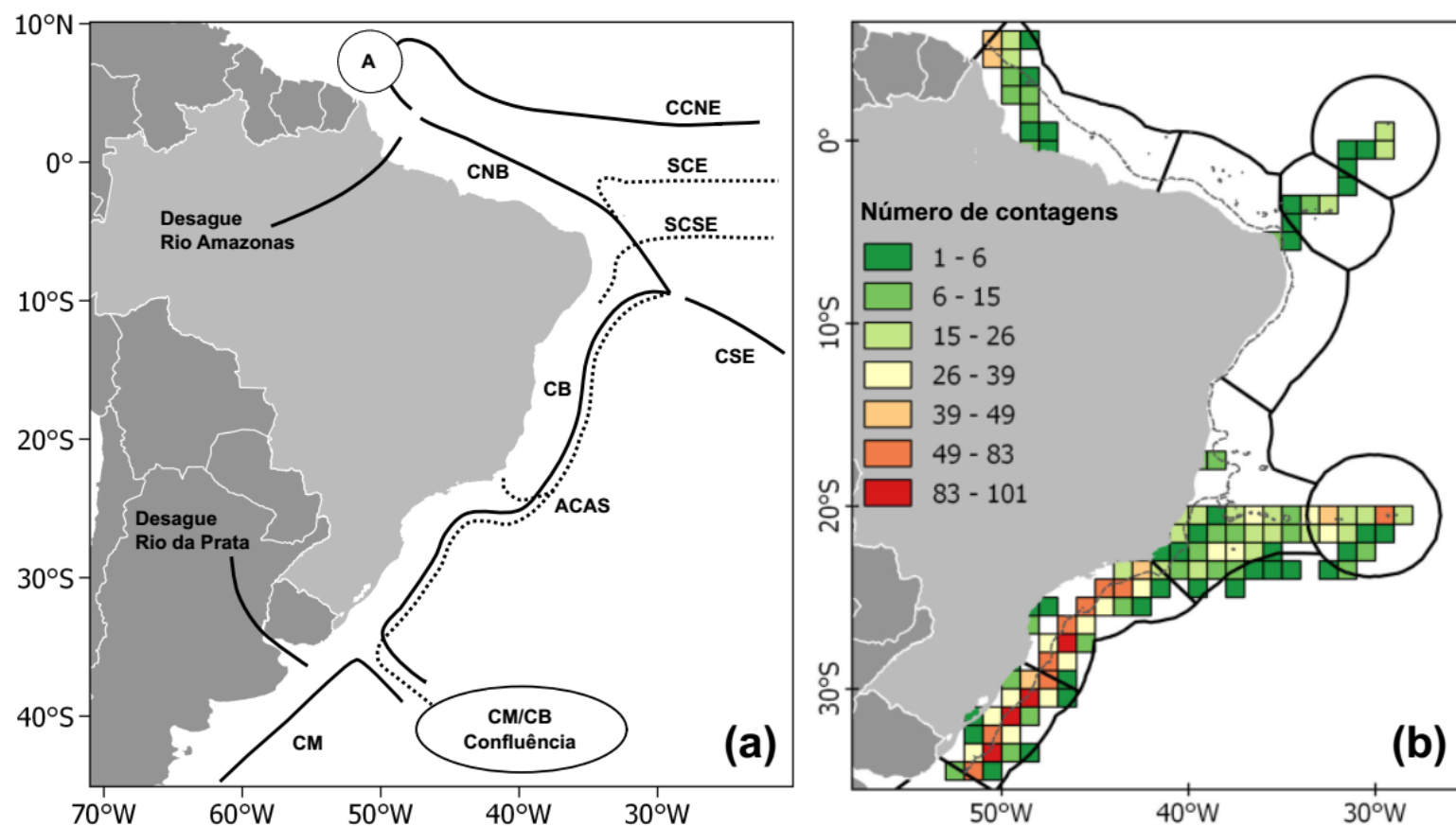
(ambiente ‘oceânico’) relaciona-se à isóbata de 200 m. Na região Norte, devido ao cone do Rio Amazonas, a plataforma interna estende-se por cerca de 300 km; no Nordeste, a plataforma é bem estreita, atingindo menos de 50 km em alguns pontos. Na região Leste, a plataforma está próxima ao continente, cerca de 40 km e, nas proximidades da Cadeia Vitória-Trindade chega a ter 140 km. Nas regiões Sudeste e Sul, a plataforma varia em torno dos 100 km de extensão, com ~220 km no Cone de Rio Grande.

**Tabela 1.** Síntese do esforço amostral realizado e alvo de estudo desta obra, por cruzeiro científico, ano, época predominante, e número de Estações de Contagem (EC) de aves marinhas, entre 2009 e 2018.

| Projeto                                                                             | Cruzeiro        | Ano         | Época predominante               | EC por cruzeiro    |
|-------------------------------------------------------------------------------------|-----------------|-------------|----------------------------------|--------------------|
| <b>Talude (23°–35°S, 41°–52°O)</b>                                                  | I/III/V/VIII    | 2009 a 2014 | Primavera                        | 121/183/227/142    |
|                                                                                     | II/IV/VI/VII/IX | 2010 a 2015 | Outono                           | 117/203/203/145/93 |
| <b>Chevron (21°–32°S, 37°–52°O)</b>                                                 | I               | 2011        | Verão                            | 143                |
| <b>Trindade (21°–23°S, 28°–43°O) <sup>a1</sup></b>                                  | I/IV/V          | 2011 a 2014 | Outono                           | 121/65/62          |
|                                                                                     | II/VII/VIII     | 2011 a 2015 | Primavera                        | 77/75/36           |
|                                                                                     | III/IX/XI       | 2012 a 2018 | Verão                            | 156/37/28          |
|                                                                                     | VI/X            | 2014 e 2017 | Inverno                          | 35/32              |
| <b>Abrolhos (c.17°S, 39°O) <sup>a2</sup></b>                                        | I               | 2011        | Verão                            | 6                  |
|                                                                                     | II/III          | 2011        | Inverno                          | 2/7                |
| <b>Atol das Rocas (c.5°S, 35°O) <sup>a2</sup></b>                                   | I               | 2010        | Primavera                        | 13                 |
| <b>Arquipélago de São Pedro e São Paulo<br/>(4°S–0,5°N, 29°–34°O) <sup>a2</sup></b> | I/II            | 2010 e 2011 | Agosto <sup>b</sup>              | 26/44              |
|                                                                                     | III             | 2012        | Verão                            | 16                 |
| <b>Amapá (1°S–5°N, 47°–51°O)</b>                                                    | I               | 2015        | Março, Abril e Maio <sup>b</sup> | 219                |
| <b>Total</b>                                                                        |                 |             |                                  | <b>2633</b>        |

<sup>a1</sup> Projeto Pró-Trindade (CNPq/Marinha do Brasil); <sup>a2</sup> Projetos Pró-Arquipélago (CNPq/Marinha do Brasil).

<sup>b</sup> Devido à amostragem em ambos os Hemisférios, optou-se por incluir os meses.



**Figura 1.** Área de estudo do presente trabalho. (a) Principais correntes superficiais e os desagues continentais mais notáveis. (b) Representação em grade com o número de Estações de Contagem (esforço amostral) por célula. CCNE = Contracorrente Norte Equatorial; SCE = Subcorrente Equatorial; SCSE = Subcorrente Sul Equatorial; CNB = Corrente Norte do Brasil; CSE = Corrente Sul Equatorial; CB = Corrente do Brasil; ACAS = Água Central do Atlântico Sul; CM = Corrente das Malvinas; A = zona de formação de vórtices.

O Brasil recebe diferentes influências oceanográficas, de acordo com a região (Fig. 1). As principais correntes que regem a costa do país originam-se a partir do Giro Subtropical do Atlântico, de onde a margem norte do Giro, a Corrente Sul Equatorial (CSE; *South Equatorial Current – SEC*), em torno de 10°S, aproximando-se do Brasil, divide-se nas quentes e oligotróficas Corrente Norte do Brasil (CNB; *North Brazil Current – NBC*) e Corrente do Brasil (CB; *Brazil Current – BC*) (Silveira et al. 1994). A CNB flui diretamente para a região Norte do país, enquanto a CB flui até a região Sudeste-Sul. Do sul da América do Sul, de águas fria e com maior aporte de nutrientes, a Corrente das Malvinas (CM; *Malvinas Current – MC*) flui em direção ao norte, influenciando, principalmente, os estados do sul do Brasil (Matano et al. 2010). O encontro dessa massa d'água com a CB, por sua vez, forma a Confluência CB/CM, ou também conhecido como a Convergência Subtropical. A seguir são evidenciados alguns processos oceanográficos notáveis de cada região.

A CNB flui em direção à costa Norte do país onde colide com a pluma do desague do Rio Amazonas. A região costeira é diretamente influenciada pelas águas turvas, quentes e ricas em nutrientes do Rio Amazonas, que é o maior desague de águas continentais no ambiente marinho do mundo (Hu et al. 2004, Coles et al. 2013). A pluma do Rio Amazonas varia de direção, posição e intensidade, de acordo com os pulsos de desagues (Coles et al. 2013), e tem contribuição direta ou indiretamente em toda a circulação da região tropical do Oceano Atlântico. A plataforma externa é regida pela oligotrófica CNB que, entre 5–10°N faz um movimento de retroflexão e retorna em direção à África, através da Contracorrente Norte Equatorial (CCNE; *North Equatorial Countercurrent – NECC*). No processo de retroflexão, a CNB interage com o desague do Rio Amazonas e forma vórtices de grande porte (anéis), com diâmetros de até 500 km (Hu et al. 2004). Esses anéis carregam as águas do Rio Amazonas no seu contorno (Ffield 2005, Silva et al. 2009), e provocam enriquecimentos locais de nutrientes, além do processo inerente de agregação de partículas dos vórtices. O braço da CNB que segue em direção ao norte, torna-se a Corrente das Guianas, que se mistura com o desague do Rio Orinoco na Venezuela e cria condições de altas produtividades (Bourlès et al. 1999a, Hu et al. 2004).

A região Nordeste é uma área de alta dinâmica oceanográfica. Águas quentes e oligotróficas de superfície, que fluem em velocidades mais elevadas, interagem com as contracorrentes e correntes de subsuperfície, de temperaturas mais frias e com maior aporte de nutrientes. As ilhas oceânicas do Arquipélago Fernando de Noronha, Atol das

Rocas e o Arquipélago de São Pedro e São Paulo são fortemente influenciadas pelas correntes CSE, Subcorrente Equatorial (SCE; *Equatorial Undercurrent – EUC*) e Subcorrente Sul Equatorial (SCSE; *South Equatorial Undercurrent – SEUC*) (Tchamabi et al. 2017, Araújo et al. 2018). Essas Subcorrentes, quando encontram um obstáculo topográfico, como as ilhas oceânicas da região, criam turbulências e influenciam na camada de mistura local, que por sua vez interagem num processo de vórtices advectivos e geram ressurgências de subsuperfície (Souza et al. 2013).

No Leste brasileiro, a corrente de superfície fundamental é a CB (Silveira et al. 2000). A circulação é menos dinâmica e o fluido das massas d'água ocorre majoritariamente para o sul. Nesse processo, margeando a plataforma interna, a CB forma meandros que, por sua vez, podem influenciar pequenos vórtices. Essa região é dominada por essas águas quentes e oligotróficas (Ekau & Knoppers 1999). Quando a CB se encontra com o Banco dos Abrolhos e com a Cadeia Vitória-Trindade, os meandros superficiais tornam-se mais intensos e, na subsuperfície dessas regiões ocorrem processos de ressurgência das Águas Centrais do Atlântico Sul (ACAS; *South Atlantic Central Water – SACW*). A ACAS tem como característica temperaturas frias, além de promover grande aportes de nutrientes. Desse modo, nesses processos, a subsuperfície fica dominada pela ACAS, e os afloramentos dessa massa d'água na superfície geram importantes ressurgências locais (Schmid et al. 1995, Gaeta et al. 1999).

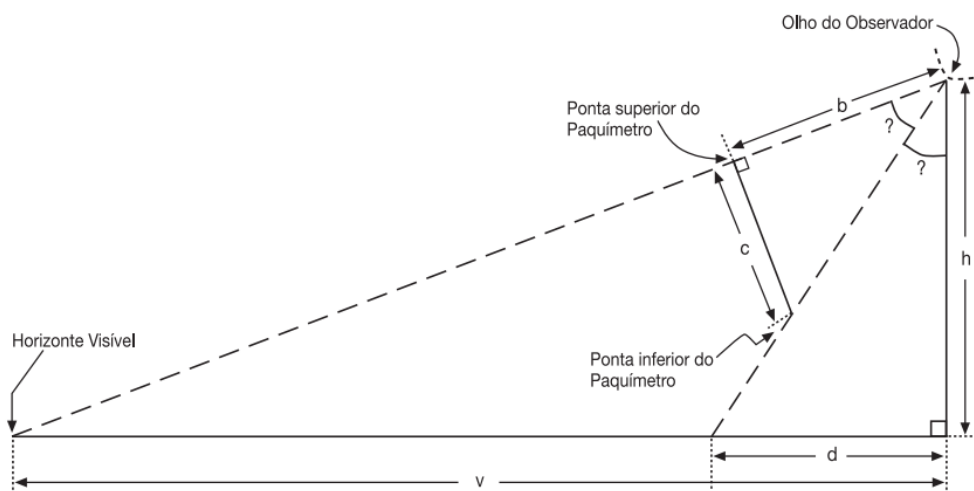
O Sudeste é uma região dominada pela CB (Silveira et al. 2000), e caracterizada pelos vórtices e ressurgências geradas nos seus dois extremos: nos Cabos de São Tomé e Cabo Frio (22°-23°S) no Rio de Janeiro, e no Cabo de Santa Marta (28°S) em Santa Catarina. A dinâmica de ventos na plataforma interna gera ressurgências da ACAS nas regiões dos Cabos mencionadas anteriormente, com influências notáveis na biota local (Coelho-Souza et al. 2012). A costa brasileira tem uma mudança de direção na região de Cabo Frio, e passa do direcionamento norte-sul para nordeste-sudoeste. Essa mudança de direcionamento da linha de costa aliado a mudanças no assoalho oceânico, cria instabilidades na CB que, por sua vez, geram vórtices de média escala (Campos et al. 2000, Palma & Matano 2009, Mill et al. 2015). Ainda, essas instabilidades criam outras condições que enriquecem ecologicamente a região, como as frentes térmicas na camada de fundo, e possíveis frentes de salinidade na superfície (Palma & Matano 2009, Brandini et al. 2018).

A região Sul é influenciada diretamente pela CM e os desagues do Rio da Prata (Argentina/Uruguai) e da Lagoa dos Patos, no Rio Grande do Sul. Do Norte, a CB traz as

águas quentes e oligotróficas, e do Sul, águas frias e com maior aporte de nutrientes são trazidas pela CM. A confluência dessas duas grandes massas d'água é conhecida como a Convergência Subtropical (Matano et al. 2010). Essa interação forma processos oceanográficos de média escala, como vórtices (Wilson & Rees 2000). Na plataforma interna, a CB traz consigo a Água Tropical (AT), quente e com alta salinidade, que interage com a pluma de água doce do Rio da Prata, e forma a Frente Subtropical de Plataforma (FSP; *Subtropical Shelf Front – SSF*) (Möller et al. 2008, Piola et al. 2008). A flutuação sazonal da FSP, as intrusões de águas doces, ricas em nutrientes continentais, e ressurgências por ação do vento pontuais na costa, fazem essa região ter alta produtividade primária (Ciotti et al., 1995, Möller et al. 2008).

### Contagem de aves

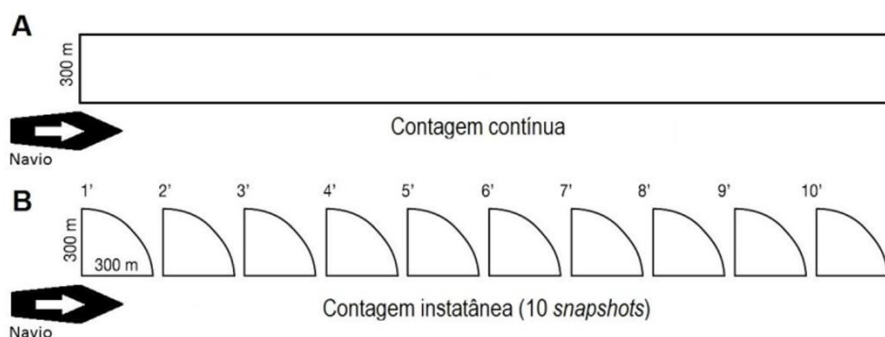
Para a contagem de aves no mar, os pressupostos necessários são de que a embarcação tenha rumo fixo e velocidade constante conhecida. As aves avistadas até a distância de 300 m a partir da embarcação, calculada para cada observador e embarcação conforme o método descrito por Heinemann (1981) (Fig. 2), e cobrindo um espaço de  $\frac{1}{4}$  de círculo adjacente e à frente da embarcação são contabilizadas conforme descrito a seguir.



**Figura 2.** Método de Heinemann (1981) para a determinação da faixa amostral do raio de 300 m. Sendo  $c$  = abertura do paquímetro,  $b$  = distância entre o paquímetro e o observador,  $h$  = altura dos olhos do observador em relação à linha d'água,  $d$  = distância a ser estimada (para este estudo, 300 m), e  $v$  = distância visível do horizonte. Imagem adaptada de Neves et al. (2006).



As unidades amostrais (Estações de Contagem – EC) são compostas por três tipos de contagens distintas. Essas contagens são realizadas de acordo com as indicações para censos de aves no mar, sendo os censos de i) aves seguidoras, ii) contagem contínua e, iii) contagens instantâneas (Tasker et al. 1984, van Franeker 1994, Neves et al. 2006). As aves associadas à embarcação (aves seguidoras) são identificadas e contabilizadas primeiro, a fim de diminuir o viés de recontagem de indivíduos, já que estas aves não são contabilizadas nas contagens seguintes. Na contagem contínua é feita a contabilização das aves durante 10 min contínuos, em um bloco amostral único de área, evitando ao máximo a recontagem de aves (identificando-as visualmente, e se mantendo ciente da sua posição em relação à embarcação) e excluindo-se as seguidoras. Assim, tem-se um retângulo amostrado, com comprimento variável determinado pela velocidade do navio (Fig. 3A). Dez contagens instantâneas são realizadas em seguida, com intervalos de 1 min entre contagens (Fig. 3B). A “varredura” é feita como uma “fotografia” (do inglês, *snapshot*) no momento inicial de cada bloco amostral, a fim de diminuir o efeito do deslocamento das aves (Gaston et al. 1987).



**Figura 3.** Desenho esquemático da área amostrada nos censos contínuos (A) e instantâneos (B). Adaptado de Neves et al. (2006).

Os diferentes métodos de contagens têm diferentes implicações nas análises de dados. As aves seguidoras podem permanecer ao redor da embarcação por vários dias, enviesando qualquer análise relacionada à abundância da assembleia e/ou determinada espécie que é propensa a esse hábito. Por outro lado, pode trazer informações importantes quanto aos padrões de ocorrência das espécies. A principal diferença entre os censos contínuos e instantâneos é a possibilidade/probabilidade de recontagem das aves, tendo,

também, diferentes implicações nas análises de abundância. Alguns autores propõem o uso de taxas de correção para essas contagens, por exemplo, levando em conta a movimentação das aves e as taxas de detecção dos observadores (Spear et al. 1992, Spear et al. 2004).

No cruzeiro realizado no Amapá, na região mais ao norte amostrada, o navio operava em estações oceanográficas durante parte do tempo. Assim, sem rumo e velocidade fixos, o método descrito anteriormente não pode ser empregado. Deste modo, as aves foram registradas em intervalos de 1 h, limitadas a uma faixa de 300 m ao redor do navio. Aves em voo e pousadas foram contabilizadas, identificando-as para evitar ao máximo as recontagens dentro de cada intervalo amostral. Algumas estações oceanográficas perduraram mais de uma hora e, assim, a cada hora, um novo bloco amostral era iniciado. Essas contagens foram chamadas de ‘estacionárias’, e aparecem no Apêndice 1 como *point-counts*.

O arranjo taxonômico utilizado para esta obra é o proposto pelo Comitê Brasileiro de Registros Ornitológicos (Piacentini et al. 2015). Quando possível, as aves foram fotografadas e, com o auxílio de guias específicos, identificadas (Harrison 1985, Olsen & Larsson 1997, Onley & Scofield 2007). Em alguns casos, fotos foram enviadas para especialistas.

#### *Variáveis ambientais e fisiográficas*

Para cada EC, a direção e a velocidade do vento, o estado do mar (em escala Beaufort), bem como a profundidade, foram registrados *in situ*. Essas, somadas à temperatura e salinidade superficial do mar, e distância da costa, serão as variáveis “base” das análises. Ainda, clorofila-*a* foi considerada como um *proxy* de produtividade primária e incluída nas análises.

Apesar de algumas variáveis serem coletadas *in situ* pelos observadores, devido a problemas/falhas nos aparelhos de anemômetro e sondas batimétricas de alguns cruzeiros, optou-se para, no conjunto de dados desta obra, os derivarmos todos das mesmas fontes de sensoriamento remoto por imagens de satélite. Assim, mantemos uma fonte de dados única, para cada variável, para todos os cruzeiros, independente das diferenças entre sensores, capacidade e disponibilidade dos equipamentos individuais das embarcações utilizadas como plataformas de observação.

Imagens de sensoriamento remoto diárias, e do horário mais próximo aos dos censos realizados, foram baixadas de banco de dados globais e livres, interpoladas, e

extraídas do ponto mais próximo à posição da EC. A interpolação permite um escalonamento na resolução espacial dos dados satelitais e, ainda, por ser uma aproximação matemática, auxilia no ‘preenchimento de dados’ para EC que, por ventura, estivessem em baixo de cobertura de nuvens. Nos Apêndices 1 e 2, diferentes resoluções espaciais de interpolações foram selecionadas, afim de suportar boas resoluções para os dados e manter o desenvolvimento computacional envolvido.

Para as variáveis de temperatura superficial do mar (TSM) e salinidade superficial do mar (SSM) os dados foram obtidos dos modelos HYCOM (*HYbrid Coordinate Ocean Model* – <<<https://hycom.org>>>). O HYCOM é um modelo de circulação oceânica global híbrido, em que as coordenadas verticais são isopicnais no oceano aberto (seguem as estratificações de densidade da água) e mudam, suavemente, para coordenadas sigma em zonas costeiras (que seguem o fundo oceânico) (Bleck 2002). Essa característica mantém as vantagens de modelos isopicnais e ainda permitem maior resolução próximo à costa. Desta forma, fornecem melhor representação dos processos oceanográficos. Em médias latitudes, o HYCOM tem resolução espacial horizontal de  $\pm 7$  km ( $0,083^\circ$ ).

Para as variáveis de direção e velocidade do vento, o banco de dados do ERA-INTERIM-ECMWF (*European Centre for Medium-Range Weather Forecasts* – <<<https://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc>>>) foi utilizado. Estes dados são considerados robustos, com precisão espacial de  $\pm 14$  km ( $0,125^\circ$ ), e mais precisos para utilização em modelos de previsão climática (Dabernig et al. 2015), com produtos em escala global a cada 6 h.

Os dados de clorofila-*a*, um *proxy* de produtividade primária, foram obtidos no banco de dados da NASA, provenientes do satélite MODIS (*Moderate Resolution Imaging Spectroradiometer* – <<<https://oceancolor.gsfc.nasa.gov/data/aqua>>>). Ao captar dados espectrais nas bandas 405–877 nm (bandas 8 a 16) um algoritmo é aplicado para calcular a concentração de clorofila-*a* de acordo com uma relação empírica derivada de medições *in situ* e das bandas azul para verde de medições remotas de reflectância. O resultado deste processo é a medição de clorofila-*a* em  $\text{mg/m}^3$  de Carbono com dados diários, numa resolução espacial variada (devido às nuvens) mas que pode chegar a  $\pm 4,6$  km ( $\sim 0,06^\circ$ ).

Os dados de profundidade foram derivados do banco de dados proveniente do GEBCO (*General Bathymetric Chart of the Oceans* – <<[https://www.gebco.net/data\\_and\\_products/gridded\\_bathymetry\\_data](https://www.gebco.net/data_and_products/gridded_bathymetry_data)>>) que possui uma resolução espacial de 30 arco-segundos, com um valor batimétrico a cada  $\sim 925$  m.

Ainda, duas variáveis foram calculadas diretamente através do software MATLAB. A distância da costa foi calculada como o valor da distância (km) entre a EC e o ponto mais próximo de terra. As ilhas costeiras foram mantidas quando no arquivo base para esse cálculo, mas as ilhas oceânicas retiradas. O gradiente de TSM foi calculado como variável para o Apêndice 2. Para isso, foi aplicada a primeira derivada, em cada imagem de TSM, na diferença de valores entre o pixel ‘ao sul’ quanto o ‘ao norte’. Assim, a primeira linha de pixels (de baixo para cima) foi ‘queimada’ para o processo – sem afetar os dados, já que nenhuma EC ficou sob ela. Essa variável pode indicar zonas de maior variação de TSM em relação às suas vizinhas, identificando, assim, potenciais zonas de frentes oceanográficas térmicas.

### *Análise de dados*

Para cada Apêndice, as análises foram feitas de modo separado, a fim de estabelecer as relações diretas entre as aves e as variáveis ambientais/fisiográficas regionais, e manter a mesma resolução espacial dos dados ambientais em cada Apêndice. Para ambos, análises exploratórias dos dados foram feitas, a fim de identificar valores extremos, distribuição dos dados, correlação entre as variáveis explanatórias e frequências numéricas (*sensu* Zuur et al. 2010), tendo em vista o ajuste de modelos adequados para os dados.

Todas as análises estatísticas foram realizadas no software livre e de código aberto R (R Core Team 2019), versão 3.6.0. Assegurando a replicação das análises, os códigos estão disponíveis nos Apêndices deste documento, onde, também, são indicados os pacotes utilizados. O software livre e de código aberto QGIS foi utilizado, versão 2.18.7 (QGIS Development Team 2018), para as confecções dos mapas.

### *Análises Apêndice 1*

Visto que a região Norte do país carece de informações básicas quanto à assembleia de aves marinhas, um sumário descritivo das espécies registradas, seus números máximos de registros, médias, e densidades foram calculadas. Para o emprego dos modelos estatísticos, a unidade amostral de cada EC foi escolhida como a dos censos contínuos (e seus números absolutos).

A análise exploratória dos dados indicou um alto número de zeros nos dados, não sendo indicado o uso de modelos de regressão amplamente utilizados, como os Modelos Lineares Generalizados (*Generalized Linear Models – GLMs*), com distribuições de

Poisson ou Binomial-negativo. Assim, para as avaliações de interação entre as aves e as variáveis ambientais/fisiográficas, unimos as espécies de mesma família, as quais também têm convergências ecológicas (del Hoyo et al. 1992, 1996).

Os grupos analisados foram: bobos, Procellariidae (*Puffinus* + *Calonectris*); petréis-das-tormentas, Hydrobatidae (*Oceanodroma* + *Oceanites*); gaivotas-rapeiras, Stercorariidae (*Stercorarius*); gaivotas, Laridae (*Leucophaeus*); e os trinta-réis, Sternidae (*Sterna*). Devido a diferenças ecológicas e poucos registros, *Thalasseus acutiflavus* e *Phaetusa simplex* não foram incluídas em ‘Sternidae’.

Para abordar o alto número de zeros no banco de dados optou-se por empregar modelos de ‘regressão múltipla em duas-partes’, análogos aos modelos *Hurdle*, onde o teste é composto de uma parte relacionada à ‘ocorrência’ das espécies e a outra para a ‘contagem’ dos indivíduos (Zeileis et al. 2008). O modelo de ocorrência é uma regressão múltipla, com base na distribuição Binomial, onde os grupos são avaliados como fatores (ausência e presença; 0 e 1). O modelo relacionado à contagem é uma regressão múltipla, baseada em uma distribuição de Poisson, sendo ‘zero-truncado’ (somente valores positivos de abundância). Para os modelos univariados, de ‘duas-partes’, os grupos definidos anteriormente foram utilizados como variável resposta. Em uma abordagem multivariada, a fim de verificar as afinidades de todos os grupos de aves juntos, em relação aos parâmetros ambientais/fisiográficos, foi realizada uma Análise de Correspondência Canônica (*Canonical Correspondence Analysis* – CCA). Essa análise ordena e ranqueia as variáveis explicativas com influência na matriz biológica (Legendre & Legendre 1998, Quinn & Keough 2002). Os eixos da CCA foram testados através do teste de Análise de Variância (*ANalysis Of VAriance* – ANOVA), com 99 permutações.

Baseado nos testes exploratórios dos dados, ‘salinidade superficial do mar’ foi retirada das análises devido à alta correlação com ‘distância da costa’ e ‘clorofila-*a*’ ( $r > 0,5$ ). Os valores da ‘direção do vento’ apontavam, quase na totalidade, vindos do quadrante nordeste. Assim, seu poder ‘explicativo’ seria baixo – devido à baixa variabilidade da própria variável. As variáveis ‘direção do vento’ e ‘intensidade do vento’ costumam interagir para influenciar as aves, deste modo, ‘intensidade’ também foi retirada das análises. Os Fatores de Inflação de Variância (*Variance-Inflation Factor* – VIF) apontam para números baixos entre as variáveis explicativas; porém, para as análises univariadas, a ‘distância da costa’ foi retirada (VIF = 12,3), assegurando apenas valores <3.

## Análises Apêndice 2

Para este Apêndice, os dados das contagens em nagegação (seguidoras, contínuos e instantâneos) e contagens estacionárias foram utilizados. De acordo com as análises, foram extraídas do banco de dados duas matrizes: uma indicativa de abundância, e outra de ocorrência. Conforme explicado anteriormente, cada Estação de Contagem (EC) é o conjunto das contagens de aves seguidoras, censos contínuos e instantâneos. Assim, a matriz de ocorrência é composta pela informação de ausência/presença (0/1) de cada espécie para cada EC, somadas às informações dos três tipos de contagem ( $n = 2633$ ). Para a matriz de abundância, foram selecionados apenas os dados de censos contínuos de cada EC ( $n = 2532$ ). A seguir, para ambas as matrizes, atribuiu-se *a priori* a qual Província e Ecorregião biogeográfica proposta por Spalding et al. (2007) encontrava-se cada EC. Devido ao baixo número de ECs na região Nordeste e pela similaridade das características oceanográficas desta região, optou-se por adaptar a proposta de Spalding et al. (2007), unindo as Ecorregiões originais *São Pedro and São Paulo Rocks*, *Fernando de Noronha and Atoll das Rocas*, e *Northeastern Brazil* em uma única ‘*Northeastern Brazil*’ (Nordeste brasileiro).

Mapas foram gerados para representar, espacialmente, como o esforço, a média de indivíduos contados, e a riqueza de espécies foram distribuídos. Essas representações foram feitas em grades, com células de  $1^{\circ} \times 1^{\circ}$ . O esforço foi contabilizado como o número de ECs por célula; a média de aves por célula foi o cálculo do número total de aves contabilizadas por EC, dividido pelo número de ECs (com base na matriz de abundância); e, a riqueza de espécies, é o número de espécies distintas registradas naquela célula (com base na matriz de ocorrência). Devido aos Procellariiformes e Charadriiformes terem sido os táxons mais registrados, optou-se por mapear a abundância média e a riqueza de espécies, também, separadamente para essas ordens.

A fim de comparar a riqueza de espécies entre as Ecorregiões, foram produzidas curvas de rarefação e extrapolação do número de espécies. A ideia é, basicamente, computar o número de espécies novas registradas a cada nova amostragem (ECs) e criar uma curva acumulativa dessas informações. Essas curvas nos permitem ter uma noção de estabilização, e inferir se a assembleia/comunidade está bem representada na amostragem. Como as áreas tiveram uma cobertura amostral diferente, com o número de ECs desbalanceado, essas curvas foram, também, construídas de acordo com um método que absorve essa desigualdade. Deste modo, fizemos as curvas ‘baseadas-em-cobertura-amostral’ (*coverage-based*) (Chao & Jost 2012). Ambas as representações, quando

interpretadas juntas, nos dão o indício do número potencial de espécies, e de quão bem foi amostrada cada área.

Pela natureza hierárquica da identificação de Ecorregiões, e devido à extensão de área em que este Apêndice abrange, hipotetizamos que as assembleias têm um padrão gradual de mudança. Para testar a similaridade entre as regiões propostas por Spalding et al. (2007), utilizamos análises de agrupamentos hierárquicos (*Hierarchical Clusters*). A matriz de distância para a análise foi obtida através da dissimilaridade de Sørensen, baseada na matriz de ocorrência de espécies, e o método de agrupamento foi o de ‘ligação simples’. Essa análise nos retorna um dendrograma, o qual evidencia a similaridade entre as Ecorregiões em relação aos seus conjuntos de espécies. Os dados oceanográficos e fisiográficos foram utilizados, em conjunto com a matriz de abundância de aves, em uma Análise Canônica de Coordenadas Principais (*Canonical Analysis of Principal Coordinates – CAP*). A CAP é uma análise que permite discriminar variáveis fatoriais (no nosso caso, as Ecorregiões) em relação à análise canônica entre dados ambientais e biológicos (Anderson & Willis 2003). Para essa análise, optamos por excluir observações (ECs) que não tivessem, no mínimo, três indivíduos. A densidade de aves marinhas é, normalmente, baixa, e adotando o critério de >3 indivíduos, mantiveram-se 394 observações.

Para investigar a relação entre a latitude e a riqueza de espécies, foram utilizados Modelos Aditivos Generalizados (*Generalized Additive Models – GAMs*). Os GAMs são modelos aditivos que consistem em diversos ‘modelos lineares curtos’ conectados por uma função de suavização (*smooth function*) (Wood 2017), representando melhor, assim, padrões não lineares de relação entre duas (ou mais) variáveis. Os modelos espaciais foram ajustados para a variável dependente ‘riqueza de espécies’, baseada na distribuição de Poisson, e a função de suavização da latitude foi a única variável explicativa independente. Foram gerados GAMs para o número total de espécies, e separadamente para as ordens Procellariiformes e Charadriiformes.

## RESULTADOS

No Apêndice 1, as primeiras informações quanto à assembleia de aves marinhas no Norte do Brasil são apresentadas. No total, 219 contagens foram realizadas, com 148 h de amostragem. Um total de 443 aves foram registradas, todas com baixas densidades, porém uma alta riqueza de espécies foi observada, dado que foram apenas dois cruzeiros de amostragem, ambos na mesma época do ano ( $S = 21$ ; Tabela 1 do Apêndice 1).

A composição é, majoritariamente, de espécies migrantes, de ambos os Hemisférios. Quatro espécies somam 54% dos registros, sendo elas: trinta-réis-boreal *Sterna hirundo* ( $n = 80$ ), trinta-réis-das-rocas *Onychoprion fuscatus* ( $n = 54$ ), bobo-pequeno *Puffinus puffinus* ( $n = 52$ ) e gaivota-alegre *Leucophaeus atricilla* ( $n = 52$ ). Para essas espécies, algum ponto de ocorrência com  $>16$  aves foi registrado (Figura 3 do Apêndice 1).

Os modelos univariados de ‘duas-partes’ indicaram, na parte de ocorrência, a importância da TSM para Procellariidae, Laridae e Sternidae, e da clorofila-*a* para Sternidae; na parte de ‘contagem’, as mesmas variáveis apontam influência para os grupos Stercorariidae, Laridae e Sternidae, mas apenas para Laridae mostrou-se estatisticamente significativa (Tabela 2 do Apêndice 1). Os estimadores ‘negativos’ de TSM (águas mais frias com mais aves, tanto em ocorrência quanto em abundância) podem estar sugerindo processos de frentes de massas d’água (diferentes propriedades de TSM e SSM), já que sempre acompanham estimadores positivos da variável clorofila-*a* (maiores valores de clorofila, maiores abundâncias e ocorrências de aves), a qual é influenciada no processo de frentes. Apesar de terem ficado com bons ajustes matemáticos no geral, para Procellariidae, erros-padrão não condizentes foram atribuídos e, para Stercorariidae, os estimadores apresentados não são realísticos. Deste modo, as interpretações devem ser cautelosas.

A análise multivariada apontou para o mesmo caminho, com a clorofila-*a* mais próxima a Sternidae e Laridae, e TSM mais próxima de Procellariidae (Figura 4 do Apêndice 1). Para Hydrobatidae, a distância da costa foi uma variável importante, visto que os petréis-das-tormentas foram registrados frequentemente na isóbata de 20 m. Os eixos 1 e 2 da CCA foram estatisticamente significantes ( $p = 0,01$ , ambos), e as quatro variáveis mostraram-se estatisticamente significantes para a construção dos eixos (todas com  $p < 0,05$ ).



Espacialmente, nota-se duas áreas de agregação de aves marinhas, uma próxima a foz do Rio Amazonas, e outra na zona de borda das formações dos vórtices (*rings*). Os mapas apresentados no Apêndice 1 demonstram essas regiões—todos os registros (Figura 2); as quatro espécies mais registradas (Figura 3); e os registros de Procellariiformes e Charadriiformes, apenas dos censos contínuos (Figura 5).

No Apêndice 2, um total de 2633 contagens foram realizadas (incluindo as contagens do Apêndice 1), registrando três ordens, nove famílias, e 46 espécies de aves marinhas (Apêndice 1 do Apêndice 2). Destas contagens, 1749 observações tiveram ao menos uma ave registrada. Dentre as espécies, 14 foram raramente registradas, com <5 incidências (Apêndice 1 do Apêndice 2).

Espacialmente, as células com maiores riquezas de espécies foram registradas em regiões nos extremos do país: no Norte, na fronteira marítima com a Guiana Francesa; ao leste, na célula ao redor da Ilha da Trindade; e ao sul, na divisa marítima com o Uruguai (Figura 2 do Apêndice 2). Na região sul, ainda, um conjunto de células com alta riqueza de espécies é notável próximo ao Cabo de Santa Marta (Santa Catarina; ~28°S). As maiores riquezas, na região sul, foram registradas próximas à isóbata de 200 m. Quando analisada a riqueza de espécies das diferentes ordens, um padrão contrastante é notado. Para a ordem dos Charadriiformes, maiores riquezas foram na região Norte (0–5°N), ao largo do Amapá, e ao redor da Ilha da Trindade (~20°S); em contraposto, a ordem dos Procellariiformes teve expressiva riqueza na região Sudeste-Sul, mas ainda mais notável, ao sul de 27°S (Figura 3 do Apêndice 2). Pela ótica da Ecorregiões, o Nordeste do Brasil tem uma baixa riqueza de espécies, enquanto que as Ecorregiões do Sudeste-Sul e das Ilhas da Trindade e Martin Vaz têm maiores riquezas (Figura 4a do Apêndice 2); a região Norte (*Amazonia*), demonstra potencial de ser a área com maior riqueza de espécies (Figura 4a do Apêndice 2). A curva de acúmulo de espécies em relação à cobertura amostral demonstra que as Ecorregiões, com exceção da Amazônica (*Amazonia*), parecem estar bem amostradas (Figura 4b do Apêndice 2).

Os agrupamentos hierárquicos confirmaram o padrão esperado em nível de Província. A Província da Plataforma Norte do Brasil (*North Brazil Shelf*) ficou distanciada das outras devido à alta peculiaridade de espécies registradas apenas naquela região; enquanto que as Províncias Tropical do Sudoeste do Atlântico e Subtropical do Sudoeste do Atlântico (*Tropical Southwestern Atlantic* e *Warm Temperate Southwestern Atlantic*, respectivamente) foram mais similares, já que compartilham diversas espécies (Figura 5a do Apêndice 2). Para o agrupamento em nível de Ecorregiões, foi demonstrado

um padrão semelhante ao das Províncias, mas com suas peculiaridades (Figura 5b do Apêndice 2). A região do Nordeste Brasileiro foi dissimilar como, e agrupada com, a região da Amazônia (apesar de terem nós distintos—evidenciando a dissimilaridade, de ambas, com as demais Ecorregiões). Curioso foi o agrupamento da Ecorregião do extremo leste (Ilhas da Trindade e Martin Vaz) com a Ecorregião do extremo sul (Rio Grande), e não com regiões mais próximas geograficamente (e.g. o Leste Brasileiro). Quando levada em conta a classificação *a priori* das contagens de aves e os dados ambientais associados às observações, a CAP indica uma porcentagem de discriminação entre as Ecorregiões de 67%. Internamente, a análise gerou 10 eixos, os quais captaram 81% da variação dos dados. No gráfico bidimensional, fica evidente a separação da Ecorregião das Ilhas da Trindade e Martin Vaz (Figura 6 do Apêndice 2). Nas porcentagens de acerto discriminatórias, a Ecorregião de Rio Grande teve a maior taxa de acerto (81%;  $n = 201$ ), seguido do Nordeste Brasileiro (80%;  $n = 10$ ), Ilhas da Trindade e Martin Vaz (74,2%;  $n = 62$ ), Leste Brasileiro (70,7%;  $n = 41$ ) e Sudeste Brasileiro (26,7%;  $n = 75$ ). A Ecorregião Amazônica não teve classificada corretamente nenhuma observação ( $n = 5$ ). O padrão de agrupamento das Ecorregiões Sudeste Brasileiro com Leste Brasileiro, a afinidade teórica (devido à classificação Provincial) da primeira com a Ecorregião de Rio Grande, junto com a baixa taxa de acerto na classificação da CAP, demonstram que a região do Sudeste Brasileiro é uma possível área de transição de assembleias.

Os modelos espaciais tiveram resultados contrastantes. Para todos, a função de suavização da variável latitude foi significativa ( $p < 0,01$ ). Os gráficos da função de suavização foram bem elucidativos. Para o somatório das espécies, o modelo teve o coeficiente de determinação  $R^2_{adj} = 0,44$  e indicou 39,3% da variância dos dados explicados; maiores riquezas ao Sul, mas com dois picos crescentes (Figura 7a do Apêndice 2): um relacionado à presença da Ilha da Trindade (20°S) e o outro à Foz do Rio Amazonas (0–5°N). Quando analisada apenas a ordem dos Procellariiformes, fica evidente a maior riqueza de espécies na região Sudeste-Sul, ao sul de 23°S (Figura 7b do Apêndice 2); o modelo teve o melhor ajuste, com coeficiente de determinação  $R^2_{adj} = 0,53$  e 52,2% da variância dos dados explicada. Para Charadriiformes, o coeficiente de determinação foi de  $R^2_{adj} = 0,08$  e a variância explicada foi de 19,8%; o gráfico da função suavizada demonstra claramente dois picos, relacionados aos mesmos detectados no modelo com todas as espécies—Ilha da Trindade e Foz do Rio Amazonas (Figura 7c do Apêndice 2).

## CONCLUSÕES

- As aves marinhas têm afinidade com feições oceanográficas de meso-escala, como vórtices, ressurgências, e ressurgências de subsuperfície relacionadas a relevos no assoalho oceânico (como os montes submarinos da Cadeia Vitória-Trindade). Nesses locais, tanto as maiores riquezas de espécies, quanto as maiores abundâncias médias, foram observadas ao largo do Brasil.
- Dentre os processos oceanográficos de meso-escala, destacamos os aportes de água doce. Tanto o desague do Rio Amazonas, no Norte, quanto a contribuição do desague do Rio da Prata (Argentina/Uruguai) somado ao desague da Lagoa dos Patos, no Sul, confirmaram-se como importantes locais de riqueza de espécies e abundância média de aves marinhas. De fato, ambas as regiões foram as de maior riqueza de espécies.
- A riqueza de espécies de aves marinhas parece estar relacionada a locais de “uso” (Norte e Sudeste-Sul do Brasil), sendo locais de “passagem” (Nordeste do Brasil) naturalmente uma região de baixa riqueza.
- A ordem dos Charadriiformes contradiz o padrão marinho de riqueza de espécies em relação à latitude, e mostra-se como um grupo intrigante para futuras análises.
- As Ecorregiões Marinhas (*sensu* Spalding et al. 2007) para animais com alta capacidade móvel, como as aves marinhas, parecem adequar-se melhor em nível de Província, portanto em escalas geográficas maiores. Por outro lado, a afinidade desse grupo com características oceanográficas de meso-escala sugere que, provavelmente, as Províncias devam ser limitadas de acordo com tais processos, e não pelo critério de endemismo.

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## **APÊNDICE 1**

**Assembleia de aves marinhas na foz do Rio Amazonas e sua relação com características ambientais**

**Seabird assemblage at the mouth of Amazon River and its relationship with environmental characteristics**

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**Seabird assemblage at the mouth of the Amazon River and its relationship with environmental characteristics**

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## ABSTRACT

There is a paucity of data on seabird assemblages at sea in tropical waters, particularly in the western Atlantic Ocean, such as distribution and species occurrence. Here, we describe the seabirds recorded near the Amazon River mouth, in North Brazil, the greatest freshwater input in the marine environment globally. Through two ship surveys conducted between March and May 2015, 443 individuals of 21 species were recorded. The species composition was almost all migrant taxa from both the Northern and Southern Hemispheres. We accessed the associations between bird assemblages (grouped by seabird families) and environmental variables, through univariate, two-part multiple regression models and canonical correspondence analysis. Seabirds aggregate in two main areas, each related to different mesoscale oceanographic features: the tidal mixing and saline front at the mouth of the Amazon River and the ring-formation zone on the border with French Guiana. For petrels (Procellariidae) and storm-petrels (Hydrobatidae), associations with sea surface temperature and distance from the coast were important. These groups were mainly observed in the ring-formation zone, and storm-petrels also occurred at the 20-m isobaths, where the advection process can cause local zooplankton enhancement. On the other hand, for terns (Sternidae), gulls (Laridae) and skuas and jaegers (Stercorariidae), chlorophyll-*a* and bathymetry were the most important factors. Their distributions were associated with the mouth of the Amazon River, where primary productivity is high. The oceanographic characteristics of these aggregation zones make them ecologically important areas for meso- and megafaunal marine taxa, particularly seabirds.

## *Keywords*

At sea counts; Community; Distribution; Hotspots; Megafauna aggregations; Procellariiformes.

## 1. Introduction

The basic attributes used to characterize ecological assemblages are species composition, richness and abundance. Assemblages, defined as ‘taxonomically related groups that occur together in space and time’ (Stroud et al., 2015), are structured based on habitat heterogeneity, species diversity and their interactions (Begon et al., 2006). In the patchy marine environment, organisms are likely to be associated with some features shaped through oceanographic and physical processes. Elevated primary production generates nutrients and physical forces accumulate biomass *per se* (Olson and Backus, 1985), creating ecologically important zones for several marine taxa (Hunt, 1990; Sournia, 1994; Bost et al., 2009). These structures are linked mainly to seabed topography, physical water properties, and oceanographic processes, such as fronts, eddies and local upwelling (Genin, 2004; Scales et al., 2014b). Therefore, one can expect that top predators, such as seabirds, aggregate in these zones (Weimerskirch, 2007; Scales et al., 2014a; Grecian et al., 2016).

The major frontal zones are well-known globally, as they are persistent in space (e.g., Acha et al., 2004; Belkin et al., 2009), but the monitoring of many of them in the Atlantic Ocean is lacking (Miloslavich et al., 2011). Many large marine regions worldwide have no data on seabirds, and this paucity of data is particularly notable in tropical regions and along the South American Atlantic coast (Mott and Clarke, 2018). In Brazil, which has over 7000 km of coastline, from 5°N to 34°S, a single published study was found in a recent global review on the study effort regarding seabird distributions (Mott and Clarke, 2018) related to satellite-tracked Spectacled Petrels *Procellaria conspicillata* (Bugoni et al., 2009). Although a few other studies on seabird assemblages are also available for the region (Coelho et al., 1990; Neves et al., 2006; Krüger and Petry, 2010; Fey et al., 2017), they are all from the Southeast and South region, including assemblages attending fishing vessels (Olmos, 1997; Bugoni et al., 2008). With its extensive coastline, Brazil’s marine environments play a key role in the entire ecosystem of the South Atlantic Ocean, which is widely variable and is thus expected to host different seabird assemblages. The composition of the bird fauna along this vast tropical area has not been described, although it is expected to be distinct from that studied from 23°S southward (Neves et al., 2006; Bugoni et al., 2008; Krüger and Petry, 2010).

Different oceanographic conditions, such as water masses and nutrients, directly influence prey types and their availability. This has led to various seabird assemblages occurring in different oceanographic domains, even crossing large marine regions in

offshore waters (Woehler et al., 2010; Commins et al., 2014; Jungblut et al., 2017). For example, environmental characteristics such as bathymetry influence seabird distributions, with distinct associations according to species (Ainley et al., 1993; Yen et al., 2004; Hunt et al., 2014). Dependence on land or ice-covered land (in Polar Regions) has also been documented for a variety of taxa (Ainley et al., 1993; Yen et al., 2004; Cushing et al., 2018). Sea surface temperature and levels of chlorophyll-*a* (a primary production proxy) have been demonstrated to influence the habitats of many species, from warm to cool, and oligotrophic to eutrophic waters (Bugoni et al., 2009; Blanco et al., 2017; Clay et al., 2017). Water masses have inherently distinct temperatures and salinities, which also play a role in shaping the assemblages and habitat use of seabirds (Hyrenbach et al., 2007; Commins et al., 2014; Jungblut et al., 2017), including plumes of freshwater discharge (Urbanski et al., 2017; Phillips et al., 2018).

At a global level, the largest freshwater discharge into the marine environment occurs by the Amazon River in northern Brazil, which influences the entire oceanographic pattern of the equatorial Atlantic Ocean (Hu et al., 2004; Coles et al., 2013). In terms of its biota and ecology, this is a poorly known area, despite its worldwide oceanographic importance (Miloslavich et al., 2011). Recently, a large mesophotic reef system discovered in the region calls attention to its ecological significance, given its unique formation and size (Moura et al., 2016; Francini-Filho et al., 2018). The northern area of the reef formation, as well as adjacent northern areas in Suriname, are regions undergoing current prospecting by the oil and gas industry (Willems et al., 2017; Francini-Filho et al., 2018), which causes concerns due to potential environmental issues. Due to the lack of information on seabird distributions in northern Brazil, in this study, we aim to describe the seabird assemblage associated with the Amazon River mouth and its adjacent areas, serving as a baseline for future studies in the region. Identifying relationships between ecological groups and environmental characteristics, we also call attention to two distinct areas of ecological importance for different assemblages that are potentially important to other marine taxa.

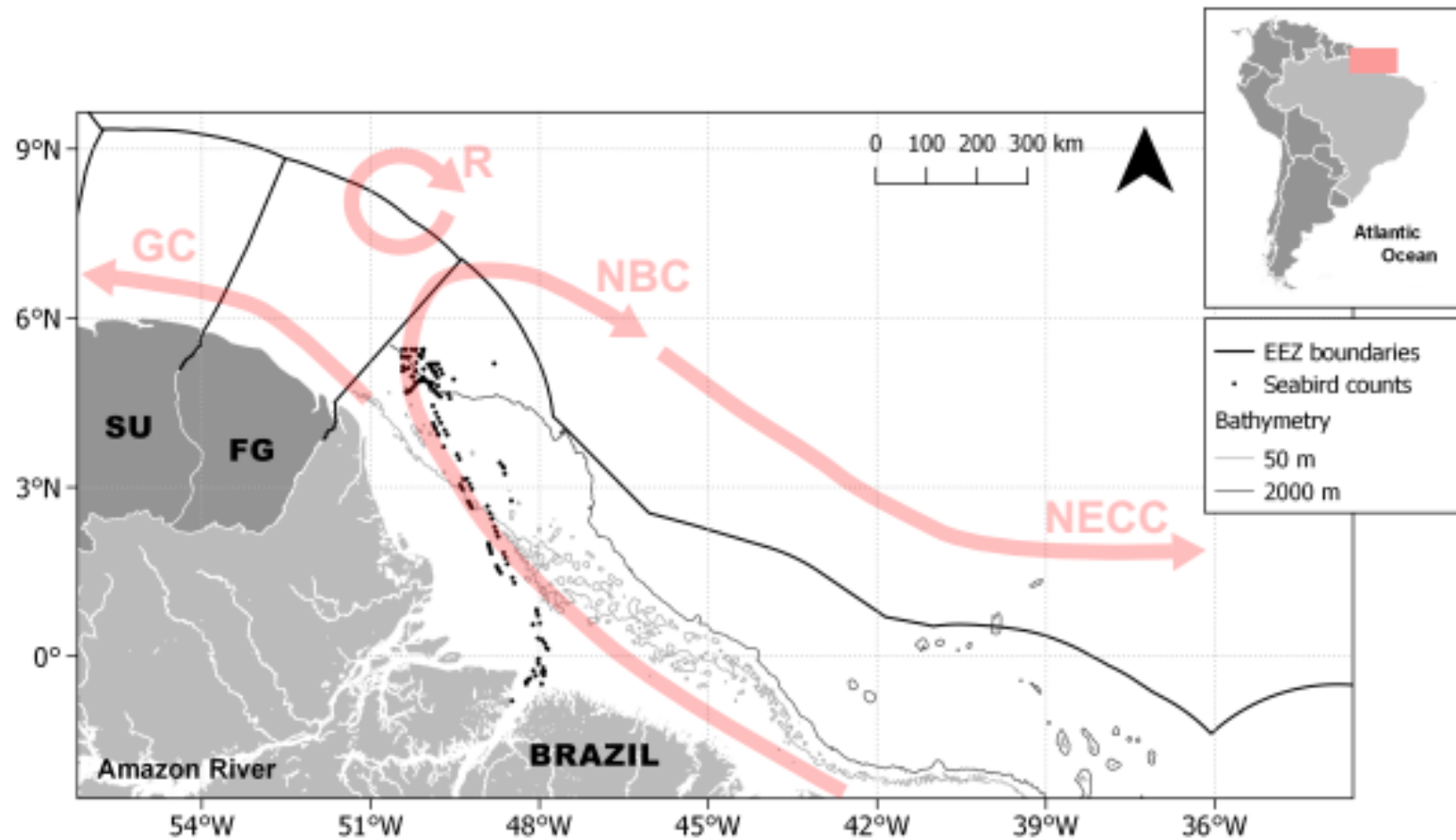
## 2. Methods

### 2.1. Study area and oceanographic characteristics



Two cruises were carried out from 27 March to 14 April, and from 23 April to 01 May 2015 onboard the F.P.V. *Jean Charcot*. Bird counts occurred between 5°26.753'N–0°02.391'S and 47°51.054'–59°57.179'W alongside the mouth of the Amazon River (Fig. 1). Transects encompassed shallow waters from ~10 m depth to offshore waters at ~3100 m depth. Two count methods were used: navigation counts while the vessel was underway, and point counts while the vessel was stationary (see section 2.2. *Seabird counts*).

The Amazon River is the largest river in the world, with a discharge of approximately  $6 \times 10^{12} \text{ m}^3/\text{year}$  of freshwater into the tropical Atlantic Ocean (Gibbs, 1967). Adjacent to the mouth of the Amazon River, the region is governed by the North Brazil Current (NBC), which flows northward to the Caribbean Sea (Bourlès et al., 1999a) through the coastal Guiana Current (GC). Near 5–10°N, the NBC retroflexes (inverts) and mixes into the North Equatorial Countercurrent (NECC), which flows eastward (Bourlès et al., 1999b; Silva et al., 2009). Shedding from the retroflexion, eddies build and drift north-northwest to the Caribbean Sea (Fratantoni et al., 1995; Bourlès et al., 1999b; Ffield, 2005). At least 2–3 rings are formed annually by this process, each of them transporting ~1 Sv (i.e.,  $10^6 \text{ m}^3/\text{s}$ ) of water, playing an important role in mass transport of Amazonian water across the equatorial-tropical gyre boundary (Fratantoni et al., 1995; Ffield, 2005; Silva et al., 2009).



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133 **Fig. 1.** Study area in northern Brazil (light grey) along the mouth of the Amazon River, with dots representing seabird counts (N = 219). A schematic  
 134 diagram of the main surface currents and the zone of ring formations (R) are given (adapted from Bourlès et al., 1999b): GC = Guiana Current;  
 135 NBC = North Brazil Current; NECC = North Equatorial Counter Current. In darker grey, South America, with SU = Suriname and FG = French  
 136 Guiana. EEZ = Exclusive Economic Zone. (2-column fitting image)

## 2.2. Seabird counts

Sampling techniques varied by ship activity, i.e., during vessel navigation and at oceanographic stations. First, during navigation to reach the northern area near French Guiana, bird censuses were carried out following Tasker et al. (1984), adapted by Neves et al. (2006). This included snapshot and continuous counts of all birds at a given distance from the vessel, after recording apart the ship-attending birds. The method involves counting birds that have typical ship-following behaviours, such as crossing the bow or flying in circles. Some birds even follow at a distance of up to 700 m from the ship; they commonly stay in the ship trail. This minimizes recounts of flying birds by identifying and counting them. Birds assigned as ship-followers were not counted nor included in the subsequent continuous and snapshot methods. Then, birds were recorded as stated by Tasker et al. (1984) by a continuous count of 10 min, followed by 10 snapshot counts one minute apart, in a 300-m strip. All birds on the water and in flight were recorded.

Second, in the northern area, the ship operated at several oceanographic stations, collecting physico-chemical data. Therefore, without continuous velocity and no fixed heading, the methods described by Tasker et al. (1984) could not be used. Thus, birds were recorded at 1 h intervals, limited by a 300-m band around the vessel; birds on the water and in flight were counted, avoiding recounts as much as possible. More than an hour of activities occurred at some stations, so each one-hour counting represented a new sampling period. Hereafter, we refer to this count method as point counts.

These methods were used in different areas; the first was during ship navigation, while point counts were used in the northern region. The two methods are not directly comparable, although available bird species and their environmental associations should be equivalent. To support bird identification, two guides were consulted (Harrison, 1985; Onley and Scofield, 2007). Photographic records of the seabirds were made with a Nikon 7300 camera, Nikkor 70–400 mm lenses, and verified in the lab; photographs were also sent to experts when necessary.

Position and weather data were recorded at the beginning of each count, i.e., date, geographic coordinates, hour, cloud cover, sea state (on the Beaufort scale), and wind speed and direction. Censuses with a Beaufort value  $> 5$  were not used in the subsequent analyses. The 300-m strips/band were calculated using the equations described by Heinemann (1981).

## 2.3. Oceanographic and physiographic variables

The environmental data used were sea surface temperature (°C; SST), sea surface salinity (SSS), wind direction (in degrees; WD) and intensity (m/s; WI), chlorophyll-*a* (mg of carbon/m<sup>3</sup>; CHL), bathymetry (meters; BAT), and distance from the coast (km; DIST). Data were obtained from open-access global source data, such as the HYbrid Coordinate Ocean Model (HYCOM – <https://hycom.org/>) for SST and SSS; for wind parameters, we used the European Centre for Medium-Range Weather Forecasts Re-Analysis (ERA-INTERIM-ECMWF – <https://www.ecmwf.int/>); chlorophyll-*a* data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua – <https://oceancolor.gsfc.nasa.gov/data/aqua/>); bathymetry data were obtained from the General Bathymetric Chart of the Oceans (GEBCO – <https://www.gebco.net>). The distance from the coast was calculated for each sample unit based on the minimum distance from the continental shoreline. Data were downloaded according to the proximate hour of the day associated with each sample and then interpolated in a 1000 × 1000 grid between 8.01°N–4.78°S and 43.26°W–52.71°W, ensuring a spatial resolution of 0.001° in longitude and 0.013° in latitude. Next, the most proximal value available for the sample unit was extracted with a nearest neighbour filter. These routines were carried out in MATLAB R2016b software.

#### 2.4. Data analysis

Descriptive statistics were calculated according to the minimum and maximum numbers, mean, mean density (birds/km<sup>2</sup>), and frequencies of occurrence for each species. Counts of ship followers and point counts did not have a fixed sampling area; therefore, we used mean values only. For subsequent analysis, sample units were considered the continuous counts during navigation. The taxonomic arrangement follows Piacentini et al. (2015).

Birds were grouped based on phylogenetic proximity, which also encompasses similar ecological traits, as follows: shearwaters, Procellariidae (*Puffinus* + *Calonectris*); storm-petrels, Hydrobatidae (*Oceanodroma* + *Oceanites*); skuas and jaegers, Stercorariidae (*Stercorarius*); gulls, Laridae (*Leucophaeus*); terns, Sternidae (*Sterna*). Cabot's Terns *Thalasseus acutiflavus* and Large-billed Terns *Phaetusa simplex* were not included in the Sternidae group due to their ecological differences (Goshfeld and Burger, 1996) and limited sampling.

To address seabird-environment associations and to cope with many zeros in the dataset, we performed two-part multiple linear regressions, which are analogous to hurdle

models (Zeileis et al., 2008). As a first step, we modelled the zero-part (i.e., the occurrence of seabird groups) based on binomial generalized linear models (GLMs) and a dataset of presence/absence matrices; then, we modelled the count-part (i.e., the abundance of seabird groups) based on a Poisson distribution with a zero-truncated dataset (Zeileis et al., 2008). Model fit was visually assessed with Quantile-Quantile plots and rootogram; the latter compares observed and expected values graphically, with observed values as bars (like those of histograms) and expected values as a curve (Kleiber and Zeileis, 2016). We also assessed the relationships between birds and their environment based on a multivariate approach through canonical correspondence analysis (CCA), which provides an ordination and ranks the influence of environmental parameters in the biological matrix (Legendre and Legendre, 1998; Quinn and Keough, 2002). This analysis helps to visualize the interactions between the seabird assemblages and environmental characteristics. The significance of the axes and explanatory variables in the CCA was assessed using ANOVA, with 99 permutations.

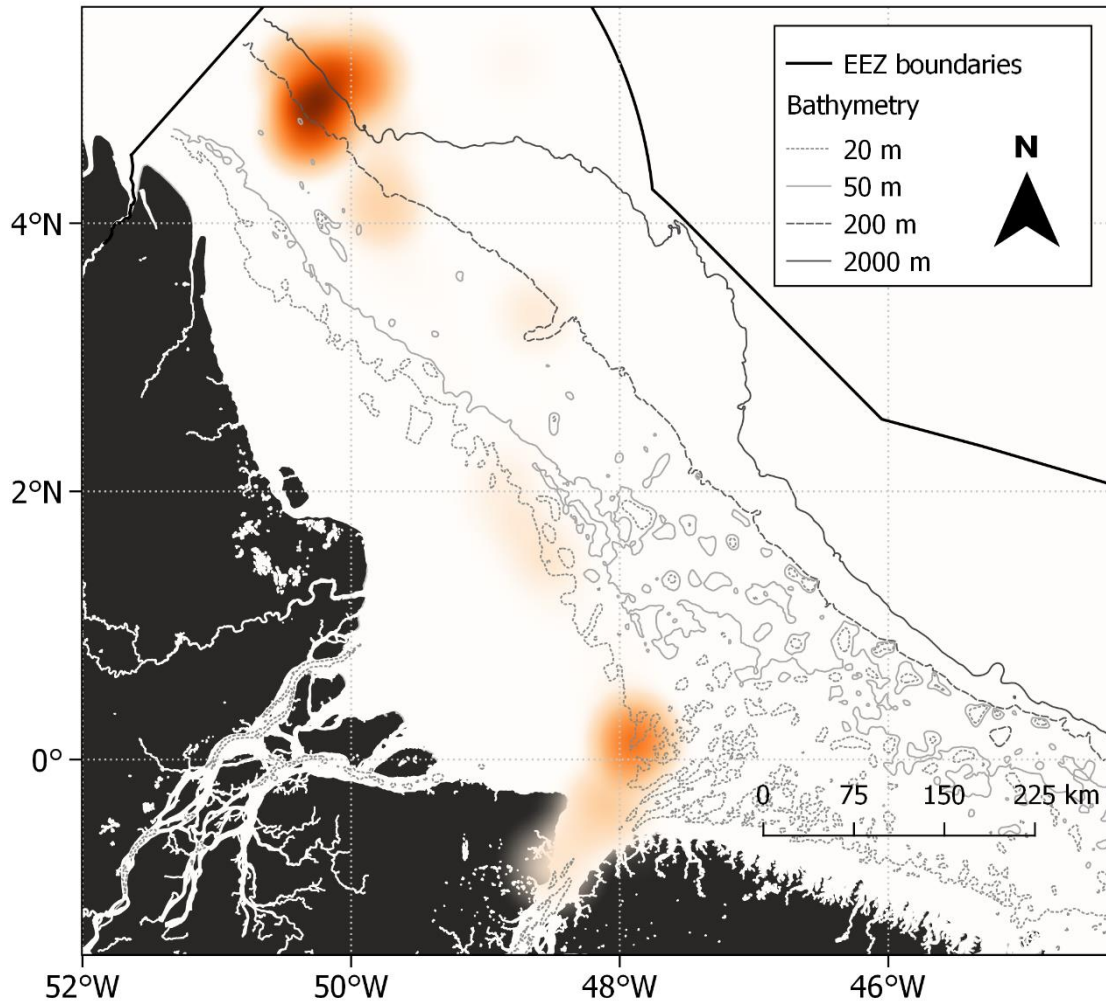
The environmental data were used as explanatory variables and bird counts as the response variable (absolute count) for grouped taxa in both analyses. The explanatory variables were selected after checking that they met assumptions of collinearity (Zuur et al., 2010). Therefore, we excluded SSS due to its high correlation with DIST and CHL ( $r > 0.5$ ). All data from wind direction were from northeast to southwest (giving no variability), so the explanatory power of this variable would have been minimal; accordingly, we excluded it and wind intensity, as these variables are likely to interact and have effects on bird abundance/distribution. The variance inflation factor (VIF) was low between the environmental variables, but, as a precaution, for the univariate linear models, we excluded DIST (VIF = 12.3) to ensure that the VIF values were  $< 3$ .

All statistical analyses were carried out in R v. 3.4.2 (R Core Team, 2017) with the packages ‘vegan’ 2.5-2 (Oksanen et al., 2018) and ‘countreg’ 0.2-0 (Zeileis and Kleiber, 2018). Spatial plots were created in QGIS 2.18.7 (QGIS Development Team, 2018). The R code used here are available in the Supplementary Material (S1).

### 3. Results

Seabird counts were collected for 27 days and represented c. 148 h of sampling effort, totalling in 219 counts: 118 during navigation and 101 point counts. Continuous

counts covered an area of 74.5 km<sup>2</sup>, whereas snapshot counts covered 166.7 km<sup>2</sup>. Spatially, a high abundance of seabirds occurred in Brazil's northern limit of the Economic Exclusive Zone, between the isobaths of 200 and 2000 m depth, followed by the coastal area adjacent to the Amazon River mouth < 20 m depth (Fig. 2).

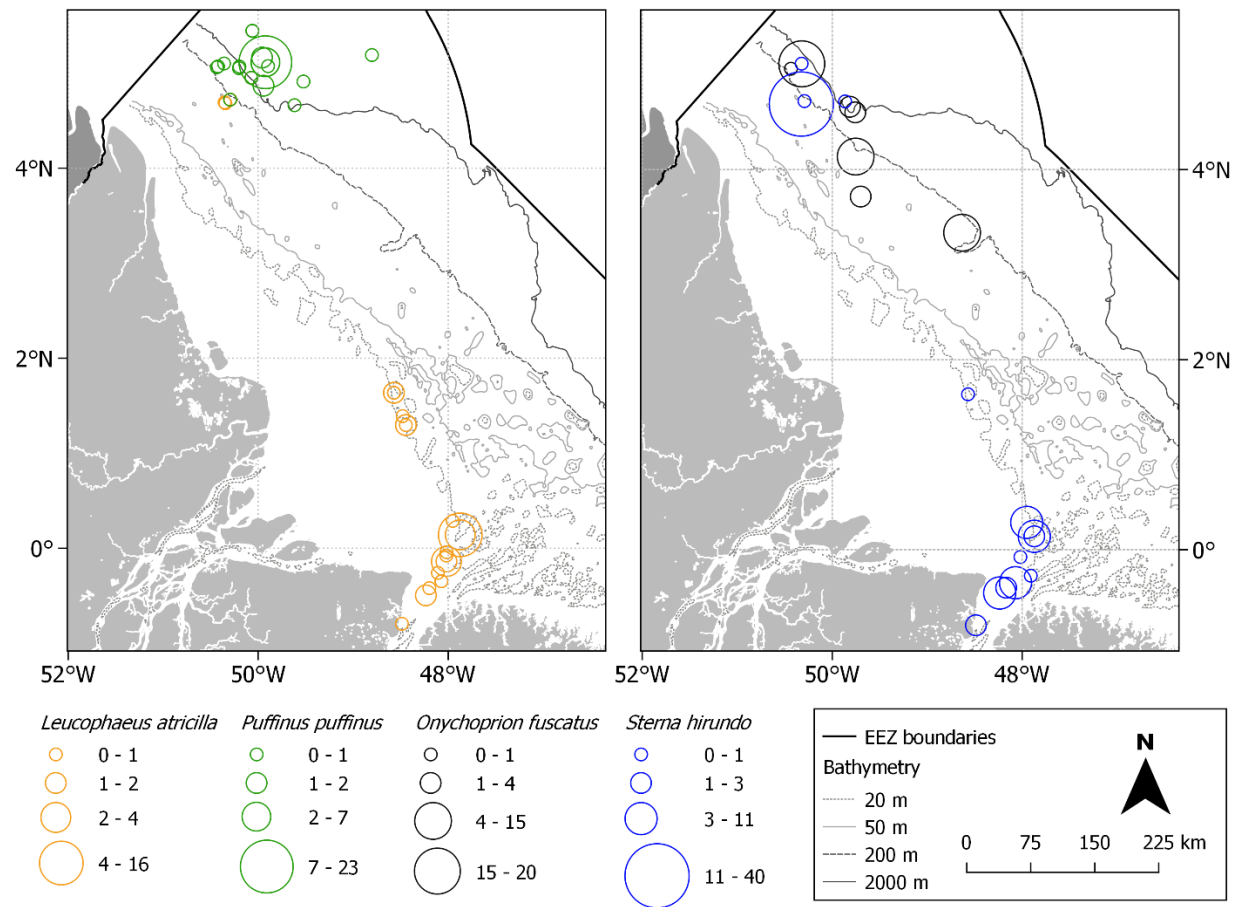


**Fig. 2.** Heatmap of all seabird records according to total count numbers, exhibiting two areas of aggregation, along the mouth of the Amazon River, Brazil, in March–May 2015. (1.5-column fitting image)

### 3.1. Seabird assemblage

A total of 443 birds from 8 families and 21 species (Table 1) were recorded. During the ship-follower and point-count methods, the numbers of birds and species richness were similar (129 and 175 birds; 20 and 17 species, respectively). Likewise, the continuous and snapshot count records of birds and richness were also similar (69 and 70 birds; nine species each, respectively) (Table 1).

Notably, four species accounted for 54% of all records: Common Tern *Sterna hirundo* (n = 80), Sooty Tern *Onychoprion fuscatus* (n = 54), Manx Shearwater *Puffinus puffinus* (n = 52) and Laughing Gull *Leucophaeus atricilla* (n = 52). These species had at least one point of occurrence with more than 15 birds in a flock, reflecting their apparent dominance when compared to other species (Fig. 3). However, such a result does not reflect directly on the frequencies of occurrences, as Wilson's Storm-Petrel *Oceanites oceanicus* was one of the most frequent species in three different types of counts (ship-followers, continuous and snapshot). Four other species were the most frequent in the point counts (*Oceanodroma leucohoa*, *Fregata magnificent*, *Stercorarius skua*, and *Phaetusa simplex*), while *Numenius hudsonicus*, *Stercorarius parasiticus*, *Thalasseus acuflavidus*, and *Sula sula* had fewer than three records (Table 1).



266

267 **Fig. 3.** Laughing Gull *Leucophaeus atricilla*, Manx Shearwater *Puffinus puffinus*, Sooty Tern *Onychoprion fuscatus*, and Common Tern *Sterna*  
 268 *hirundo* distributions along the mouth of the Amazon River, Brazil, in March–May 2015. Records based on all count methods are included.

269 (2-column fitting image)



**Table 1.** Summary of seabird assemblage data from northern Brazil, along the mouth of the Amazon River, in March–May 2015. Data are presented for the four different count methods. For each species, the maximum, total and mean number per count method is given. Density (birds/km<sup>2</sup>) is computed for continuous and snapshot counts, which have an associated defined area. The minimum count for all species across all count methods was zero. Therefore, these values are not shown. FO = frequency of occurrence (%); N = sample size, n = number of birds counted.

| Count-method                | Navigating (N = 118) |    |        |      |                   |   |        |         |      |                 |    |        |         |      | Stations (N = 101) |   |        |      | Total |
|-----------------------------|----------------------|----|--------|------|-------------------|---|--------|---------|------|-----------------|----|--------|---------|------|--------------------|---|--------|------|-------|
|                             | Ship followers       |    |        |      | Continuous counts |   |        |         |      | Snapshot counts |    |        |         |      | Point counts       |   |        |      |       |
| Taxon                       | Max                  | n  | Mean   | FO%  | Max               | n | Mean   | Density | FO % | Max             | n  | Mean   | Density | FO % | Max                | n | Mean   | FO % |       |
| Procellariiformes           |                      |    |        |      |                   |   |        |         |      |                 |    |        |         |      |                    |   |        |      |       |
| Procellariidae              |                      |    |        |      |                   |   |        |         |      |                 |    |        |         |      |                    |   |        |      |       |
| (shearwaters)               |                      |    |        |      |                   |   |        |         |      |                 |    |        |         |      |                    |   |        |      |       |
| <i>Calonectris borealis</i> | 1                    | 2  | 0.0169 | 1.69 | 2                 | 2 | 0.0169 | 0.0268  | 0.85 | 1               | 1  | 0.0008 | 0.0060  | 0.85 | 1                  | 1 | 0.0099 | 0.99 | 6     |
| <i>Puffinus puffinus</i>    | 5                    | 11 | 0.0932 | 5.93 | 7                 | 9 | 0.0763 | 0.1208  | 1.69 | 23              | 24 | 0.0203 | 0.1439  | 1.69 | 2                  | 8 | 0.0792 | 6.93 | 52    |
| <i>Puffinus</i> sp.         | 0                    | 0  | 0      | 0    | 1                 | 1 | 0.0085 | 0.0134  | 0.85 | 0               | 0  | 0      | 0       | 0    | 1                  | 1 | 0.0099 | 0.99 | 2     |
| Hydrobatidae                |                      |    |        |      |                   |   |        |         |      |                 |    |        |         |      |                    |   |        |      |       |
| (storm-petrels)             |                      |    |        |      |                   |   |        |         |      |                 |    |        |         |      |                    |   |        |      |       |
| Hydrobatidae                | 0                    | 0  | 0      | 0    | 0                 | 0 | 0      | 0       | 0    | 1               | 1  | 0.0008 | 0.0060  | 0.85 | 1                  | 1 | 0.0099 | 0.99 | 2     |
| <i>Oceanites oceanicus</i>  | 2                    | 8  | 0.0678 | 5.93 | 1                 | 5 | 0.0424 | 0.0671  | 4.24 | 3               | 5  | 0.0042 | 0.0300  | 2.54 | 1                  | 2 | 0.0198 | 1.98 | 20    |

|                                    |   |   |        |      |   |   |        |        |      |   |   |        |        |      |   |    |        |      |    |
|------------------------------------|---|---|--------|------|---|---|--------|--------|------|---|---|--------|--------|------|---|----|--------|------|----|
| <i>Oceanodroma leucorhoa</i>       | 1 | 2 | 0.0169 | 1.69 | 1 | 2 | 0.0169 | 0.0268 | 1.69 | 1 | 3 | 0.0025 | 0.0180 | 2.54 | 2 | 9  | 0.0891 | 7.92 | 16 |
| <b>Suliformes</b>                  |   |   |        |      |   |   |        |        |      |   |   |        |        |      |   |    |        |      |    |
| Fregatidae (frigatebirds)          |   |   |        |      |   |   |        |        |      |   |   |        |        |      |   |    |        |      |    |
| <i>Fregata magnificens</i>         | 1 | 3 | 0.0254 | 2.54 | 0 | 0 | 0      | 0      | 0    | 1 | 2 | 0.0017 | 0.0120 | 1.69 | 2 | 11 | 0.1089 | 8.91 | 16 |
| Sulidae (boobies)                  |   |   |        |      |   |   |        |        |      |   |   |        |        |      |   |    |        |      |    |
| <i>Sula dactylatra</i>             | 1 | 6 | 0.0508 | 5.08 | 0 | 0 | 0      | 0      | 0    | 0 | 0 | 0      | 0      | 0    | 0 | 0  | 0      | 0    | 6  |
| <i>Sula sula</i>                   | 1 | 1 | 0.0085 | 0.85 | 0 | 0 | 0      | 0      | 0    | 0 | 0 | 0      | 0      | 0    | 0 | 0  | 0      | 0    | 1  |
| <b>Charadriiformes</b>             |   |   |        |      |   |   |        |        |      |   |   |        |        |      |   |    |        |      |    |
| Scolopacidae (curlew)              |   |   |        |      |   |   |        |        |      |   |   |        |        |      |   |    |        |      |    |
| <i>Numenius hudsonicus</i>         | 1 | 1 | 0.0085 | 0.85 | 0 | 0 | 0      | 0      | 0    | 0 | 0 | 0      | 0      | 0    | 1 | 2  | 0.0198 | 1.98 | 3  |
| Stercorariidae (skuas and jaegers) |   |   |        |      |   |   |        |        |      |   |   |        |        |      |   |    |        |      |    |
| <i>Stercorarius skua</i>           | 1 | 1 | 0.0085 | 0.85 | 0 | 0 | 0      | 0      | 0    | 0 | 0 | 0      | 0      | 0    | 1 | 10 | 0.0990 | 9.90 | 11 |
| <i>Stercorarius pomarinus</i>      | 1 | 1 | 0.0085 | 0.85 | 0 | 0 | 0      | 0      | 0    | 0 | 0 | 0      | 0      | 0    | 3 | 7  | 0.0693 | 3.96 | 8  |

|                                 |    |    |            |      |    |        |            |        |      |    |    |            |        |      |    |    |        |           |    |
|---------------------------------|----|----|------------|------|----|--------|------------|--------|------|----|----|------------|--------|------|----|----|--------|-----------|----|
| <i>Stercorarius parasiticus</i> | 0  | 0  | 0          | 0    | 1  | 1      | 0.008<br>5 | 0.0134 | 0.85 | 0  | 0  | 0          | 0      | 0    | 1  | 2  | 0.0198 | 1.98      | 3  |
| <i>Stercorarius longicaudus</i> | 4  | 6  | 0.050<br>8 | 2.54 | 0  | 0      | 0          | 0      | 0    | 1  | 2  | 0.001<br>7 | 0.0120 | 1.69 | 1  | 1  | 0.0099 | 0.99      | 9  |
| <i>Stercorarius</i> sp.         | 1  | 1  | 0.008<br>5 | 0.85 | 2  | 5      | 0.042<br>4 | 0.0671 | 3.39 | 0  | 0  | 0          | 0      | 0    | 3  | 5  | 0.0495 | 2.97      | 11 |
| Laridae (gulls)                 |    |    |            |      |    |        |            |        |      |    |    |            |        |      |    |    |        |           |    |
| <i>Leucophaeus atricilla</i>    | 4  | 17 | 0.144<br>1 | 6.78 | 16 | 2<br>3 | 0.194<br>9 | 0.3087 | 5.93 | 3  | 8  | 0.006<br>8 | 0.0480 | 3.39 | 1  | 4  | 0.0396 | 3.96      | 52 |
| Sternidae (terns)               |    |    |            |      |    |        |            |        |      |    |    |            |        |      |    |    |        |           |    |
| <i>Anous stolidus</i>           | 1  | 2  | 0.016<br>9 | 1.69 | 0  | 0      | 0          | 0      | 0    | 0  | 0  | 0          | 0      | 0    | 1  | 5  | 0.0495 | 4.95      | 7  |
| <i>Onychoprion fuscatus</i>     | 15 | 17 | 0.144<br>1 | 1.69 | 0  | 0      | 0          | 0      | 0    | 4  | 6  | 0.005<br>0 | 0.3598 | 1.69 | 20 | 31 | 0.3069 | 2.97      | 54 |
| <i>Phaetusa simplex</i>         | 0  | 0  | 0          | 0    | 9  | 9      | 0.076<br>3 | 0.1208 | 0.85 | 0  | 0  | 0          | 0      | 0    | 6  | 22 | 0.2178 | 10.8<br>9 | 31 |
| <i>Sterna hirundo</i>           | 11 | 30 | 0.254<br>2 | 5.08 | 3  | 5      | 0.042<br>4 | 0.0671 | 1.69 | 1  | 3  | 0.002<br>5 | 0.0180 | 2.54 | 40 | 42 | 0.4158 | 2.97      | 80 |
| <i>Sterna dougalli</i>          | 1  | 1  | 0.008<br>5 | 0.85 | 0  | 0      | 0          | 0      | 0    | 0  | 0  | 0          | 0      | 0    | 7  | 7  | 0.0693 | 0.99      | 8  |
| <i>Sterna paradisaea</i>        | 3  | 3  | 0.025<br>4 | 0.85 | 0  | 0      | 0          | 0      | 0    | 0  | 0  | 0          | 0      | 0    | 1  | 2  | 0.0198 | 1.98      | 5  |
| <i>Sterna</i> sp.               | 1  | 3  | 0.025<br>4 | 2.54 | 2  | 5      | 0.042<br>4 | 0.0671 | 2.54 | 15 | 15 | 0.012<br>7 | 0.0900 | 0.85 | 2  | 2  | 0.0198 | 0.99      | 25 |

|                         |   |     |        |      |   |   |        |        |      |   |    |   |   |   |   |     |   |   |     |
|-------------------------|---|-----|--------|------|---|---|--------|--------|------|---|----|---|---|---|---|-----|---|---|-----|
| <i>Thalasseus</i>       |   |     |        |      |   |   |        |        |      |   |    |   |   |   |   |     |   |   |     |
| <i>acuflavidus</i>      | 1 | 1   | 0.0085 | 0.85 | 1 | 2 | 0.0169 | 0.0268 | 1.69 | 0 | 0  | 0 | 0 | 0 | 0 | 0   | 0 | 0 | 3   |
| <i>Thalasseus</i>       |   |     |        |      |   |   |        |        |      |   |    |   |   |   |   |     |   |   |     |
| <i>maximus</i>          | 7 | 12  | 0.1017 | 2.54 | 0 | 0 | 0      | 0      | 0    | 0 | 0  | 0 | 0 | 0 | 0 | 0   | 0 | 0 | 12  |
|                         |   |     |        |      |   | 6 |        |        |      |   |    |   |   |   |   |     |   |   |     |
| <b>Total</b>            |   | 129 |        |      |   | 9 |        |        |      |   | 70 |   |   |   |   | 175 |   |   | 443 |
| <b>Species richness</b> |   | 20  |        |      |   | 9 |        |        |      |   | 9  |   |   |   |   | 17  |   |   | 21  |

### 3.2. Seabird-environmental relationships

According to the univariate multiple regression approach, the zero-part of the models points to the importance of cooler SSTs (negative estimators) for three groups: Procellariidae, Laridae, and Sternidae (Table 2). Although the model estimators were low, this result may indicate that these groups associate with different water edges, which influence the chlorophyll-*a* levels, also a significant parameter for Sternidae. Effects of SST and CHL were additionally identified in the count-models for Stercorariidae, Laridae and Sternidae, with negative estimates for SST and positive estimates for CHL, even though they reached statistical significance only for Laridae (Table 2). However, some models with good mathematical fit had unreliable estimates, such as for Procellariidae, or had large standard errors, e.g., for Stercorariidae, likely due to the low amount of available data, which were fit using zero-truncated GLMs, and thus interpretation should be undertaken with caution. For Hydrobatidae, the count-model did not fit.

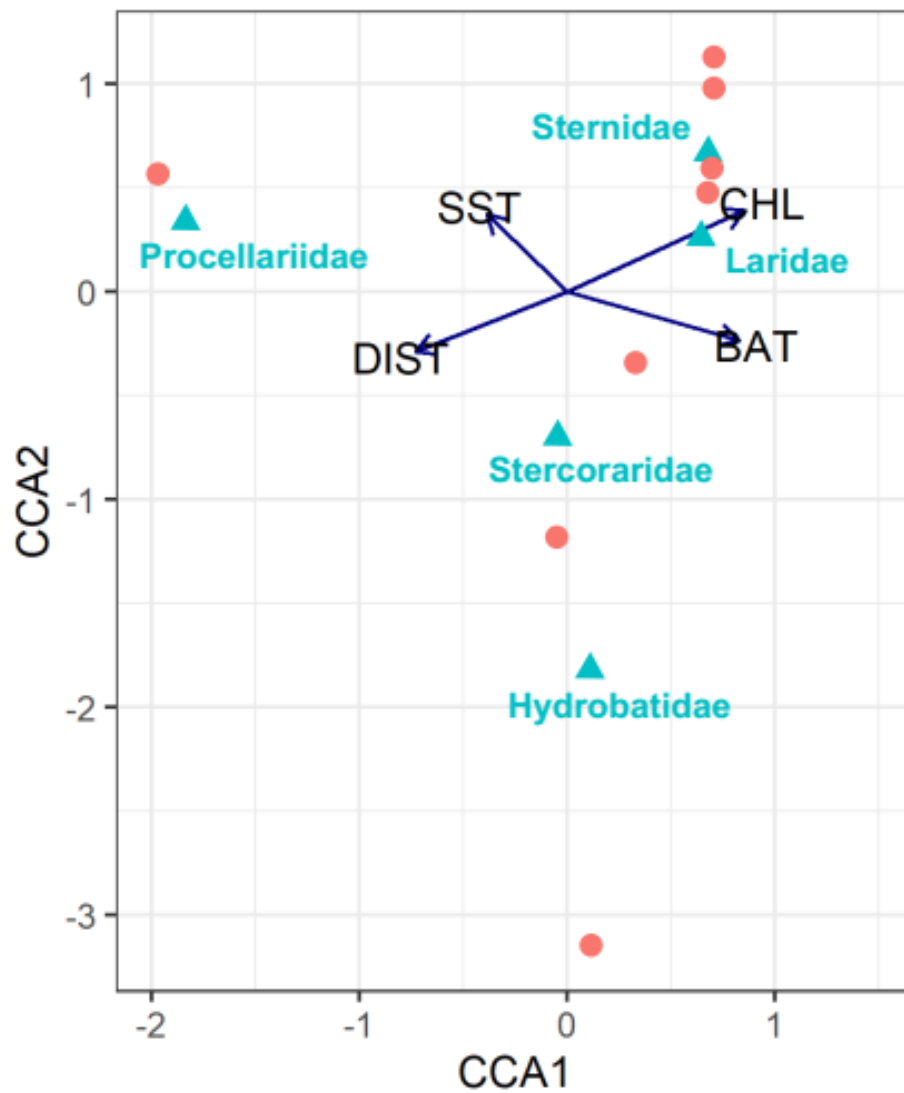
The two principal CCA axes were statistically significant (CCA1,  $F = 10.05$ ,  $p = 0.01$ ; CCA2,  $F = 6.21$ ,  $p = 0.01$ ), while the other two axes were non significant. All variables were significant in terms of building the axes (DIST,  $F = 6.06$ ,  $p = 0.01$ ; BAT,  $F = 5.16$ ,  $p = 0.01$ ; CHL,  $F = 3.39$ ,  $p = 0.03$ ; SST,  $F = 3.03$ ,  $p = 0.03$ ). The CCA indicated a similar pattern to the GLM models, with Procellariidae associated with SST and DIST; DIST was also important for Hydrobatidae, as they were frequently recorded near the 20-m isobaths. Laridae and Sternidae, were associated most highly with CHL and BAT (Fig. 4). Maps with records of the continuous counts for both Procellariiformes and Charadriiformes demonstrated distinct patterns of occupancy, with the former concentrated in the northern areas, whereas the latter occurred mostly near the mouth of the Amazon River (Fig. 5). This reinforces, spatially, the results from the CCA.

**Table 2.** Summary of the two-part regression models, grouped by seabird families. Full models are presented ( $y \sim \text{SST} + \text{CHL} + [\text{BAT}*(-1)]$ ) to represent the importance of each explanatory variable for each family. SST = sea surface temperature; CHL = chlorophyll-*a*; BAT = bathymetry; SE = standard error.

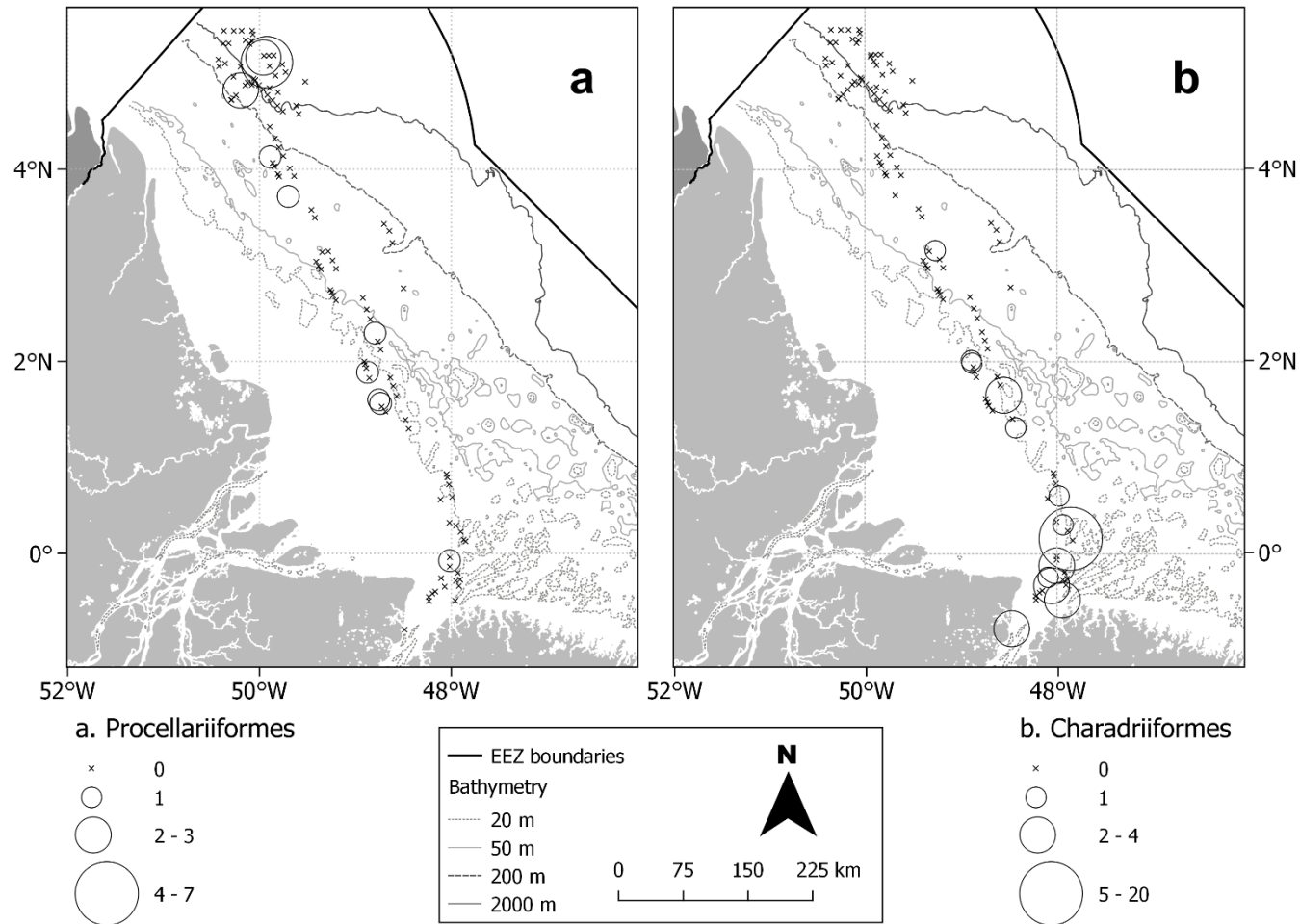
|                       | Zero-part            |                 | Count-part           |                 |
|-----------------------|----------------------|-----------------|----------------------|-----------------|
|                       | Estimate $\pm$ SE    | <i>p</i> -value | Estimate $\pm$ SE    | <i>p</i> -value |
| <b>Procellariidae</b> |                      |                 |                      |                 |
| SST                   | -0.117 $\pm$ 0.063   | 0.063           | -6.490 $\pm$ NA      | NA              |
| CHL                   | -1.037 $\pm$ 2.393   | 0.665           | 342.366 $\pm$ 0.705  | <0.001***       |
| BAT                   | -0.0003 $\pm$ 0.0006 | 0.627           | -0.056 $\pm$ NA      | NA              |
| <b>Hydrobatidae</b>   |                      |                 |                      |                 |
| SST                   | 0.003 $\pm$ 0.048    | 0.935           | n.f.                 | n.f.            |
| CHL                   | -0.183 $\pm$ 0.117   | 0.118           | n.f.                 | n.f.            |
| BAT                   | 0.028 $\pm$ 0.018    | 0.129           | n.f.                 | n.f.            |
| <b>Stercorariidae</b> |                      |                 |                      |                 |
| SST                   | 0.013 $\pm$ 0.057    | 0.809           | -0.565 $\pm$ 232.273 | 0.998           |
| CHL                   | -0.202 $\pm$ 0.133   | 0.129           | 2.037 $\pm$ 113.363  | 0.986           |
| BAT                   | 0.043 $\pm$ 0.026    | 0.096           | 0.658 $\pm$ 488.841  | 0.999           |
| <b>Laridae</b>        |                      |                 |                      |                 |
| SST                   | -0.149 $\pm$ 0.087   | 0.089           | -0.591 $\pm$ 0.186   | 0.001**         |
| CHL                   | 0.231 $\pm$ 0.149    | 0.121           | 0.662 $\pm$ 0.221    | 0.002**         |
| BAT                   | 0.016 $\pm$ 0.044    | 0.705           | -0.418 $\pm$ 0.107   | <0.001***       |
| <b>Sternidae</b>      |                      |                 |                      |                 |
| SST                   | -0.433 $\pm$ 0.203   | 0.033*          | -0.765 $\pm$ 0.636   | 0.229           |
| CHL                   | 0.724 $\pm$ 0.386    | 0.060           | 0.984 $\pm$ 0.798    | 0.218           |
| BAT                   | -0.001 $\pm$ 0.005   | 0.810           | -0.390 $\pm$ 0.296   | 0.188           |

*p*-values = '\*\*\*' 0.001 - '\*\*' 0.01 - '\*' 0.05

n.f. = no fit.



**Fig. 4.** Canonical correspondence analysis of seabird-environmental relationships from the data from two cruises in the mouth of the Amazon River, Brazil, in March–May 2015. Data represent scores of families of seabirds (triangles) and scores of environmental variables (arrows).



314

315 **Fig. 5.** Procellariiformes (a; Procellariidae + Hydrobatidae) and Charadriiformes (b; Stercorariidae + Laridae + Sternidae) distribution along the  
 316 mouth of the Amazon River, Brazil, in March–May 2015. Only records from the continuous count method are included. (2-column fitting  
 317 image)



#### 4. Discussion

This is the first study describing the at-sea seabird assemblages adjacent to the mouth of the world's largest river, demonstrating high species richness at the Amazon River delta in northern Brazil. The species compositions were similar to those described for Suriname, being composed mainly of migratory species (de Boer et al., 2014; Willems et al., 2017). Procellariiformes, and Stercorariidae and Scolopaciidae (Charadriiformes) are all migrants from the Southern and Northern Hemispheres (Harrison, 1985). The recorded Suliformes can be both from islands off north-eastern Brazil or from the Caribbean Sea (Harrison, 1985); however, *Sula* are likely from the Caribbean, as they do not disperse widely, while *Fregata* can be from either location. On the other hand, Sternidae are both resident (e.g., Large-billed Terns, which breed on sand banks in Amazonian rivers or the coast) and migratory (e.g., Common Tern *Sterna hirundo*); Laughing Gulls (Laridae) are also migrants from the Northern Hemisphere (Harrison, 1985).

Seabirds recorded along the mouth of the Amazon River have low frequencies of occurrence and lower densities than other areas. This might be due to their distinct species composition, with approximately 18 out of 21 species being migrants. Indeed, northern Brazil serves as a pathway for many transequatorial migrants, including pelagic (such as shearwaters and skuas) and coastal (terns and gulls) species (Guilford et al., 2009; Mostello et al., 2014; Neves et al., 2015; van Bemmelen et al., 2017; Pollet et al., 2019). Low density of seabirds is expected for tropical waters, like in Pacific and Indian Oceans (Ribic et al., 1997; Jaquemet et al., 2004), as the composition of tropical seabird assemblages is usually based on species breeding on nearby lands (Jaquemet et al., 2004; Ballance et al., 2006). The recorded coastal seabirds, mainly terns, commonly feed at sea and roost on the coast, being able to feed more than once a day (Bugoni et al., 2005).

Spatially, two seabird aggregation sites were noted. In patchy environments, this likely indicates potential feeding zones (e.g., Davoren, 2013). Oceanographically, these two areas have their own singularities, pointing to important ecological features in each one. The surveyed northern area is where the NBC retroflects into the NECC, generating the starting point of ring development (Bourlès et al., 1999b; Ffield, 2005). The edges of these rings have Amazon water, which is fresher, more nutrient-rich and warmer than the NBC water, entrapped in the ring (Ffield, 2005). In the same way, but through different physical processes, the discharge at the mouth of the Amazon River produces a suitable foraging area for seabirds. River discharges influence the vertical turbulence at the

boundaries of their plume and the edge of the salt-water mass (Largier, 1993); this frontal zone causes mixture that influence physical and biological processes (Largier, 1993; Karati et al., 2018). The position, extent and intensification of the Amazon River salinity front is driven by its discharge, amount of suspended sediment in the water column, and tidal processes (Geyer, 1995). The bottom saline front extends ahead of the mouth of the Amazon River to between the isobaths of 10 and 20 m, where it supports strong frontogenesis (Geyer, 1995). As a result, the bottom-up process in the trophic chain creates dynamic opportunities for seabird feeding (Cox et al., 2013; Scales et al., 2014b; Phillips et al., 2018).

Seabirds are known to be associated with eddies, shelf-fronts, and river plumes (Scales et al., 2014b; Cox et al., 2016; Phillips et al., 2018), and the two areas of aggregation shown here seem to attract seabirds through the coupling of physical and biological processes. Procellariiforms, which comprise the majority of birds in the northern region, are known to be associated with mesoscale features (100–1000 km scale, Weimerskirch, 2007; Phillips et al., 2018). As they are predominantly oceanic, not surprisingly, they are concentrated in this area off the 200-m isobath, near the NBC retroflexion, which is supported by the CCA results that show association with sea surface temperature (SST) and distance from the coast (DIST) for Procellariidae. However, some Hydrobatidae were recorded on the border of the 20-m isobath. In that region, tidal processes appear to sustain conditions for the accumulation of zooplankton (see Geyer, 1995; Santos et al., 2008), possibly through the advection of bottom water, likely benefiting storm-petrels (which are mainly zooplanktivores).

The tidal process and the salinity front are key elements at the mouth of such a source of freshwater discharge. Coupling these oceanographic processes that influence lower trophic-level accumulation, with the coastal habit of the majority of the charadriiforms recorded, explains seabird aggregations next to the mouth of the Amazon discharge. The CCA results indicate a positive association with chlorophyll-*a* (CHL) for Sternidae and Laridae, in addition to bathymetry (BAT), as their main densities occurred in shallow waters. At the confluence of the Amazon River and the Atlantic Ocean, the water is very productive, with high concentrations of CHL (Santos et al., 2008). The salinity front and tidal processes likely also influenced seabird foraging sites (Cox et al., 2013; Phillips et al., 2018), although we removed salinity from our models due to its collinearity with DIST and CHL. Proximity to shore was additionally documented in

other seabirds (Ainley et al., 1993), likely allowing them to expend less energy during their commute between feeding sites and coastal breeding and/or roosting sites.

The seabird survey presented here shows a species-rich assemblage, even with limited at-sea sampling and data from a single season (boreal spring). With a typical migratory seabird assemblage, there is room for increased species richness with increasing sampling effort. In Suriname, six seabird species were documented as new for the country in a two-and-a-half month at-sea survey (in boreal spring to summer), totalling 18 species (de Boer et al., 2014). Likewise, Willems et al. (2017) recorded 25 seabird species (in boreal spring, winter, and early fall), with Bulwer's Petrel *Bulweria bulwerii* being new to Suriname. We did not record some of the species documented by these studies, though it is plausible that they all pass through Brazilian waters (e.g., Bulwer's Petrel, Red-billed Tropicbird *Phaethon aethereus*, and Audubon's Shearwater *Puffinus lherminieri*). In fact, northern Brazil and Caribbean South America have a paucity of marine biological studies (Miloslavich et al., 2011). For seabirds, new records are frequently reported in this region (de Boer et al., 2014; França et al., 2016; Flood et al., 2017; Willems et al., 2017).

The absence of studies in the Amazon River delta allows for remarkable new discoveries, such as the formation of mesophotic reefs (Moura et al., 2016; Francini-Filho et al., 2018). The improvement of biological surveys and environmental understanding is urgently needed. Given the comprehension of the macro- and meso-oceanographic processes at the mouth of the Amazon River and in adjacent areas, biological studies should focus on the two aggregation sites reported here, at the mouth of the Amazon River per se and the zone of ring formation near the French Guiana border. The process of tidal mixing along the 20-m isobath may provide insights into the bottom-up process influencing meso- and megafauna distributions associated with the Amazon River discharge. Notwithstanding, these two areas seem to be profitable hotspots, serving as ecologically important areas for seabirds.

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**Supplementary material (S1)** – R code.

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687       210X.2009.00001.x  
688

```

689 Supplementary material (S1) – R code
690
691 #####
692 ## Seabird assemblage at the mouth of Amazon River and its relationship with
693 environmental characteristics
694 ## Journal of Sea Research (20XX), v. XX, pp. XXX-XXX
695 ##
696 ## Code by Nicholas W Daudt
697 ## R version 3.4.2
698 #####
699
700 ####Load required packages####
701 library(tidyverse)
702 library(matrixStats)
703 library(lattice)
704 library(vegan)
705 library(MASS)
706 library(ggplot2)
707 library(ggvegan) # the 'install code' is on the relative section
708 library(countreg) # the 'install code' is on the relative section
709
710 ####Open data####
711 ## {utils} function 'read.csv'
712 ## {base} function 'subset'
713 ## {dplyr} function 'filter'
714
715 allData <- read.csv("./allData.csv", sep = ";", dec = ",", header = TRUE)
716 allData$Date <- as.Date.character(allData$Date)
717
718 ## Subset of the respective types of seabird-counts (in this case, 'ccTotal' refers to
719 'continuous-count' (cc))
720 ccTotal <- subset(x = allData, subset = CensusDescription %in% c("Contínuo"))
721 #'Contínuo' refers to 'continuous-count'.
722 # [...]

```

```

723
724  ## In the 'ccTotal' subset, seabird families were grouped to subsequent analysis
725  ccTotal$abundTot <- rowSums(ccTotal[,c(18:42)]) #abundTot = total abundance
726  ccTotal$Procellariidae <- ccTotal$Calonectris.borealis + ccTotal$Puffinus.puffinus +
727  ccTotal$Puffinus.sp.
728  ccTotal$Hydrobatidae <- ccTotal$Oceanites.oceanicus +
729  ccTotal$Oceanodroma.leucorhoa + ccTotal$Hydrobatidae.sp
730  ccTotal$Stercorariidae <- ccTotal$Stercorarius.parasiticus + ccTotal$Stercorarius.sp.
731  ccTotal$Laridae <- ccTotal$Leucophaeus.atricilla
732  ccTotal$Sternidae <- ccTotal$Sterna.hirundo + ccTotal$Sterna.sp.
733
734  ## For multivariate CCA, delete the counts that sum 'zero'
735  ccTotalMultivar <- ccTotal[-ccTotal$abundTot !=0,]
736
737  ## Subset just birds
738  ccBirdsGroups <- subset(x = ccTotalMultivar, select = Procellariidae:Sternidae)
739  ccBirdsGroups$abundTotGr <- rowSums(ccBirdsGroups[,c(1:5)])
740  ccBirdsGroups <- ccBirdsGroups[-ccBirdsGroups$abundTotGr !=0,]
741
742  ccBirdsGroups <- subset(x = ccBirdsGroups, select = Procellariidae:Sternidae)
743
744  ## Subset environmental variables
745  ccEnvMultivar <- subset(x = ccTotalMultivar, select = SSS:BAT)
746
747  #####Summary#####
748  ## {base} package function 'summary'.
749  ## {matrixStats} package functions 'sum2' and 'colSums2'
750
751  ## Min, Max, Mean: summary function from {base}
752
753  ## Density from 'continuous-counts' (cc). For 'snapshot-counts' (ci) the same procedure
754  was made.
755  ccAreaTotal <- sum2(ccTotal$Area)
756  colSums2(as.matrix(ccBirds))/ccAreaTotal

```

```

757
758  ## Frequency of occurrence (%FO) from 'continuous-counts' (cc). For 'ship-followers',
759  'snapshot-counts', and 'point-counts' the same procedure was made.
760  zero.cc <- as.vector(print(colCounts(x = as.matrix(ccBirds), value = 0)))
761  cc.fo <- as.vector(100-((zero.cc/118)*100))
762  cc.fo
763
764  #####Exploratory analysis#####
765  ## {lattice} package
766  ## Codes used directed from the following reference:
767  ## Alain F. Zuur et al. (2010) A protocol for data exploration to avoid common
768  statistical problems. Methods Ecol. Evo.
769  ## doi: 10.1111/j.2041-210X.2009.00001.x
770
771  #####CCA#####
772  ## {vegan} package function 'cca'
773  ## {ggvegan} package function 'autoplot'
774  ## {ggplot2} package functions to 'theme_bw' and 'expand_limits'
775
776  ccaGroups <- cca (ccBirdsGroups ~ SST+DIST+CHL+BAT, data = ccEnvMultivar[-
777  c(1),]) #
778  anova(ccaGroups, by = "axis", permutations = 99)
779  anova(ccaGroups, by = "term", permutations = 99)
780
781  # To plot the CCA, the following package was used {ggvegan}
782  devtools::install_github("gavinsimpson/ggvegan")
783  library(ggvegan)
784
785  ccaPlot <- autoplot(ccaGroups) + theme_bw() + expand_limits(x = 1.5)
786  ccaPlot
787
788  #####Multiple-regression linear models (GLM)#####
789  ## {stats} package function 'glm'
790  ## {countreg} package functions 'zerotrunc', 'qqrplot' and 'rootogram'

```

```

791
792  install.packages("countreg", repos="http://R-Forge.R-project.org")
793  library(countreg)
794
795  ## Zero-part: Binomial GLM
796  Procella.bin <- glm(factor(ccTotal$Procellariidae>0) ~ SST + CHL + ((BAT)*-1), data
797  = ccTotal, family = binomial)
798  summary(Procella.bin)
799      # and so on, for each group...
800
801  ## Checking zero-part model fitting
802  plot(Procella.bin)
803      # and so on, for each group...
804
805  ## Count-part: Zero-truncated GLM
806  Procella.zt.p <- zerotrunc(ccTotal$Procellariidae ~ SST + CHL + ((BAT)*-1), data =
807  ccTotal, subset = ccTotal$Procellariidae>0)
808  summary(Procella.zt.p)
809      # and so on, for each group...
810
811  ## Checking count-part model fitting
812  qqplot(Procella.zt.p)
813  rootogram(Procella.zt.p)
814      # and so on, for each group...
815
816

```



## **APÊNDICE 2**

**As aves marinhas desafiam os limites das Ecorregiões marinhas e os gradientes  
latitudinais de riqueza de espécies**

**Seabirds challenge the limits of marine ecoregions and latitudinal  
gradient theory of species richness**

Nicholas W. Daudt; Maurício G. Camargo; Eduardo P. Kirinus; Leandro Bugoni

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# Seabirds challenge the limits of marine ecoregions and latitudinal gradient theory of species richness

Running header: Marine Ecoregions and seabirds

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## ABSTRACT

**Aim** To identify spatial patterns of seabird diversity and abundance off the Brazilian coast, based on at-sea surveys, test the Marine Ecoregion concept to highly mobile seabirds, and the latitudinal gradient theory of species richness using seabirds as model group.

**Location** The South Atlantic Ocean off Brazil, from 5°N to 34°S.

**Taxa** Seabirds, Aves, Procellariiformes, Charadriiformes, and Suliformes.

**Methods** Seabird assemblages were *a priori* classified by linking at-sea bird counts to the proposed Marine Ecoregions of the World. We used occurrence data in Hierarchical Clusters to explore assemblage affinities (with Sørensen dissimilarities), and abundance data in Canonical Analysis of Principal Coordinates (CAP) to account for the influence of environmental characteristics on the assemblage structure. Generalized Additive Models (GAMs) were performed to assess the influence of latitude on species richness for all seabird species, as well as for the two species-richest orders.

**Results** Hierarchical Clusters and CAP analysis suggest that biogeographic realms for seabirds fit better at the province-scale than at the larger or smaller, i.e. global and regional scales. Provinces delineated by oceanographic processes were the best way to aggregate assemblages for seabirds, based on both occurrence and abundance. Latitude was significant for all GAMs, and the smooth functions indicated contrasting patterns between seabird orders, i.e. Procellariiformes had a southward increase in species richness, richer at ~34°S (Brazil/Malvinas Confluence zone), while Charadriiformes had two peaks, on 0–5°N (Amazon River outflow) and at 20°S (where Trindade Island is located).

**Main conclusions** Biogeographic realms for seabirds fit better at a province-level scale than at regional or global scales, as delineated by oceanographic processes. Seabirds comprise a polyphyletic group, with intrinsic differences in lifecycles, and tests of the

latitudinally increasing gradient of species richness indicated different patterns between Procellariiformes and Charadriiformes.

**Keywords** Biogeography; Charadriiformes; Habitat heterogeneity; Latitudinal gradient; Marine birds; Marine Ecoregions of the World; Procellariiformes.

## INTRODUCTION

For over a century, biogeographers have discussed and proposed geographical units that represent organisms and their environmental surroundings. Thus, biogeography identifies, delimits, and names bioregions. Regions were historically delimited by taxonomy-derived approaches, such as the influence of barriers on endemism or occurrence patterns of species (see Spalding et al., 2012 for a brief review). On the other hand, proposals exist to use ecological, geochemical, and oceanographic processes to delineate ecoregions in the marine environment, with more emphasis on the environment rather than purely biological component (Longhurst, 1998; Robertson et al., 2017). Although bioregionalization approaches are still in progress, the hierarchical characteristic of the bioregions is a well-recognized pattern in both terrestrial and marine environments (Olson et al., 2001; Spalding et al., 2012; Vilhena and Antonelli, 2015; Robertson et al., 2017). This means that, nested within biologically-driven large-scale processes are local-scale processes, such as species use/competition for a resource ruled by the physical environment.

In the dynamic marine environment, which has a variety of fluid processes, bioregions are still in debate. The proposed Marine Ecoregions of the World (MEOW; Spalding et al., 2007) is probably one of the most popular nowadays. This study tried to create a worldwide classification of bioregions, hierarchically arranged, for coastal environments. For this, Spalding et al. (2007) used mainly distribution data of benthic animals, reported in scientific papers and reports, as well as expert opinions, to propose the aforementioned classification scheme. The MEOW classification is based on shelf areas (<200 m isobaths) and defines 62 Provinces and 323 Marine Ecoregions (Spalding et al., 2007). More recently, aiming to expand the MEOW approach to the pelagic environment, Spalding et al. (2012), proposed Pelagic Provinces, classifying 37 Provinces into 7 Biomes. The focus was epipelagic organisms, which occupy the first 200 m of the

water column in high seas, but the authors suggest that both MEOW and Pelagic Provinces complements well their boundaries (Spalding et al., 2012).

Assemblage structure is a key aspect of ecological regionalization. Identifying the species that occur in an area is the basis to assembling a biological unit, which should contain ecological (oceanographical) features shared among all of those species, like predictable fronts and eddies. Marine megafauna usually has a wide home-range, and identifying areas of transition and feeding for these groups is key to understanding the processes that lead to their occurrence in a given area. Advances in tracking technologies allow us to recognize staging and transition areas for many migratory species (Hussey et al., 2015). Expanding studies from single to multiple taxa tracked at the same time can identify hotspot zones and familiar features in a variety of regions (Reisenger et al., 2018; Yurkowski et al., 2019). From a diversity point of view, these areas are keystone structures (Tews et al., 2004), and should embrace a variety of taxa by their ecological importance.

Processes that influence the entire community build these important aggregation zones into hotspots. In the patchy marine environment, hotspots of mega-fauna are mainly linked to oceanographic processes, such as fronts and eddies (Weimerskirch, 2007; Scales et al., 2014). For top-predators, these hotspots are zones with the highest occurrence, and are usually species-richer in comparison with surrounding areas. At a global scale, the diversity of oceanic taxa has a pattern with more species at mid-latitudes, and top-predators contribute to this pattern (Tittensor et al., 2010). However, studies carried out during the last decade that search for patterns of diversity in the marine environment at broader scales do not yet include any seabird species (Tittensor et al., 2010; Powell et al., 2012; Chaudhary et al., 2016).

Seabirds are a polyphyletic group that encompasses a variety of habits (Schreiber and Burger, 2001). They are prone to disperse widely, due to high-flying capabilities. In fact, many species are transequatorial migrants (e.g. Guilford et al., 2009), and even during the breeding season can fly thousands of kilometres in foraging trips. These long-distance foraging trips, and migrations to non-breeding areas, barely influence population structure (Friesen, 2015), because seabirds are highly philopatric (Schreiber and Burger, 2001). Because of these attributes, seabirds are interesting model organisms to test a variety of ecological theories. Here, we aim to identify spatial patterns in the diversity and abundance of seabirds off the Brazilian coast, based on at-sea surveys along 40° of latitude. We also test the Marine Ecoregion concept as proposed by Spalding et al. (2007)

applied to highly mobile seabirds. In addition, we explore the latitudinal gradient of species richness using all observed seabird taxa as a model group, and focus on the two most frequently recorded bird orders (Procellariiformes and Charadriiformes).

## MATERIALS AND METHODS

### Study area

The study was carried out with at-sea seabird counts over the continental shelf, shelf break and adjacent waters along the entire Brazilian coast, from the boarder with French Guiana (5°N; 50°W), at the Saint Peter and Saint Paul Archipelago (1°N; 29°W) and Trindade Island (20°S; 28°W), to the south, at the Uruguayan boarder (34°S; 52°W). Along these 7000 km of the Brazilian coast, the continental shelf extension is highly variable, with the 200-m isobath ranging from c. 300 km in the North, to c. 50 km in Northeast, 40–150 km in East, and 100–200 km in Southeast-South regions (Fig. 1).

Oceanographically, the northern region is influenced offshore by the oligotrophic North Brazil Current (NBC) (Bourlès et al., 1999a), and the coastal shelf by the nutrient-rich Amazon River (AR) discharge (Silva et al., 2009). The intensity of AR rules many oceanographic processes, such as tidal-mixing and saline fronts (Geyer, 1995). On the offshore border with French Guiana (5–10°N), NBC retroflects and blends into the North Equatorial Countercurrent (NECC) (Bourlès et al., 1999b); in this process NBC builds eddies (rings) that flow northeastwards through the Caribbean Sea carrying AR water in its core (Bourlès et al., 1999b; Silva et al., 2009). The South Equatorial Current (SEC) splits near 10°S, generating the NBC that flows equatorward, and its south branch forms the oligotrophic Brazilian Current (BC) (Silveira et al., 1994).

The northeast region is a highly dynamic low-productive environment, as a corridor to both the NBC and BC (Ekau and Knoppers, 1999). Offshore, the region has a dynamic system of surface and subsurface currents; where the Rocas Atoll, Fernando de Noronha Island, and Saint Peter and Saint Paul Archipelago were mainly influenced by the SEC, the Equatorial Undercurrent (EUC), and the South EUC (SEUC) (Tchamabi et al., 2017; Araújo et al., 2018). Such currents, by hitting these oceanic islands, create local-scale mixing turbulences, and advection eddies, which influence the subsurface chlorophyll (Souza et al., 2013).

In the east, BC is the fundamental water mass, being the west boundary of the Subtropical Gyre of the Atlantic Ocean (Silveira et al., 2000). Its meander process on the shelf-edge, intensified in its encounter with the Abrolhos Bank and Vitória-Trindade-

Chain as topographical barriers is noteworthy (Ekau and Knoppers, 1999). It has important implications on the primary-production and local circulation patterns, bringing local upwelling of the nutrient-rich South Atlantic Central Water (SACW; Schmid et al., 1995; Gaeta et al., 1999).

The southeastern region is dominated by a current-eddy-upwelling system, named the South Brazil Bight. Its main water mass is the BC that flows over the continental shelf and beyond, in the upper 500–750 m (Silveira et al., 2000). The major processes that influence its dynamics and productivity are an inner-shelf wind-driven upwelling, variable mid-shelf surface haline and bottom thermal fronts, and a shelf-break, with topographical subsurface upwelling (Palma and Matano, 2009, Brandini et al., 2018). In addition, hydrographical instabilities in water mass boundaries and topographical variations at the bottom layer build eddies off Cabo Frio and São Tomé Cape, at 22° and 23°S, respectively (Campos et al., 2000; Palma and Matano, 2009; Mill et al., 2015).

The southern region is ruled offshore by the confluence of the warmer, nutrient-poor BC with the cooler, nutrient-rich Malvinas Current (MC) (Matano et al., 2010). The interactions between BC/MC build mesoscale features, as meanders and eddies (Wilson and Rees, 2000). Inshore, the wide shelf is dominated by the freshwater discharges of the La Plata River (Argentina/Uruguay) and the interaction of coastal currents (Tropical Water, carried out by BC), which form the Subtropical Shelf Front (SSF) (Möller et al., 2008; Piola et al., 2008). The SSF fluctuation, freshwater inputs, and local upwelling dictated by winds causes a high primary production in this area (Ciotti et al., 1995; Möller et al., 2008).

## **Data collection**

Seabird counts were recorded from several platforms, including Fishing, Research, and Brazilian Navy vessels (50–330 feet). Trips occurred from 2009–2018 during the four seasons, ranging from shallow waters <10 m to offshore waters >5000 m depth. The effort was not equally distributed both in space and time, as each research project had its own goals, but we treated them with the same weight.

Birds were recorded in motion, with near constant vessel bearing and speed. As all cruises were of research priority, no offal was used to attract birds. We followed Tasker et al. (1984) and Neves et al. (2006) protocols for counting seabirds at-sea. The latter authors slightly modified the Tasker et al. (1984) protocol, by recording the ship-attending birds in a separate sheet - as the presence of the ship *per se* can influence bird

movements, and attract ship followers (e.g. Hyrenbach 2001). From Tasker et al. (1984), both continuous and snapshot counts were carried out. First, “ship-attending” birds were identified and counted, according to characteristic behaviours (flying in circles, following the ship wake), to ensure not recounting them in the following count methods (Neves et al. 2006). Then, all flying and sitting birds were recorded in a 10 min “continuous count”, followed by ten “snapshot counts” separated by 1-min each (Tasker et al. 1984). Continuous and snapshot counts have the same purposes, i.e. they are a sample of seabird abundance, and are collected independently, i.e. the same birds were plausibly counted in both methods, although neither recorded again any ship-attending bird. These three count-methods were computed at the same sample-point, according to geographic coordinate, date and hour. These sample-points were used as the basis to extract remotely-sensed environmental data.

Oceanographic and physiographic data were gathered in online, open-access platforms. Sea surface temperature (SST; °C) and sea surface salinity (SSS) were from HYCOM models (<https://hycom.org/>); chlorophyll-*a* (CHL; mg/m<sup>3</sup>), as proxy for primary production, were from MODIS-Aqua (<https://oceancolor.gsfc.nasa.gov/data/aqua/>); and bathymetry (in m) were from the GEBCO (<https://www.gebco.net>). Data were downloaded to the proximate hour of the day associated with each sample-point; then, all raster images were interpolated in MATLAB R2016b software, ensuring that all environmental data had the same 0.040° in longitude (~4.5 km) and 0.045° latitude in (~5 km) spatial resolution. Through the neighbour filter, the proximal value of each environmental data point was associated with each seabird count. The distance from the proximal mainland shoreline (in km) for each sample was calculated. In addition, we performed a first derivate of SST raster pixels, to identify zones of major variance in SST values (a proxy for thermal fronts).

## **Data analysis**

For the following analyses, two matrices were built. First, an occurrence matrix, based on the three seabird counting-methods described. As the three methods were used sequentially, they have the same geographic coordinates, date and hour; so, we used these attributes as an identifier to assign species occurrence (presence/absence) for each sample ( $n = 2633$ ). The second matrix was for abundance data, based only on “continuous-count” method ( $n = 2532$ ). Then, seabird counts were assigned to the specific Province and Marine Ecoregion, proposed by Spalding et al. (2007), as an *a priori* classification of



assemblages, given that counts inside the biogeographic polygons. For Marine Ecoregions a slightly adaption was used, due to local oceanography affinities and lower number of counts, with Northeastern Brazil encompassing São Pedro and São Paulo Rocks, Fernando de Noronha and Atoll das Rocas, and Northeastern Brazil Ecoregions.

A spatial description of the data is presented for effort, mean abundance and species richness. Grid cells of  $1^{\circ} \times 1^{\circ}$  were used as the basis for calculations. The effort was recorded as the number of sample-points in each grid, based on the occurrence matrix. Abundance was represented as the mean number of seabirds, dividing the sum of flock size per count by number of counts in each grid cell. Species richness was calculated as the number of species recorded in each grid cell (i.e. alpha-diversity). In addition, because the albatrosses and petrels (Procellariiformes) and the terns, skuas, and gulls (Charadriiformes) were the most representative of the recorded seabirds, we performed separated spatial representations of mean abundance and species richness for each order, following the same procedures.

To estimate species richness of each Marine Ecoregion, we used the coverage-based rarefaction and extrapolation curves (Chao and Jost, 2012). This method allows comparing species richness based on completeness of samples between different locations. We used the `iNEXT::iNEXT` function, with default specifications, i.e. the endpoint as double of reference value, 50 bootstraps replications, and confidence interval of 95% (Hsieh et al., 2019). Data entry was species incidence from the raw occurrence matrix.

A gradual change in assemblages was expected, thus we ran a Hierarchical Cluster based on species occurrence (occurrence matrix) to test for similarities between biogeographic zones (Provinces and Ecoregions). We used the `stats::hclust` function and a distance-matrix based on Sørensen dissimilarities (using `labdsv::dsvdis` function), with the single linkage method as the clustering algorithm. Additionally, to test seabird assemblage values related to biogeographic realms, we ran a Canonical Analysis of Principal Coordinates (CAP), based on the abundance matrix and the environmental data, plus the Ecoregion as factor. The CAP is a constrained canonical multivariate analysis that best separates groups, by finding the axis that maximizes differences of dummy variables (Anderson and Willis, 2003). We excluded observations with  $\leq 2$  individuals, resulting in 394 seabird counts for CAP. The dissimilarity measure used was Bray-Curtis, and the analysis was run with the `BiodiversityR::CAPdiscrim` function (Kindt and Coe, 2005).

To test the influence of the latitudinal variation in species richness, we specified Generalized Additive Models (GAM), expecting non-linear relationships (Chaudhary et al., 2016). The GAMs were fitted with the `mgcv::gam` function, with a Poisson distribution. Based on the occurrence matrix, we summed the number of species of each sample, and used it as an independent count (for all species, as well as for Procellariiformes and Charadriiformes); for the explanatory variable, we used latitude.

All data were processed in R environment 3.6.0 (R Core Team, 2019), using the following packages for statistical analysis: ‘vegan’ 2.5-5 (Oksanen et al., 2019), ‘labdsv’ 1.8-0 (Roberts, 2016), ‘BiodiversityR’ 2.11-1 (Kindt and Coe, 2005), and ‘mgcv’ 1.8-28 (Wood, 2017), ‘iNEXT’ 2.0.19 (Hsieh et al., 2019). Graphical outputs were produced with ‘ggplot2’ 3.2.0 (Wickham, 2016) or specific functions of packages already cited. Spatial data were manipulated in R, with the packages ‘sf’ 0.7-4 (Pebesma, 2018) and ‘dplyr’ 0.8.1 (Wickham et al., 2019), and maps were built under QGIS 2.18.7 (QGIS Development Team, 2018).

## RESULTS

A total of 2633 seabird counts were carried out, covering mainly the southern-portion of the study area, 23°S to 33°S (Table 1, Fig. 2). From all counts, 1749 had at least one individual recorded. In total, 3 orders, 9 families, and 46 species were recorded; though 14 species were rarely seen, recorded in less than five counts (Appendix 1). Procellariiformes and Charadriiformes dominated the seabird assemblage, with 24 and 18 species, respectively.

Larger numbers of species (>12) were recorded in extreme regions off Brazil, on the border with French Guiana to the north, around Trindade and Martin Vaz Islands, to eastward bounds, on the Uruguayan boarder to the south, as well as in front of Cabo de Santa Marta (24°S); the latter two were at the 200 m isobath (Fig. 2). Procellariiformes and Charadriiformes showed a contrasting pattern, with the greatest richness 27–34°S for the former, and in the northern region and around Trindade Island for the latter (Fig. 3). The rarefaction/extrapolation curves showed that Northeastern Brazil has notably lower species richness among Ecoregions, and that Amazonia has potential to increase its richness with increasing sampling effort (Fig. 4a). Although there were differences in seabird counts between each Marine Ecoregion (see Table 1), all but Amazonia were well covered (Fig. 4b).

The Hierarchical Clusters pointed to minimal separation from both east Brazilian Provinces (Tropical Southwestern Atlantic and Warm Temperate Southwestern Atlantic), though the North Brazilian Shelf had a major dissimilarity from them (Fig. 5a), as expected. The Ecoregion clustering presented a similar pattern but included the Northeastern Brazil as dissimilar as Amazonia from the southeast-southern Ecoregions. The offshore Trindade and Martin Vaz Islands were most similar to Rio Grande (Fig. 5b). The overall CAP discrimination was 67.5%, with Trindade and Martin Vaz Islands the most distinguished assemblage in the biplot (Fig. 6). The analysis produced 10 axes, accounting for 81% of the variance. The correct classification of observations were 81% for Rio Grande ( $n = 201$ ), 80% for Northeastern Brazil ( $n = 10$ ), 74.2% for Trindade and Martin Vaz Islands ( $n = 62$ ), 70.7% for Eastern Brazil ( $n = 41$ ), 26.7% for Southeastern Brazil ( $n = 75$ ), and 0% for Amazonia ( $n = 5$ ).

The GAM with all species explained 39.3% of the deviance of species richness by latitude, with an  $R^2_{\text{adj}} = 0.44$ . The smooth function plot shows the greatest richness in southern Brazil, decreasing by eastern Brazil, though with a peak at 20°S (where Trindade and Martin Vaz Islands are located), and increasing again towards the north (Fig. 7a). For Procellariiformes and Charadriiformes, contrasting patterns emerged. In the former, species richness had it highest south of 23°S (52.2% deviance explained,  $R^2_{\text{adj}} = 0.53$ ; Fig. 7b); in the latter, two peaks appeared, at 20°S and between 0–5°N (19.8% deviance explained,  $R^2_{\text{adj}} = 0.08$ ; Fig. 7c). The smooth parameter for Latitude was significant for all models ( $p < 0.01$ ).

## DISCUSSION

This is the first study describing the spatial distribution of seabirds along almost 40 degrees of latitude off Brazil. Data presented here are based on scientific excursions rather than fisheries-attending birds, and emphasize different assemblage structures through this large latitudinal extension, dominated by Procellariiformes and Charadriiformes. Biogeographic realms seem to fit better for seabirds at the Province-scale, and we argue that these Provinces must be based on oceanography processes. Some adaptations in the Provinces defined off the Southwest Atlantic by Spalding et al. (2007) are proposed, to improve the definition of seabird assemblages. Seabirds prove to be a complex model for testing latitudinal gradients in species richness. Procellariiformes seem to follow a bimodal pattern in the marine environment (i.e. mid-latitudes with highest diversity), though they increase in species richness on the tropics. On the other

hand, Charadriiformes show opposite patterns (highest diversity in the tropics, decreasing through the south, but not monotonically).

### Biogeographic realms

It has been recognized that biogeographic realms should be hierarchically organized (Spalding et al., 2007), as are foundational oceanographic and biological processes. Therefore, in the heterogeneous seascape off Brazil, different currents and structures should sustain different seabird assemblages. Using the *a priori* classification based on Spalding et al. (2007) applied to the seabird data, results are broadly in agreement with the hierarchical idea, but some particularities are detected. From a wide-to-fine scale, the Province clusters show the intuitive pattern of similarity between assemblages. This is given the division of the North Brazil Shelf due to oceanographic processes (mainly Amazon River influence) and given that Charadriiformes were the bulk of the recorded species, with some records only there (e.g. Laughing Gull *Leucophaeus atricilla*). The Tropical Southwestern Atlantic and Warm Temperate Southwestern Atlantic share oceanographic influences (e.g. Brazil Current; Silveira et al., 2000), as well as species occurrence (e.g. Brown Booby *Sula leucogaster*, Yellow-nosed Albatross *Thalassarche chlororhynchos*), so the similarity between them was expected. Yet, differences are noticeable due to oligotrophic characterization of the Tropical vs. the upwelling, freshwater inputs and Convergence zone from the Warm Temperate regions; also by species composition, as some seabirds occur only in Tropical (e.g. Brown Noddy *Anous stolidus*) and others just in Warm Temperate (e.g. Cape Petrel *Daption capense*).

When we examined the Marine Ecoregions cluster, Northeastern Brazil segregated from the other nearby Ecoregions of their Province, apart with/from Amazonia. In addition, seabirds in Eastern Brazil are more similar to Southeastern Brazil, than to their congeners Northeastern Brazil and Trindade and Martin Vaz Islands. Rio Grande Ecoregion appears more similar to Trindade and Martin Vaz Islands, than to Southeastern Brazil. Again, when we analyse the oceanographic features of these regions, some of these affinities emerge. For Amazonia, the dynamics is mainly linked to Amazon River discharge. Northeastern Brazil is an oligotrophic environment, with low richness assemblage, mainly based on breeding species. Southeastern Brazil and Eastern Brazil are both strongly influenced by the Brazil Current, with wind and topographical upwelling-eddy-processes, so their assemblage is expected with share many species. Rio Grande has the influence of the continental freshwater discharges and the Subtropical

Shelf Front (Ciotti et al., 1995; Möller et al., 2008), and the cool nutrient-rich Malvinas Current offshore (Matano et al., 2010). The topographical subsurface upwelling process at Trindade and Martin Vaz Islands, and the distance from the mainland coast (1140 km) were probably the most influential environmental characteristics to structure that assemblage. The CAP results, which considers together species abundance/occurrence and environmental data, provide a basis to discriminate Trindade and Martin Vaz Islands and Rio Grande Ecoregions quite well (74% and 81%, respectively). In addition, Northeastern and Eastern Brazil were well discriminated too, although their lower number of counts. On the other hand, Southeastern Brazil, which had more samples than the latter two, only reached 26% of correct discrimination. This is due to a mixture of characteristics, with environmental and seabird assemblage proprieties shared with neighbouring Ecoregions.

Environmental characteristics can act as ecological barriers or bridges to some highly mobile vertebrates (Briscoe et al., 2017), particularly distinct oceanographic bodies of water, as described above. Indeed, in Northeastern Brazil, Brown Booby populations are strongly influenced by their local environment pressures (Nunes and Bugoni, 2018). For fishes over the Vitória-Trindade Chain, local environmental conditions such as the advection of bottom water and reduced dispersion (even for good dispersal species) are causes of population structure, with Trindade Island as a rich site (Pinheiro et al., 2015; Pinheiro et al., 2017). In the Pacific Ocean, dolphins have been separated into biogeographic units according to oceanographic domains, from different water-masses, salinities and temperatures in the water column (Kanaji et al., 2016). Tunas and billfishes, large and highly mobile fishes, present distinct assemblages related to specific biogeochemical environments (Reygondeau et al., 2012).

Altogether, this scenario suggests that, at least for seabirds, biogeographic realms should be defined at mesoscales, such as at Province levels. Given the Uruguayan and north Argentinean seabird assemblages (Veit, 1995; Gandini and Seco-Pon, 2007; Jiménez et al., 2011), in addition to the oceanographic context that these regions are associated with, i.e. the La Plata River discharge (Ciotti et al., 1995; Möller et al., 2008), we suggest that the Rio Grande and Uruguay–Buenos Aires Shelf (from Spalding et al. 2007 Ecoregions), form a distinct Province. We advocate for Province scales as the best approach for biogeographic realms, and propose a re-classification for seabirds from Southeastern Brazil as belonging to the Tropical Southwestern Atlantic Ocean. In addition, even though Province-scale seems to fit best for seabirds, another region must

be considered as distinct: the Northeastern Brazil has its unique characteristics, oceanographically and from the seabirds' perspective, with the bulk of species breeding on islands (Mancini et al., 2016). For sure, other species use that region, but mainly en-route, instead of as a staging area. Therefore, the rationale that we make for the analysis aggregating three original Ecoregions of Spalding et al. (2007) as the Northeastern Brazil, for seabirds, fits well.

We call attention to the proposed Marine Ecoregions proposed by Spalding et al. (2007) that were defined to occur at 200 m isobath as the maximum. On the other hand, Provinces as stated by Spalding et al. (2012) for the pelagic environment, are a quite simple regionalization, even for oceanic seabirds. The ideas of biogeochemical provinces of Longhurst (1998) should be tested for seabirds, as they appear to be better as boundaries for these highly mobile vertebrates.

#### **Latitudinal gradient of species richness**

Studies with a large study area bring us the opportunity to look at latitudinal variation in species richness. Thirty-nine degrees of latitude were covered by this study, from equator to mid-latitudes. To the best of our knowledge, for seabirds, only Procellariiformes have been subject to a similar sampling and analysis (Chown et al., 1998). The general pattern of species richness highlights three peaks of richness, between 0–5°N, around 20°S, and ~27–34°S. Disentangling this by searching for patterns in the two most diverse orders, Procellariiformes and Charadriiformes, we noted a contrasting pattern. The GAMs emphasized a high sinuosity pattern for Charadriiformes, with peaks related to the Amazon River discharge (0–5°N) and Trindade Island (20°S). Mostly terns depend on land for roosting, and in these two areas the foraging opportunities are near to the coast. In addition, north Brazil is a staging/passage area for some transequatorial migrants, such as the Roseate Tern *Sterna dougallii* and Laughing Gull, and Trindade Island has its breeding species (Mancini et al., 2016). Southwards, oceanic skuas *Stercorarius* spp. are the major representatives of Charadriiformes, and so the richness was expected to be lower.

As previously noted, Procellariiformes has a peak in species richness around 37–43°S (Chown et al., 1998). Although our study area covers up to 34°S, a step back from the latitudinal band of the maximum species richness, the GAM indicates that the southern portion is in fact the richest of the whole study area. The seabird assemblage of Uruguay and Argentina has more influence of the sub-Antarctic assemblage, with species

rarely seen in Brazilian waters as dark albatrosses *Phoebetria* spp., and Grey-headed Albatrosses *Thalassarche chrysostoma* (Croxall and Wood, 2002; Jiménez et al., 2011). There, the oceanographic processes influenced by the cooler Malvinas Current in the shelf break is notable (Matano et al., 2010), which, coupled with freshwater discharges (Möller et al., 2008), enhance the richness and abundance of large marine animals (Croxall and Wood, 2002; Tittensor et al., 2010). In addition, an increase in species richness in the 5°N band was observed. Migratory shearwaters and zooplanktivorous storm-petrels aggregate there, possibly due to the mesoscale processes of the ring-formation, the saline and tidal-mixing fronts (Weimerskirch, 2007; Daudt et al., [Chapter 1]).

Latitudinal gradients in the marine environment are still under scrutiny when compared to the better-studied terrestrial environment (Hillebrand, 2004; Chaudhary et al., 2016). Efforts had been done to track latitudinal patterns in the marine environment, with small- to mega-fauna, multi-taxa, but the mechanism underlying patterns are still lacking (Tittensor et al., 2010; Chaudhary et al., 2016; Edgar et al., 2017). Here, we did not test directly the hypothesis of bi-modal species richness for seabirds. On the other hand, the data presented show that, even for seabirds, the bi-modal hypothesis could not explain its richness. Seabirds are a polyphyletic group, which encompass a variety of taxa and different life histories, from penguins to albatrosses; strictly coastal vs. oceanic ones; some that just occur in one Hemisphere vs. transequatorial species (Harrison, 1985). Latitudinal patterns in species richness can be distinct even inside a monophyletic group, as for amphipods (Burrige et al., 2017). Moreover, results for Charadriiformes demonstrated that this group differs from Procellariiformes, and from other marine taxa, that has its major richness at mid-latitudes (Chown et al., 1998; Tittensor et al., 2010; Chaudhary et al., 2016). Charadriiformes are intriguing taxa for testing latitudinal patterns of species richness, as their diversity, morphologies, and habits are variable.

### **General patterns of richness and abundance**

Species richness had its own spatial patterns, considering that most commonly recorded taxa were migrants, and so pathways and staging areas were the more plausible sites to observing them. The highest species richness grid-cell was observed in the north, near the Amazon River discharge, with 20 species recorded. Several species use that region as a wintering area, as well as a stepping-stone for transequatorial migration, such as petrels (Guilford et al., 2009; Pollet et al., 2019) and terns (Mostello et al., 2014; Neves et al., 2015). There, high numbers of Charadriiformes were recorded, mainly North

Hemisphere migrants. Around Trindade and Martin Vaz Islands, half the richness is composed of species that breed there (Mancini et al., 2016). However, North Hemisphere migrant petrels that pass through there (*Calonectris* spp.), and Temperate-Subtropical petrels such as gadfly petrels *Pterodroma* spp. and White-chinned Petrels *Procellaria aequinoctialis* with a nearby distributional limit (Harrison, 1985) were also recorded. On southeast–south Brazil, a rich assemblage was found, dominated by Procellariiformes, but also by oceanic Charadriiformes. In the northeast, only species that breed in nearby islands were recorded (Mancini et al., 2016), plus Wilson's Storm-petrel *Oceanites oceanicus*, a widespread transequatorial seabird (Harrison, 1985). This region is a migration corridor for transequatorial migrants, and so, individuals use it as ‘passage’ area (e.g. Metcalf, 1966; Hedd et al., 2012). Therefore, specific temporal frames should be surveyed to detect these species (Metcalf, 1966). On the other hand, north and southeast–south regions can be considered as staging/living areas for a variety of species, as the main oceanographic processes there influence prey abundance, such as local upwelling, fronts, and eddies.

Looking at the spatial distribution of orders, Charadriiformes were mainly associated with land. In fact, typical oceanic Charadriiformes were composed only of skuas and jaegers (*Stercorarius* spp.). Terns were seen mainly at Trindade Island, and in north Brazil, though southern Brazil is also an important site for several tern species (Bugoni and Vooren, 2005). On the other hand, Procellariiformes were recorded in refuelling areas for migrants (in north Brazil) and mainly in southern Brazil, which is an area of aggregation by diverse species at different life stages (juveniles, immatures and adults; Bugoni and Furness, 2009).

Areas of greatest mean abundance were linked to major oceanographic processes. Seabirds are known to aggregate in mesoscale features, such as frontal zones, tidal mixing fronts, eddies, and local upwellings (Weimerskirch, 2007; Scales et al., 2014). In north Brazil, the retroflexion zone of NBC and the freshwater discharge of the Amazon River seem to play an important role for seabirds, that associate with the ring formation structure, and a tidal-mixing and saline front, respectively (Daudt et al., [Chapter 1]). The wind and topographical upwelling-eddy-processes off east–southeast Brazil (Mills et al., 2015; Brandini et al., 2018) seems to play an important role as aggregator of seabirds. In coastal transects, highest seabird abundances were recorded adjacent to Cabo Frio, possibly due to the local upwelling (Coelho et al., 1990). In the south, greatest abundances were bordering the Uruguayan waters. That region is directly influenced by huge



freshwater discharges, which affects the nutrient and chlorophyll inputs (Ciotti et al., 1999), besides the subtropical shelf front (Piola et al., 2008). Other high abundance areas were located around Trindade and Martin Vaz Islands, where there are several colonies of Brown Noddy and White Tern *Gygis alba*, and large numbers of Sooty Terns *Onychoprion fuscatus* (Mancini et al., 2016).

## CONCLUSIONS

Here we provide a spatial analysis of the seabird assemblages from the tropics to the Southwestern Atlantic Ocean, along almost 40° of latitude. Our data support the idea that marine animal abundance and richness are not directly associated (Whitehead et al., 2010); abundance is related to ephemeral (yet predictable) oceanographic process that influence prey availability, whereas richness appears to be related to staging areas (even for different life times). We highlight two major topics in biogeography: the biogeographic realms and the latitudinal gradient in species richness. The former relates to the zoogeographic regionalization for highly mobile marine animals, such as seabirds, that needs further discussion, but seems to fit best at the Province-level scale. Biogeochemical provinces (Longhurst, 1998) should also be tested for seabirds. In the marine environment, the concept of latitudinal gradients in species richness is a complex theme. Seabirds are a polyphyletic group, with coastal vs. oceanic, sedentary vs. migratory species, and restricted vs. vast home-ranges, and serves as a complex model on which to test macroecological rules.

**DATA AVAILABILITY STATEMENT** Data will be available on request.

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**APPENDIX 1** Orders, families, and species of seabirds recorded off Brazil, 2009–2018,  
based on at-sea counts.

**APPENDIX 2** R code.

**Author contributions:** N.W.D and L.B. conceived the ideas; E.P.K. gather the  
environmental data; N.W.D and M.G.C. analysed the data; N.W.D wrote the paper; all  
authors revised the manuscript and contributed to the final version.



**Table 1** Number of at-sea seabird counts (*n*) for species richness and total abundance recorded in each biogeographic realm off Brazil, Atlantic Ocean. Provinces and Ecoregions according to Spalding et al. (2007)\*.

| Biogeographic realm                    | Species richness            | Total abundance               |
|----------------------------------------|-----------------------------|-------------------------------|
| <b>PROVINCE</b>                        |                             |                               |
| North Brazil Shelf                     | 21 ( <i>n</i> = 220)        | 70 ( <i>n</i> = 119)          |
| Tropical Southwestern Atlantic         | 27 ( <i>n</i> = 882)        | 1159 ( <i>n</i> = 883)        |
| Warm Temperate Southwestern Atlantic   | 29 ( <i>n</i> = 1531)       | 2419 ( <i>n</i> = 1530)       |
| <b>ECOREGION</b>                       |                             |                               |
| Amazonia (Am)                          | 21 ( <i>n</i> = 220)        | 70 ( <i>n</i> = 119)          |
| Northeastern Brazil* (NE-Br)           | 7 ( <i>n</i> = 99)          | 54 ( <i>n</i> = 99)           |
| Eastern Brazil (E-Br)                  | 21 ( <i>n</i> = 463)        | 318 ( <i>n</i> = 463)         |
| Trindade and Martin Vaz Islands (T-MV) | 21 ( <i>n</i> = 320)        | 787 ( <i>n</i> = 321)         |
| Southeastern Brazil (SE-Br)            | 24 ( <i>n</i> = 768)        | 736 ( <i>n</i> = 768)         |
| Rio Grande (RGr)                       | 22 ( <i>n</i> = 763)        | 1683 ( <i>n</i> = 762)        |
| <b>Total</b>                           | <b>46 (<i>n</i> = 2633)</b> | <b>3648 (<i>n</i> = 2532)</b> |

\*Northeastern Brazil includes the São Pedro and São Paulo Islands, Fernando de Noronha and Atoll das Rocas, and Northeastern Brazil Ecoregions from Spalding et al. (2007).

## FIGURE LEGENDS

**Figure 1** Study area with (a) main surface and subsurface currents off Brazil (light grey), and (b) with bold line representing the Marine Ecoregions of the World adapted from Spalding et al. (2007). Colour represents Provinces by Spalding et al. (2007): darker green = North Brazil Shelf; blue = Tropical Southwestern Atlantic; light green = Warm Temperate Southwestern Atlantic. Acronyms for Ecoregions below the map. In (a), R = ring-formation zone; NBC = North Brazil Current; NECC = North Equatorial Counter Current; EUC = Equatorial Undercurrent; SEUC = South Equatorial Undercurrent; SEC = South Equatorial Current; BC = Brazil Current; SACW = South Atlantic Central Water; MC = Malvinas Current. In (b), symbols represents São Pedro and São Paulo Rocks (triangle), Fernando de Noronha and Atoll das Rocas (circle), and Trindade and Martin Vaz Islands (square).

**Figure 2** Spatial number ( $n$ ) of seabird counts (effort), mean abundance, and species richness, per  $1^{\circ} \times 1^{\circ}$  grids, between 2009–2018 at-sea surveys off Brazil, Atlantic Ocean. Dashed line represents the 200 m isobath, and the bold line represents the Marine Ecoregions of the World by Spalding et al. (2007).

**Figure 3** Spatial distribution of Charadriiformes (green) and Procellariiformes (blue) species richness and mean abundance, per  $1^{\circ} \times 1^{\circ}$  grids, between 2009–2018 at-sea surveys off Brazil, Atlantic Ocean. Dashed line represents the 200 m isobath, and the bold line represents the Marine Ecoregions of the World by Spalding et al. (2007).

**Figure 4** Species richness rarefaction/extrapolation curves based on (a) number of samples and (b) sample coverage, constructed with incidence data recorded in each Marine Ecoregion of the World (adapted from Spalding et al., 2007), 2009–2018, off Brazil, Atlantic Ocean.

**Figure 5** Hierarchical Clusters based on occurrence data of seabirds recorded off Brazil, 2009–2018, Atlantic Ocean, for *a priori* biogeographic units. (a) Provinces and (b) Marine Ecoregions of the World (adapted from Spalding et al., 2007).

**Figure 6** Canonical Analysis of Principal Coordinates for abundance data of seabirds recorded at-sea off Brazil, 2009–2018, Atlantic Ocean, in each Marine Ecoregion of the World (adapted from Spalding et al., 2007).

**Figure 7** Generalized Additive Model for species richness related to latitude, for occurrence data of seabirds off Brazil, 2009–2018, Atlantic Ocean. (a) All species; (b) Procellariiformes; (c) Charadriiformes.

Fig. 1 –

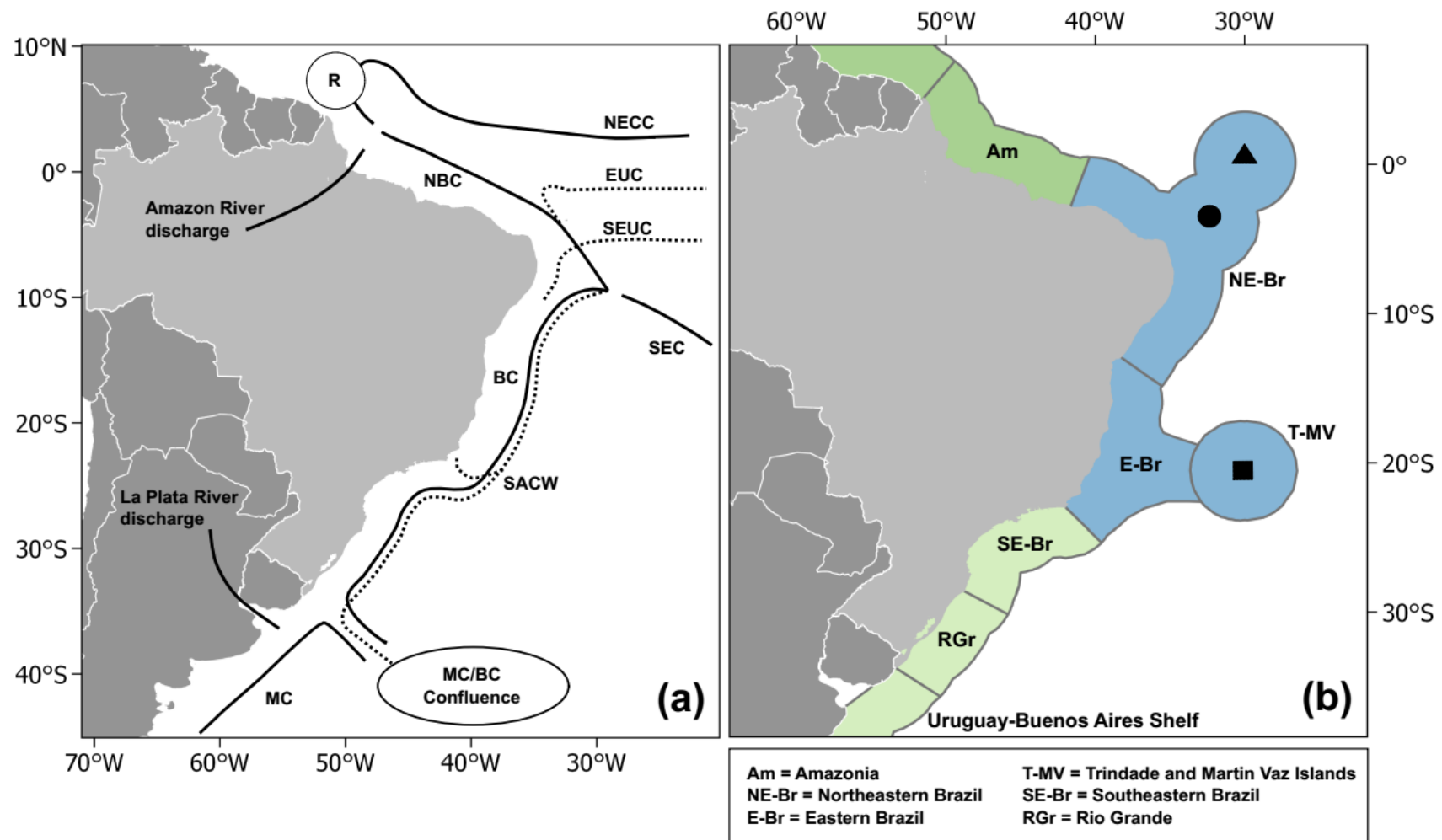


Fig. 2 –

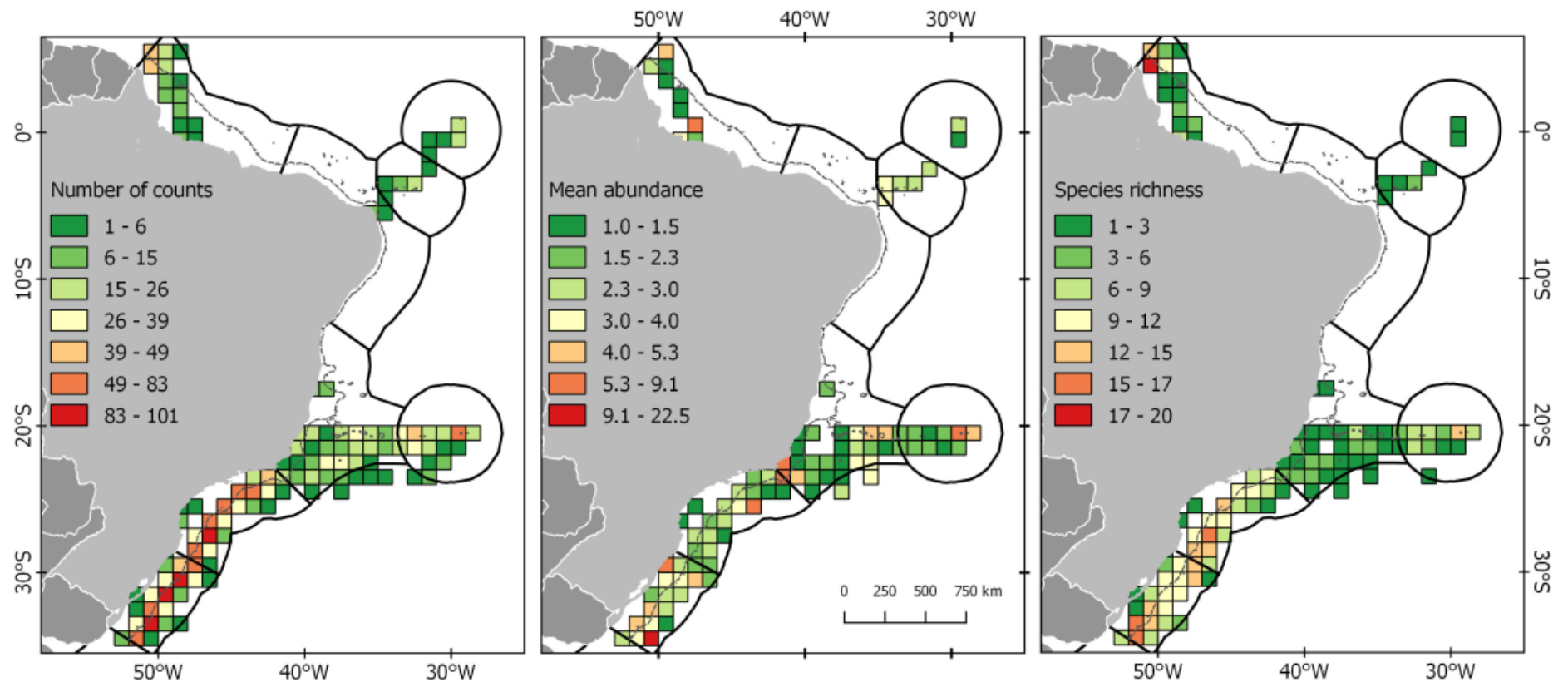


Fig. 3 –

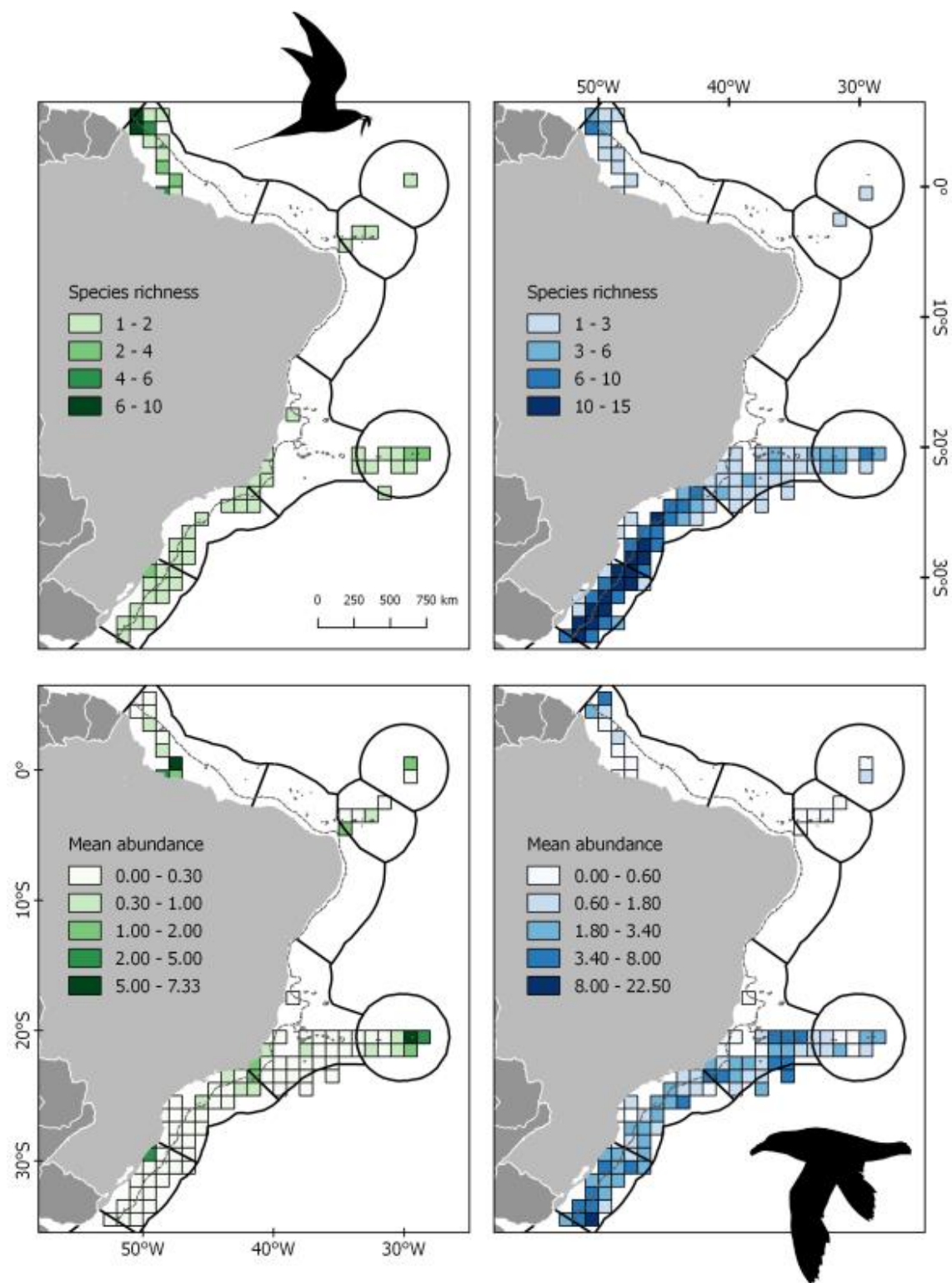


Fig. 4 –

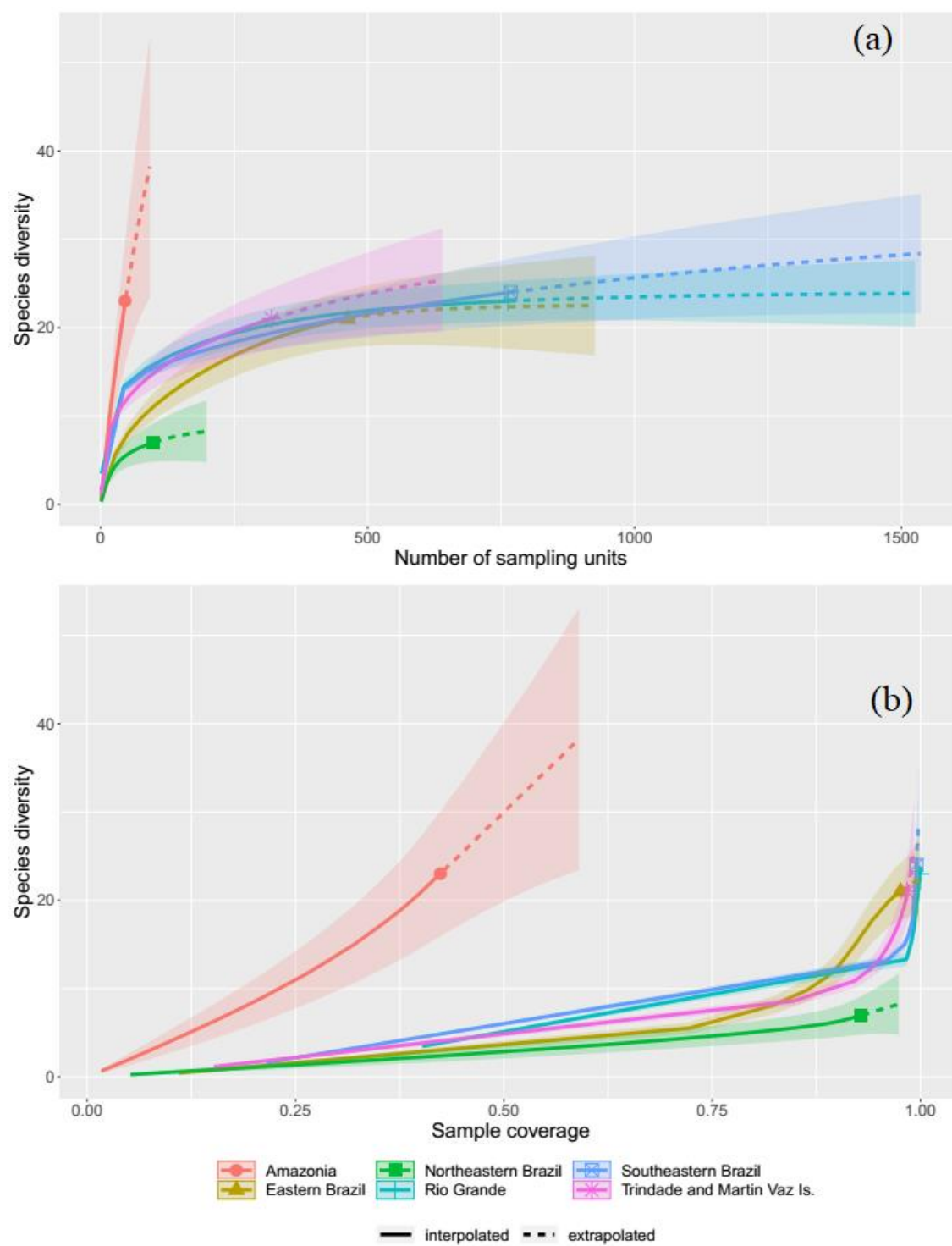
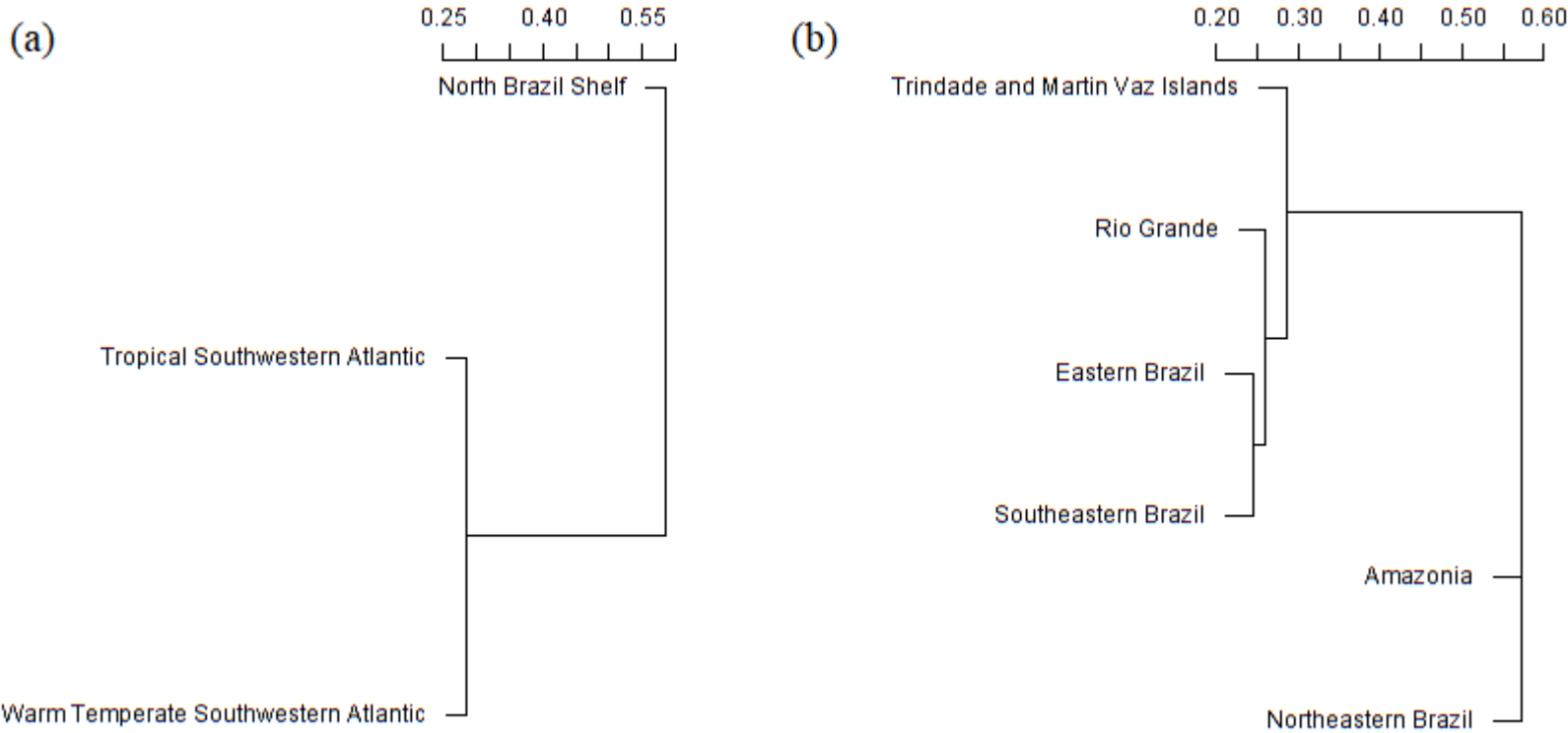


Fig. 5 –





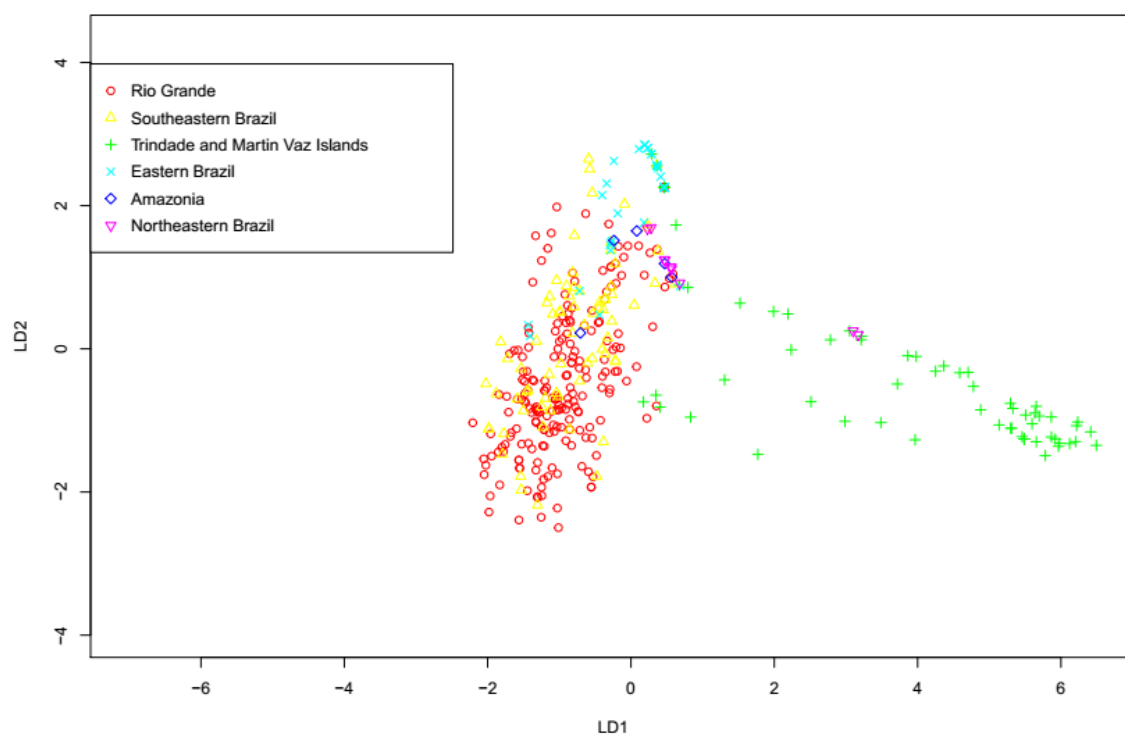
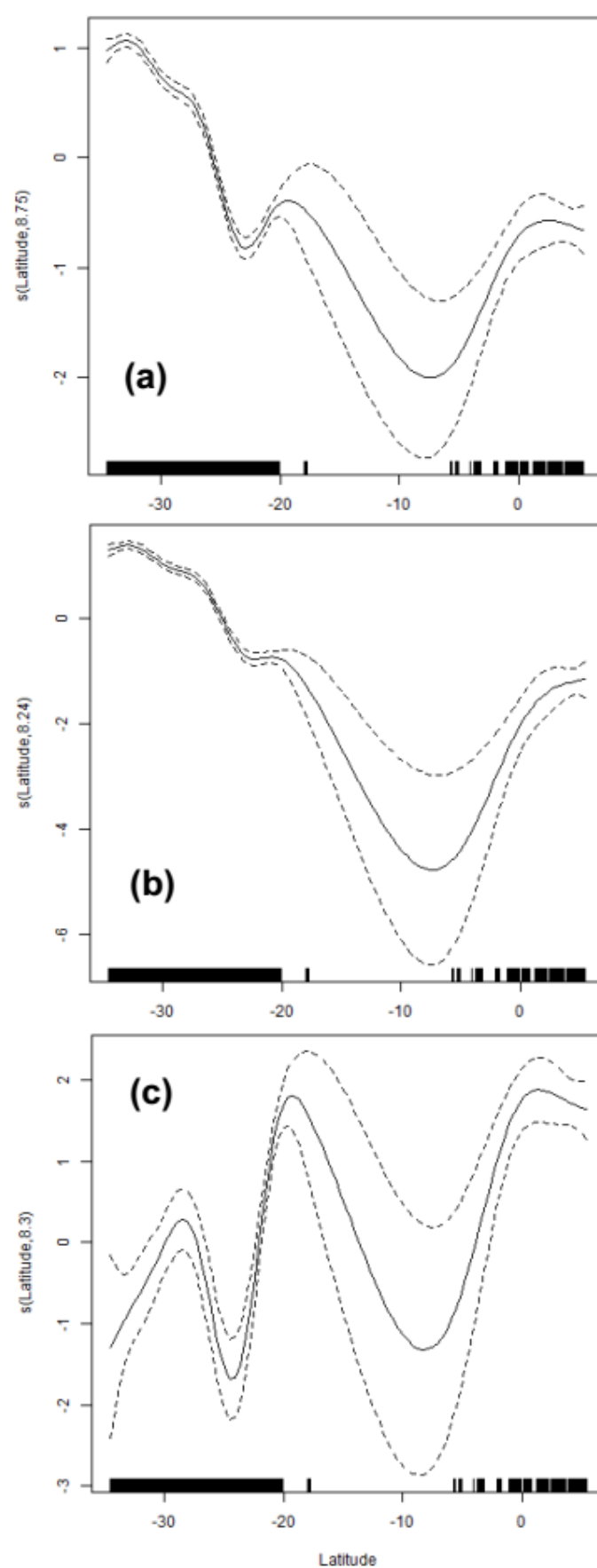
**Fig. 6 –**

Fig. 7 –



**APPENDIX 1** Orders (bold), families (normal), and species (italics) of seabirds recorded off Brazil, Atlantic Ocean, 2009–2018, based on at-sea counts. In addition, migrant/resident status, Ecoregion' occurrence, and incidence (number of total occurrences) for each species is given.

| Taxon                              | Status <sup>a</sup> | ECOREGIONS <sup>b</sup> |       |      |       |     |      | Incidence |
|------------------------------------|---------------------|-------------------------|-------|------|-------|-----|------|-----------|
|                                    |                     | Am                      | NE-Br | E-Br | SE-Br | RGr | T-MV |           |
| Procellariiformes (24 species)     |                     |                         |       |      |       |     |      |           |
| Diomedidae                         |                     |                         |       |      |       |     |      |           |
| <i>Thalassarche chlororhynchos</i> | M (S)               |                         |       | X    | X     | X   |      | 672       |
| <i>Thalassarche melanophris</i>    | M (S)               |                         |       | X    | X     | X   |      | 465       |
| <i>Diomedea sanfordi</i>           | M (S)               |                         |       |      | X     |     |      | 1         |
| <i>Diomedea exulans</i>            | M (S)               |                         |       |      | X     |     |      | 9         |
| Procellariidae                     |                     |                         |       |      |       |     |      |           |
| <i>Macronectes giganteus</i>       | M (S)               |                         |       |      |       | X   |      | 3         |
| <i>Macronectes halli</i>           | M (S)               |                         |       |      |       | X   |      | 2         |
| <i>Daption capense</i>             | M (S)               |                         |       |      | X     | X   |      | 74        |
| <i>Pterodroma mollis</i>           | M (S)               |                         |       |      | X     | X   | X    | 13        |
| <i>Pterodroma incerta</i>          | M (S)               |                         |       | X    | X     | X   | X    | 373       |
| <i>Pterodroma arminjoniana</i>     | R                   |                         |       |      |       |     | X    | 85        |
| <i>Pachyptila desolata</i>         | M (S)               |                         |       |      | X     |     |      | 1         |

|                                   |       |   |   |   |   |   |   |     |
|-----------------------------------|-------|---|---|---|---|---|---|-----|
| <i>Bulweria bulwerii</i>          | M (N) |   |   | X | X |   |   | 3   |
| <i>Procellaria aequinoctialis</i> | M (S) |   |   | X | X | X |   | 315 |
| <i>Procellaria conspicillata</i>  | M (S) |   |   | X | X | X | X | 689 |
| <i>Calonectris borealis</i>       | M (N) | X |   | X | X | X | X | 210 |
| <i>Calonectris edwardsii</i>      | M (N) |   |   | X | X | X | X | 49  |
| <i>Puffinus griseus</i>           | M (S) |   |   | X | X | X | X | 11  |
| <i>Puffinus gravis</i>            | M (S) |   |   | X | X | X | X | 685 |
| <i>Puffinus puffinus</i>          | M (N) | X |   | X | X | X | X | 223 |
| Hydrobatidae                      |       |   |   |   |   |   |   |     |
| <i>Fregatta grallaria</i>         | M (S) |   |   |   | X |   |   | 3   |
| <i>Fregatta tropica</i>           | M (S) |   |   |   | X |   | X | 6   |
| <i>Oceanites oceanicus</i>        | M (S) | X | X | X | X | X | X | 319 |
| <i>Oceanodroma leucorhoa</i>      | M (N) | X |   |   |   |   |   | 14  |
| <i>Hydrobates pelagicus</i>       | M (N) |   |   |   |   |   | X | 1   |
| <b>Suliformes (4 species)</b>     |       |   |   |   |   |   |   |     |
| Fregatidae                        |       |   |   |   |   |   |   |     |
| <i>Fregata magnificens</i>        | R     | X | X | X | X | X |   | 48  |
| Sulidae                           |       |   |   |   |   |   |   |     |
| <i>Sula dactylatra</i>            | R     | X | X | X | X |   | X | 56  |
| <i>Sula sula</i>                  | R     | X | X | X |   |   | X | 20  |

|                                     |       |   |   |   |   |   |   |    |
|-------------------------------------|-------|---|---|---|---|---|---|----|
| <i>Sula leucogaster</i>             | R     |   | X | X | X |   | X | 37 |
| <b>Charadriiformes (18 species)</b> |       |   |   |   |   |   |   |    |
| Scolopacidae                        |       |   |   |   |   |   |   |    |
| <i>Numenius hudsonicus</i>          | M (N) | X |   |   |   |   |   | 3  |
| Stercorariidae                      |       |   |   |   |   |   |   |    |
| <i>Stercorarius skua</i>            | M (N) | X |   |   |   |   |   | 11 |
| <i>Stercorarius maccormicki</i>     | M (S) |   |   |   | X | X |   | 4  |
| <i>Stercorarius pomarinus</i>       | M (N) | X |   |   | X | X | X | 55 |
| <i>Stercorarius parasiticus</i>     | M (N) | X |   |   |   |   |   | 3  |
| <i>Stercorarius longicaudus</i>     | M (N) | X |   |   |   |   |   | 5  |
| Laridae                             |       |   |   |   |   |   |   |    |
| <i>Leucophaeus atricilla</i>        | M (N) | X |   |   |   |   |   | 20 |
| Sternidae                           |       |   |   |   |   |   |   |    |
| <i>Anous stolidus</i>               | R     | X | X |   |   |   | X | 51 |
| <i>Gysis alba</i>                   | R     |   |   |   |   |   | X | 64 |
| <i>Onychoprion fuscatus</i>         | R     | X | X | X |   |   | X | 41 |
| <i>Phaetusa simplex</i>             | R     | X |   |   |   |   |   | 12 |
| <i>Sterna hirundo</i>               | M (N) | X |   |   | X | X |   | 18 |
| <i>Sterna dougallii</i>             | M (N) | X |   |   |   |   |   | 2  |
| <i>Sterna paradisaea</i>            | M (N) | X |   |   |   |   |   | 3  |

|                              |   |   |   |   |   |   |    |
|------------------------------|---|---|---|---|---|---|----|
| <i>Sterna hirundinacea</i>   | R |   | X |   | X | X | 10 |
| <i>Sterna trudeaui</i>       | R |   | X | X |   | X | 6  |
| <i>Thalasseus acufavidus</i> | R | X |   |   |   |   | 3  |
| <i>Thalasseus maximus</i>    | R | X | X |   |   |   | 4  |

---

<sup>a</sup>R = Resident taxa; M = Migratory taxa, from South (S) or North (N) Hemisphere. According to Piacentini et al. (2015).

<sup>b</sup>Am = Amazonia; NE-Br = Northeastern Brazil; E-Br = Eastern Brazil; SE-Br = Southeastern Brazil; RGr = Rio Grande; T-MV = Trindade and Martin Vaz Islands. Ecoregions according to Spalding et al. (2007), unless for 'Northeastern Brazil' that was adapted (see main text)

## APPENDIX 2 R code

```
#####
## Seabirds challenge the limits of marine ecoregions and latitudinal gradient theory of
species richness
## Journal of Biogeography (20XX), v. XX, pp. XXX-XXX
##
## Code by Nicholas W Daudt
## R version 3.6.0
#####
```

### ### Load required packages###

```
library(readxl) ##For read and export .xlsx files
library(openxlsx) ##For read and export .xlsx files
library(lubridate) ##Date manipulation
library(plyr) ##Data manipulation
library(tidyverse) ##Data manipulation
library(reshape2) ##Data manipulation
library(matrixStats) ##Data manipulation and summaries
library(sf) ##Spatial join
library(ggplot2) ##Graphical plots
library(BiodiversityR) ##Multivariate ecological analysis
library(vegan) ##Multivariate ecological analysis
library(labdsv) ##Multivariate ecological analysis
library(mgcv) ##GAM
library(iNEXT) ##Species richness extrapolation
```

### ### Spatial join – Seabird data with MEOWs###

```
allData.env <- read_excel("./allData.env.xlsx")

# Transform the data.frame as a 'simple-feature' shapefile
```

```

allData.env_MEOW <- as.data.frame(allData.env)%>%
  sf::st_as_sf(coords = c(86,85)) %>% #'coords' pick up 'Lat' and 'Long' columns and
  create a 'geometry' column with that information
  sf::st_set_crs(4326)

# Read the data to join (MEOW's shapefile)
MEOW <- st_read("./MEOW_SWAtlantic.shp")

# Join the MEOW's arguments in the allData data.frame
allData.env_MEOW <- st_join(allData.env_MEOW,MEOW)
# Removing undesired columns created in the last steps
allData.env_MEOW <- allData.env_MEOW[,-c(91,93,95,97:100)]

allData.env_MEOW_df <- as.data.frame(allData.env_MEOW)
allData.env_MEOW_df <- allData.env_MEOW_df[,-c(94)] # 'geometry' excluded [type
= "list"]...

#### Ten (10) sample-points were off the MEOW's border, so, do not 'join' into any
MEOW.
# Manualy, I designate MEOW classifications for:
#
allData.env_MEOW_df$ECOREGION <-
replace_na(allData.env_MEOW_df$ECOREGION, "Eastern Brazil")
allData.env_MEOW_df$PROVINCE <-
replace_na(allData.env_MEOW_df$PROVINCE, "Tropical Southwestern Atlantic")
##
# All from "Eastern Brazil" Ecoregion, and "Tropical Southwestern Atlantic"
PROVINCE.
####

## For this work, we consider "Northeastern Brazil" as 'NE Brazil + ASPSP + Rocas
Atoll and Noronha':

```



```
allData.env_MEOW_df$ECOREGION[allData.env_MEOW_df$ECOREGION=="Fernando de Naronha and Atoll das Rocas" |
```

```
    allData.env_MEOW_df$ECOREGION=="Sao Pedro and Sao Paulo Islands"]
<- "Northeastern Brazil"
```

```
## Saving it...
```

```
write.xlsx(allData.env_MEOW_df, "./allData.env_MEOW.xlsx")
```

```
### Open abund_allData, occ_allData####
```

```
# allData <- read_excel("./allData.env_MEOW.xlsx")
```

```
abund_allData <- read_excel("./abund_allData.xlsx")
```

```
occ_allData <- read_excel("./occ_allData.xlsx")
```

```
### iNEXT ####
```

```
### Subset just SPP and ECOREGIONS
```

```
df<-occ_allData[,c(2:47,62)] #62 = ECOREGIONS
```

```
### Subset ECOREGIONS
```

```
North <- subset(df, df$ECOREGION %in% c("Amazonia"))
```

```
Northeast <- subset(df, df$ECOREGION %in% c("Northeastern Brazil"))
```

```
East <- subset(df, df$ECOREGION %in% c("Eastern Brazil"))
```

```
Trindade <- subset(df, df$ECOREGION %in% c("Trindade and Martin Vaz Islands"))
```

```
Southeast <- subset(df, df$ECOREGION %in% c("Southeastern Brazil"))
```

```
RioGrande <- subset(df, df$ECOREGION %in% c("Rio Grande"))
```

```
### Removing the column 'ECOREGION', and transposing the data.frame
```

```
North <- data.frame(t(North[,1:46]))
```

```
Northeast <- data.frame(t(Northeast[,1:46]))
```

```
East <- data.frame(t(East[,1:46]))
```

```
Trindade <- data.frame(t(Trindade[,1:46]))
```

```
Southeast <- data.frame(t(Southeast[,1:46]))
```

```

RioGrande <- data.frame(t(RioGrande[,1:46]))

### Adding it to a 'list'
list_Ecoregion <- list('Amazonia'=North,
                      'Northeastern Brazil'=Northeast,
                      'Eastern Brazil'=East,
                      'Trindade and Martin Vaz Is.'=Trindade,
                      'Southeastern Brazil'=Southeast,
                      'Rio Grande'=RioGrande)

### iNEXT function
obj <- iNEXT(list_Ecoregion, q=c(0), datatype = "incidence_raw")
      #q=0 <- spp richness itself

curve.sample_size_based <- ggiNEXT(obj, type = 1, se = TRUE) # Sample-size-based
R/E curve
curve.sample_completeness <- ggiNEXT(obj, type = 2, se = TRUE) # Sample
completeness curve
curve.coverage_based <- ggiNEXT(obj, type = 3, se = TRUE) # Coverage-based R/E
curves

### Hierarchical cluster####
###
# Based on ALL data...
###

allData_occ <- read_excel("./allData_MEOW.xlsx")

### Hierarchical cluster -- Ecoregions####
allData_occ$ECOREGION <- replace(allData_occ$ECOREGION,
allData_occ$ECOREGION=="Sao Pedro and Sao Paulo Islands", "Northeastern
Brazil")

```

```

allData_occ$ECOREGION <- replace(allData_occ$ECOREGION,
allData_occ$ECOREGION=="Fernando de Naronha and Atoll das Rocas",
"Northeastern Brazil")

## Calculate the sum, for each species (selected columns), on each Ecoregion, using
melt
occ_all_melt <- as.data.frame(allData_occ[c(18:87,97)]) #18:87 refers to species, 97 to
"ECOREGION"

## Excluding 'Genus sp.' and 'Family' taxa
occ_all_melt <- occ_all_melt[,-c(2,6,13,15,20,21,27,30,34,38,39,43,47,55,60,64,68)]

## Melt
occ_all_melt <- melt(occ_all_melt, id = c("ECOREGION"))

## Sum the occurrences
occ_all_melt <- occ_all_melt %>%
  group_by(ECOREGION,variable) %>%
  summarise(a = sum(value, na.rm = TRUE))

## Replace any count >=1 for 1 -- then we have just '0' and '1' values
occ_all_melt$a <- replace(occ_all_melt$a, occ_all_melt$a>=1, 1)

### Unmelt (dcast) -- rows of species to columns
all_occ <- dcast(occ_all_melt, Ecoregion ~ variable)

# Excluding columns that sum zero
rownames(all_occ) <- c("Amazonia","Eastern Brazil","Northeastern Brazil","Rio
Grande","Southeastern Brazil","Trindade and Martin Vaz Islands")
all_occ <- all_occ[,-1]
all_occ <- all_occ[, -colSums2(as.matrix(all_occ)) != 0]

```

```

### write.xlsx(all_occ, "./MEOW_occ.xlsx")

## CLUSTER ---
# Dissimilarity distance matrix "d" -- Sorensen --
d.sorensen.ecoregions <- labdsv::dsvdis(as.matrix(all_occ),index="sorensen")

## Hierarchical cluster
cluster.sorensen.ecoregions <- hclust(d.sorensen.ecoregions, method = "single") ## N
and NE as 'single' clusters
plot(cluster.sorensen.ecoregions)

### Hierarchical cluster -- Provinces####
## Calculate the sum, for each species (selected columns), on each ECOREGION, using
melt
occ_all_melt <- as.data.frame(allData_occ[c(18:87,98)]) #18:87 refeers to species, 97 to
"PROVINCE"

## Excluding 'Genus sp.' and 'Family' taxa
occ_all_melt <- occ_all_melt[,-c(2,6,13,15,20,21,27,30,34,38,39,43,47,55,60,64,68)]

## Melt
occ_all_melt <- melt(occ_all_melt, id = c("PROVINCE"))

## Sum the occurences
occ_all_melt <- occ_all_melt %>%
  group_by(PROVINCE,variable) %>%
  summarise(a = sum(value, na.rm = TRUE))

## Replace any count >=1 for 1 -- then we have just '0' and '1' values
occ_all_melt$a <- replace(occ_all_melt$a, occ_all_melt$a>=1, 1)

### Unmelt (dcast) -- rows of species to columns

```

```

all_occ <- dcast(occ_all_melt, PROVINCE ~ variable)

rownames(all_occ) <- c("North Brazil Shelf","Tropical Southwestern Atlantic","Warm
Temperate Southwestern Atlantic")
all_occ <- all_occ[,-1]
all_occ <- all_occ[, -colSums2(as.matrix(all_occ)) != 0]

### write.xlsx(all_occ, "./PROVINCE_occ.xlsx")

## CLUSTER --
# Dissimilarity distance matrix "d" -- Sorensen --
d.sorensen.provinces <- labdsv::dsvdis(as.matrix(all_occ),index="sorensen")

##
cluster.sing.province <- hclust(d.sorensen.provinces, method = "single")
plot(cluster.sing.province)

### CAP #####
# Canonical Analysis of Principal Coordinates
# BiodiversityR::CAPdiscrim()

abund_allData <- read_excel("./abund_allData.xlsx")

# Subset rows that sum, at least, 3 birds...
xx=subset(abund_allData,abund_allData$totalAbund != 0 & abund_allData$totalAbund
!= 1 & abund_allData$totalAbund != 2)

write.xlsx(xx, "./cap.xlsx")

xx <- read_excel("./cap.xlsx")
abund_birds <- xx[,c(9:71)]

```

```
abund_birds1 <- abund_birds[,-colSums(abund_birds)!=0] #Removing columns (taxa)
that sum zero
```

```
abund_env <- xx[,c(85:90,91)] # 91 = ECOREGION
abund_env$dSST<-as.numeric(abund_env$dSST) #Correcting the cell format
abund_env$ECOREGION<-as.factor(abund_env$ECOREGION) #Correcting the cell
format
```

```
zz <- BiodiversityR::CAPdiscrim(data.frame(abund_birds1) ~ ECOREGION, data =
data.frame(abund_env), dist = "bray", axes = 2, m = 0, add = FALSE)
```

```
plot1 <- ordiplot(zz, type = "none", xlim = c(-7,6.5))
ordisymbol(plot1, abund_env , "ECOREGION", legend = TRUE)
```

### **### GAM -- spRichness ~ Lat ####**

```
## Total spp richness
gam_sp.rich.lat <- gam(spRichness ~ s(Latitude), data = occ_allData, method =
"REML", family = "poisson")
gam.check(gam_sp.rich.lat)
summary(gam_sp.rich.lat)
plot(gam_sp.rich.lat)
# plot.gam(gam_sp.rich.lat, shade = TRUE, shade.col = "gray")
```

```
## Procellariiformes richness ~ Lat
occ_allData$richnessProcellariiformes <-
rowSums(occ_allData[,c(3:8,10:11,13,15:16,18:19,21,23:30,44:45)])
```

```
gam_Procella.rich.lat <- gam(richnessProcellariiformes ~ s(Latitude), data =
occ_allData, method = "REML", family = "poisson")
gam.check(gam_Procella.rich.lat)
summary(gam_Procella.rich.lat)
```

```
plot(gam_Procella.rich.lat)
```

```
## Charadriiformes richness ~ Lat
```

```
occ_allData$richnessCharadriiformes <-
```

```
rowSums(occ_allData[,c(2,12,14,17,20,22,31:40,46:47)])
```

```
gam_Charadrii.rich.lat <- gam(richnessCharadriiformes ~ s(Latitude), data =  
occ_allData, method = "REML", family = "poisson")
```

```
gam.check(gam_Charadrii.rich.lat)
```

```
summary(gam_Charadrii.rich.lat)
```

```
plot(gam_Charadrii.rich.lat)
```