



The role of island physiography and oceanographic factors in shaping species richness and turnover of nesting seabird assemblages on islands across the south-eastern Pacific

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Funding information

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Handling Editor: Leo Joseph

Abstract

Aim: For seabirds, food supplies and nest sites are largely driven by oceanographic gradients and island habitats, respectively. Research into seabirds' ecological roles in insular ecosystems is crucial to understanding processes that structure seabird nesting assemblages. We examined the influence of island physiography and oceanographic factors on the spatial variation in α - and β -diversity of nesting seabird assemblages.

Location: South-eastern Pacific Ocean.

Taxon: Birds.

Methods: We compiled data from 53 seabirds breeding on 41 coastal and oceanic islands using different sources: our field records, online databases, environmental reports and literature. We used generalized linear models (GLM) to describe the effect of island physiography (area, elevation and isolation) and oceanographic factors (surface temperature, salinity and primary productivity) on seabird species richness (α -diversity). We applied multivariate GLM to test the effects of physiographic and oceanographic predictors on species composition (β -diversity). We used Jaccard dissimilarities on species occurrences per island to calculate β -diversity partitioned into turnover and nestedness. Polynomial models allowed us to model these metrics against geographical and environmental gradients and so analyse patterns in seabird β -diversity across spatial scales.

Results: Species richness was highest in Galápagos, Pitcairn and Rapa Nui. Changes in seabird α -diversity across islands were determined by island area and distance to South America but not by oceanographic variables. Physiographic and oceanographic factors were significant in determining β -diversity. Changes in β -diversity were mostly due to species replacement (β -turnover) across three major island Systems (Galápagos Archipelago, Chilean coastal islands and oceanic islands of the south-eastern Pacific). The contribution of β -nestedness was restricted to small scales (within archipelagos).

Main conclusions: Physiographic and oceanographic factors explain species diversity of seabird assemblages on islands of the south-eastern Pacific. Oceanographic

variables did not affect species richness but significantly influenced species composition. Change in species composition reflects gradients across three marine biogeographical realms: Temperate South, Eastern Indo-Pacific and Tropical Eastern Pacific. The low degree of species nestedness may reflect multiple evolutionary origins.

KEYWORDS

assemblage structure, beta diversity, biogeography, coastal islands, oceanic islands, seabirds, species richness

1 | INTRODUCTION

Islands are high-priority targets for conservation for multiple taxa (Bellard, Rysman, Leroy, Claud, & Mace, 2017; Spatz et al., 2014). The sparse islands and islets distributed along oceanic and coastal waters are the nesting grounds of many seabird species. The seabirds represent not only one of the most conspicuous groups of the marine environment but also one of the most endangered (Croxall et al., 2012; Spatz et al., 2014; Webb & Mindel, 2015). Seabirds perform a crucial role in insular ecosystems by linking terrestrial and marine food webs (McCauley et al., 2012; Otero, Peña-lastra, Pérez-alberti, Ferreira, & Huerta-diaz, 2018), and are frequently described as top consumers that modulate nutrient transfer across ecosystems by feeding on productive waters and depositing nutrient-rich guano inland (Sekercioglu, 2006).

Processes controlling alpha and beta diversity patterns in seabirds on islands are rarely addressed in ecological studies. General studies that do not explicitly address islands typically have stressed the importance of oceanographic factors as drivers of seabird diversity in oceanic waters (Bost et al., 2009; Chown & Gaston, 1999; Davies, Irlich, Chown, & Gaston, 2010; Hashmi & Causey, 2008; Wahl, Ainley, Benedict, & DeGange, 1989). The importance of island physiography (i.e., island area, elevation and isolation) in driving local species richness, as predicted by the classical theory of island biogeography (MacArthur & Wilson, 1963; Whittaker, Triantis, & Ladle, 2008), has focused primarily on terrestrial birds (Chown, Gremmen, & Gaston, 1998; Harrison, Ross, & Lawton, 1992; Luna-Jorquera, Fernández, & Rivadeneira, 2012; Melo, Rangel, & Diniz-Filho, 2009; Veech & Crist, 2007). In contrast, the diversity of seabirds nesting on islands has been rarely studied (e.g., Luna-Jorquera et al., 2012; Wahl et al., 1989). As far as we are aware, no studies have addressed how the β -diversity of nesting seabirds is affected by island physiography and gradients in oceanographic parameters.

Previous studies have highlighted the strong dependence of seabirds on bottom-up processes that regulate food availability (Pakhomov & McQuaid, 1996; Weichler, Garthe, Luna-Jorquera, & Moraga, 2004). Such processes are strongly affected by large-scale oceanographic factors and processes that modulate pelagic primary production (Schneider, 1991). Besides large-scale oceanic processes, seabird assemblages on oceanic islands can be affected by local factors, such as the presence of predators

(mostly terrestrial vertebrates; Bolton, Stanbury, Baylis, & Cuthbert, 2014; Jones et al., 2008), distance from foraging zones (Ballance, Ainley, Ballard, & Barton, 2009; Weimerskirch et al., 2003) and availability of suitable nesting habitats (e.g., cliffs, shelters, soil, or trees; Newton, 1994; Pöysä & Pöysä, 2002). Therefore, oceanographic factors that modulate food availability on foraging grounds and island physiography could explain the various seabird α - and β -diversity patterns within and across archipelagos.

Considering the ecological role that seabirds play in insular ecosystems and their current conservation threats, it is crucial to elucidate patterns and processes that regulate α - and β -diversity patterns. An understanding of species turnover and nestedness, the two components of β -diversity, offers additional insights into the processes that structure seabird communities. For instance, significant nestedness at large scales suggests rather strong biogeographical connections (Greve, Gremmen, Gaston, & Chown, 2005). In contrast, lack of nestedness at small geographical scales may suggest the role of local factors affecting extinction/colonization (Luna-Jorquera et al., 2012). In this study, we investigated how the role of physiographic and oceanographic factors control local species richness (α -diversity) and composition (β -diversity) of nesting seabirds in insular systems (coastal and oceanic), using the south-eastern Pacific as a study model. We tested the following four working hypotheses:

1. α -diversity will be positively affected by island area and elevation as these variables are directly related to the availability of nesting habitats.
2. Oceanographic variables will also significantly affect α -diversity as they govern ocean productivity and, hence, the distribution of foraging grounds near islands.
3. As oceanographic gradients observed across large spatial scales impose major filters for species establishment, we expect that increasing geographical and environmental distance will be positively related to species turnover (β -diversity).
4. In contrast, we expect that species nestedness will be dominant at the smallest spatial scales (i.e. within archipelagos), as it reflects differences in availability and quality of nesting habitat among islands. Thus, we expect a negative relationship between nestedness and geographical and spatial distances.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area extended longitudinally from 130°44'W to 70°31'W and latitudinally from 1°40'N to 38°22'S. The dataset included 42 islands of six archipelagos: Pitcairn (4 islands), Rapa Nui (4), Desventuradas (3), Juan Fernández (3), Galápagos (13) and Chilean coastal islands (15). Thus, the islands of our dataset have varying degrees of isolation from other islands and the mainland and are distributed within different biogeographical realms (Costello et al., 2017; Figure 1). Most of the oceanic islands are located on the Nazca Tectonic Plate, except for the Pitcairn Archipelago which is located on the Pacific Plate. These islands are all part of chains of volcanic islands and seamounts.

2.2 | Environmental variables

We compiled information on island characteristics from the literature and online databases. After removing highly collinear variables (i.e., correlation coefficient > 0.8), we considered seven environmental variables as predictors in the analyses: island area (km²), island elevation (m), distance to the mainland (km), human density (individuals per km²), sea surface salinity (PSS), sea surface temperature (°C) and primary productivity (g m⁻³ day⁻¹; Appendix S1). Island area, elevation and distance from the mainland were obtained from the literature or estimated using tools available in 'R' (R Core Team, 2016) and 'Google Earth' (www.google.com/earth). We derived data on human density from public databases provided by national institutes

of statistics and censuses (see metadata in Appendix S1). All oceanographic variables were extracted from the raster maps available in the 'Bio-ORACLE' online database (Assis et al., 2018; Tyberghein et al., 2012). The raster resolutions of these maps were approximately 9.2 km at the equator. We used a 50 km radius buffer around the centre of each island to calculate the average values of each oceanographic variable using the R package 'raster' (Hijmans, 2017).

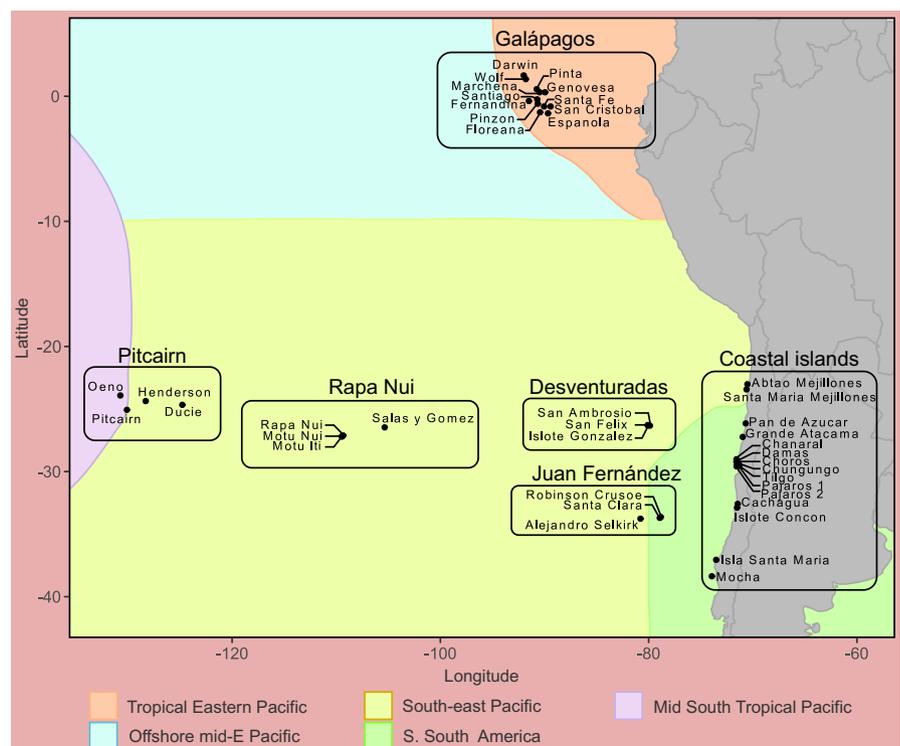
2.3 | Seabird assemblages

We compiled data on nesting occurrences of 53 seabird species (Appendix S1) in coastal and oceanic islands of the south-eastern Pacific from the literature, online databases and unpublished reports. Most of the consulted literature was published in the past 30 years, although we also included older publications to reference confirmed reports on some islands (see metadata in Appendix S1). For the majority of the Chilean islands, we used information on seabirds from our field records from multiple expeditions conducted over 19 years (1999–2018) on Chilean coastal islands, and 5 years (2013–2018) on Chilean oceanic islands (i.e., Desventuradas, Rapa Nui and Juan Fernández). All of the seabird information was organized in a binary matrix of species occurrence (1 = presence, 0 = absence) for each island (Appendix S1).

2.4 | Data analysis

We performed all analyses and graphs in the 'R' software (R Core Team, 2016) and its associated packages. Our data and R scripts are

FIGURE 1 Locations of the oceanic and coastal islands included in the study. Coloured zones indicate biogeographical realms, as described in Costello et al. (2017)



available at https://datadryad.org/stash/share/cHIMef7q6Z2Mf8IsWW3ge_O0R8_yKfBOsBiKd-aG1cs.

2.4.1 | Seabird α -diversity – Hypotheses 1 and 2

We measured the α -diversity of seabirds of each island by quantifying species richness, measured as the total sum of nesting seabird species on each island. Before the analyses, we used the Shapiro–Wilk test to check the normality of all environmental variables (i.e., island characteristics and oceanographic variables). Environmental variables that differed from the normal distribution were adjusted by applying either square root or $\log_{10}(x + 1)$ transformations. We analysed the relationships between seabird species richness and environmental variables by fitting generalized linear models (GLM) based on *Poisson* distribution and *log*-link function. Model selection and averaging were performed using the R package ‘MuMIn’ (Barton, 2018). The function *dredge* was used to perform a model selection routine based on the lowest second-order Akaike information criterion (AICc) and applied to 128 different model subsets. We applied the function *model.avg* to perform full model averaging, considering the best model subsets ($AIC_w > 0.05$). We plotted the partial residuals associated with each environmental variable to depict their effect on species richness. The final model considered the environmental variables island area (\log_{10} transformed), island elevation (square root transformed), distance from the mainland (square root transformed), human density (square root transformed), salinity, superficial primary productivity and sea surface temperature. Finally, we used residual-distance correlograms and the Moran’s *I* test routines in the R packages ‘ape’ (Paradis, Claude, & Strimmer, 2004) and ‘ncf’ (Bjornstad & Cai, 2018) to assess the spatial independence of the GLM results.

2.4.2 | Seabird β -diversity – Hypotheses 3 and 4

We applied the routines in the R package ‘betapart’ (Baselga & Orme, 2012) to calculate the partitioned β -diversity, which separates the turnover and nestedness-resultant components. The β -turnover component reflects species replacement, while β -nestedness reflects differences in species richness. These components are derived from the dissimilarity index chosen to describe β -diversity, which is frequently referred to as β -total. We used Jaccard dissimilarities on species occurrences per island to calculate β -diversity. The relationship between β -diversity and geographical and environmental distances was analysed using linear models based on a third-degree polynomial fit. Geographical distances were calculated using the *distm* routine in the R package ‘geosphere’ (Hijmans, 2017). Environmental distances were represented as Euclidean distances of a scaled and centred environmental data matrix. The correlation between geographical and environmental distances was analysed using the Mantel test in the R package ‘ade4’ (Dray & Dufour, 2007).

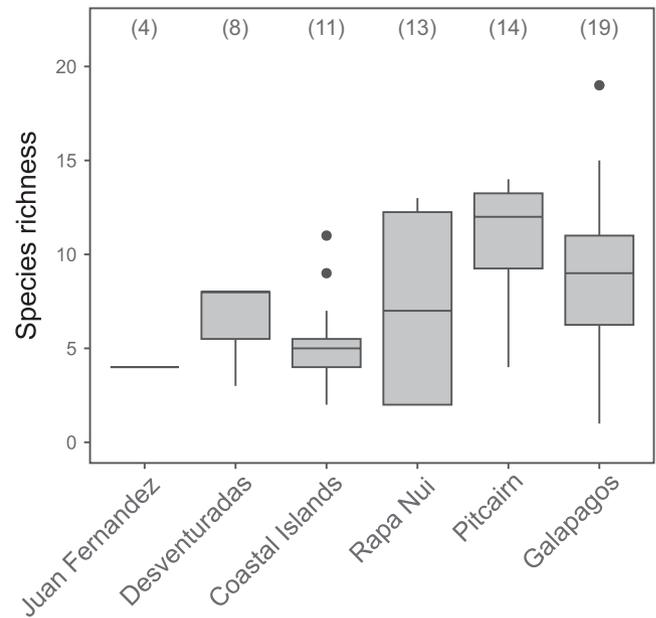


FIGURE 2 Species richness of nesting seabirds across archipelagos of the south-eastern Pacific Ocean. Values in parentheses indicate the total species richness of each archipelago

We fitted multivariate GLM models to analyse the effect of environmental variables on seabird species composition (i.e., spatial turnover). The multivariate GLM was based on a *binomial* distribution and included the same predictor variables used in the global model for univariate analyses. The analysis was performed using the function *manyglm* of the R package ‘mvabund’ (Wang, Naumann, Wright, & Warton, 2012). The significance of the model terms was assessed using analysis of deviance considering $\alpha = 0.01$. Since ordinations are a good way to represent multivariate data graphically, we performed a canonical analysis of principal coordinates (CAP, or distance-based redundancy analysis; Anderson & Willis, 2003; Legendre & Andersson, 1999) to depict changes in seabird assemblage composition across islands in relation to environmental variables. CAP is a model-based ordination technique that can represent changes in species composition given specific hypotheses (i.e., environmental variables). The analysis was based on a resemblance matrix of Jaccard distances of species occurrences and all of the environmental predictors. Although CAP does not necessarily represent the fitted values of multivariate GLMs, we observed that the function *capscale* in the R package ‘vegan’ (Oksanen et al., 2009) produced CAP ordinations that were consistent with our multivariate GLM results (data not shown). The ordination was plotted using the R package ‘ggplot2’ (Wickham, 2009).

3 | RESULTS

3.1 | Seabird α -diversity

Seabird species richness varied markedly across archipelagos and islands (Figure 2). The islands with the highest species richness were

Santa Cruz (Galápagos, 19 nesting species) and the Polynesian islands of Henderson (Pitcairn, 14), Motu Nui (Rapa Nui, 13) and Ducie (Pitcairn, 13). The Pitcairn Islands presented the highest average species richness, with 10.5 ± 4.5 (mean \pm standard deviation) nesting species per island. Even though Pinta Island in the Galápagos Archipelago showed the lowest species richness (only one nesting species), the Juan Fernández Archipelago had the lowest average species richness, with four species per island.

Only six of the 128 possible model fits for species richness had $AIC_w > 0.05$ (Table 1), and these were averaged together to produce a final model (Tables 2). Species richness showed a significant positive relationship with island area ($p < 0.05$, Figure 3a) and distance from the continent ($p < 0.01$, Figure 3b). Island elevation, water temperature, salinity, primary productivity and human density had no significant effects on species richness. There was no evidence of significant spatial autocorrelation of the residuals (Figure S1).

3.1.1 | Seabird β -diversity

The structure of seabird assemblages changed notably across the different island systems, and it was highly related to water temperature, primary productivity, island area, island elevation and distance to the continent (Figure 4; Table 3). The CAP ordination showed clear gradients in seabird species assemblages along latitudinal and longitudinal gradients, which also reflected differences across archipelagos (Figure 4). The first axis of the ordination explained 22% of the total variation and was most related to gradients in temperature, primary productivity and distance from the continent (Table 4). This axis separated oceanic islands from coastal islands, which were mostly driven by species such as the Humboldt penguin (*Spheniscus humboldti*) and the kelp gull (*Larus dominicanus*). The second axis accounted for 13% of the total variation and was most related to salinity, island area and elevation, and distance to the continent (Table 4).

This axis separates the Galápagos Archipelago from the other islands, which is mostly explained by the high number of seabird species that do not nest in the southern Pacific, such as the Nazca booby (*Sula granti*), the Galápagos shearwater (*Puffinus subalaris*), the brown pelican (*Pelecanus occidentalis*) and the wedge-rumped storm-petrel (*Hydrobates tethys*). This axis also divides the oceanic islands of the south-eastern Pacific from the other islands. The archipelagos of Desventuradas and Juan Fernández were grouped with Polynesian islands, indicating similarities in the composition of their seabird assemblages.

Partitioning β -diversity revealed that changes in seabird assemblage structure were primarily explained by the β -turnover component (species replacement), which increased with geographical and environmental distances (Figure 5). The β -turnover component tended to be predominant at large spatial scales (i.e., across archipelagos; Figure 5b). The β -nestedness component decreased with increasing geographical distances and tended to be higher at smaller spatial scales (i.e., within archipelagos; Figure 5c). The positive relationship between geographical and environmental distances (Mantel test: $p < 0.001$, $r = 0.59$) explains the similarities of their respective effects on seabird β -diversity (Figure 5). The global values of β -diversity also indicated large and small contributions of species turnover (β -turnover = 0.96) and nestedness (β -nestedness = 0.01), respectively.

4 | DISCUSSION

Our results show that even though both α - and β -diversity of nesting seabirds respond to physiographic variables, oceanographic variables only affected seabird β -diversity. Species richness was positively related to the island area, which is consistent with our first hypothesis. Contrary to our expectations, island elevation did not affect species richness. This result partially rejects our first hypothesis and suggests

TABLE 1 Summary of the model selection and averaging routines used to estimate the best model fit that describes the general effects of island physiography and oceanographic variables on the species richness of nesting seabirds on islands of the south-eastern Pacific Ocean. It shows the resulting coefficients of the global GLM model, the selected models for model averaging (i.e., full averaging on models with $AIC_w > 0.05$) and the final averaged model. Different generalized linear models fits were compared using corrected Akaike information criterion (AICc), Akaike weights (AICw) and adjusted R^2

	(Int.)	Area	Prim. prod.	Salinity	Distance	Elevation	Human d.	Temp.	df	AICc	AICw	Adj. R^2
Global model	5.999	0.223	11.322	-0.130	0.021	-0.020	-0.021	-0.016	8	235.80	0.004	0.56
Model selection table (only the 6 best models)												
	1.345	0.227	10.785	—	0.015	-0.020	—	—	5	227.88	0.20	0.56
	1.868	0.279	—	—	0.007	-0.024	—	—	4	229.44	0.09	0.51
	1.037	0.098	12.647	—	0.017	—	—	—	4	229.87	0.07	0.51
	4.375	0.206	11.173	-0.089	0.018	-0.020	—	—	6	230.15	0.06	0.56
	1.355	0.236	10.862	—	0.015	-0.020	-0.012	—	6	230.44	0.05	0.56
	1.235	0.222	10.876	—	0.014	-0.020	—	0.007	6	230.53	0.05	0.56
Final averaged model												
	1.743	0.216	9.274	-0.011	0.014	-0.018	-0.001	0.0007	8			

TABLE 2 Results of the averaged generalized linear models (6 of 128, $AIC_w > 0.95$) based on Poisson distribution and log-link function to test the effect of physiographic and environmental variables on the species richness of nesting seabirds on islands of the south-eastern Pacific Ocean.

Term	Estimate	SE	Adj. SE	z-value	p-value	Importance	N. cont. models
(Intercept)	1.7433	1.854	1.900	0.92	0.40	-	-
Area	0.2159	0.089	0.091	2.37	0.02	1	6
Primary productivity	9.2737	6.342	6.462	1.44	0.20	0.83	5
Distance to the continent	0.0144	0.006	0.006	2.49	0.01	1	6
Elevation	-0.0179	0.011	0.012	1.55	0.10	0.86	5
Salinity	-0.0107	0.054	0.055	0.19	0.80	0.12	1
Human density	-0.0013	0.010	0.011	0.12	0.90	0.1	1
Sea surface temperature	0.0007	0.008	0.008	0.008	0.90	0.1	1

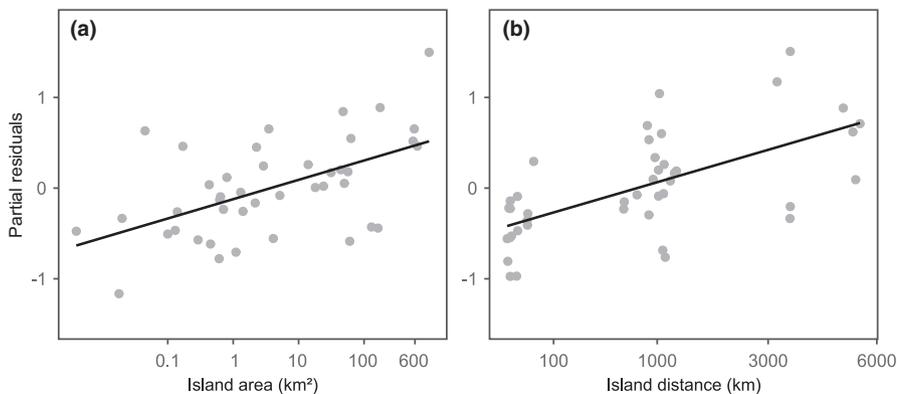


FIGURE 3 Partial residual plots based on generalized linear models modelling the species richness of nesting seabirds on islands of the south-eastern Pacific Ocean. The black lines are simple linear regressions representing the general effects of island area (a) and distance to the continent (b) on the species richness of nesting seabirds

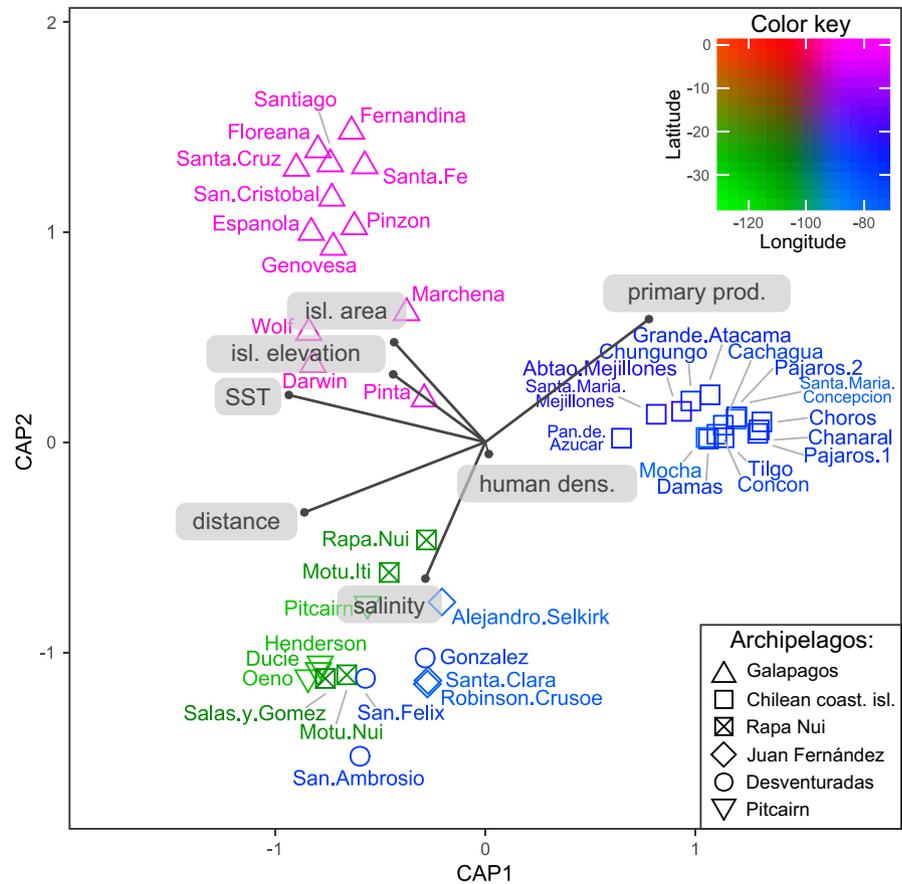
that island elevation does not necessarily correlate with an increased availability of nesting habitats for seabirds in the south-eastern Pacific Ocean. Species richness increased from coastal waters towards Polynesia, which explains the significant effect of island distance on seabird richness. However, species richness was not significantly affected by any of the oceanographic variables, which leads us to reject our second hypothesis. This indicates that the α -diversity of nesting seabirds is governed by factors related to habitat availability on islands rather than oceanographic variables. For β -diversity, we detected that both physiographic and oceanographic variables determine the changes in seabird species composition. The CAP ordination depicted three major groups of islands with contrasting species compositions: the first was formed by the Galápagos Archipelago, the second by all Chilean coastal islands and the third by the oceanic islands of the south-eastern Pacific Ocean. The differences among these groups were mostly related to gradients in oceanographic variables, especially primary productivity and sea surface temperature. These changes in β -diversity at large spatial scales tended to be driven by the turnover component of β -diversity and increased with increasing geographical and environmental distances, which is consistent with our third hypothesis. In contrast, species nestedness decreased with increasing geographical and environmental distance. This result is consistent with

our fourth hypothesis and indicates that differences in availability and quality of nesting habitat among islands have a significant effect on the variation in species richness within an archipelago. These results suggest that diversity patterns of nesting seabirds on islands are explained by the interaction of physiographic and oceanographic factors and that they may ultimately reflect the operation of both ecological and evolutionary processes.

4.1 | Seabird species richness

Species richness was mainly determined by the physiographic characteristics of the island, with large islands tending to present the highest number of nesting species. This possibly reflects a species-area relationship in which larger islands, with their greater area, allow for the existence of colonies of multiple species (Chown et al., 1998; Warham, 1996). One could argue that this positive effect might be related to island mass effect, which is a physical process related to flow perturbations. Such perturbations enhance vertical exchange among water layers, thereby causing phytoplankton blooms in the vicinity of oceanic islands (Gove et al., 2016; Hasegawa, Lewis, & Gangopadhyay, 2009). As island mass effect is a local process, it would

FIGURE 4 CAP ordination depicting changes in the species composition of nesting seabirds across islands of the south-eastern Pacific Ocean. Each point represents an island, with the colours reflecting their geographical position (similar colours indicate geographical proximity as indicated in the colour key). Vectors of each environmental variable are also shown. Vector names: human dens., human density; isl. area, island area; isl. elevation, island elevation; primary prod., primary productivity; SST, sea surface temperature



primarily benefit seabirds that feed locally in the waters surrounding their nesting grounds and, consequently, would favour the establishment of more species on an oceanic island. However, we have no direct evidence that this process explains the relationship between island area and seabird richness. In fact, our findings that marine productivity had no significant effect on species richness suggest the contrary. Studies have pointed out that oceanographic processes that sustain increased secondary productivity are not the main drivers of seabird species richness at sea, although they have a significant impact on seabird abundance (Jenkins & Van Houtan, 2016; Serratos et al., 2020).

TABLE 3 Results of the analysis of deviance on a multivariate generalized linear model that tested the effect of each environmental variable on the species composition of nesting seabird assemblages on islands of the south-eastern Pacific Ocean.

Term	Res. df	df	Deviance	p-value
(Intercept)	41			
Area	40	1	227.2	0.001
Elevation	39	1	166.5	0.001
Distance	38	1	387.4	0.001
Human density	37	1	89.4	0.020
Temperature	36	1	162.8	0.001
Salinity	35	1	73.6	0.020
Primary prod.	34	1	119.4	0.001

Indeed, a recent study found a mismatch between abundance and species richness in different taxa, including birds (Storch, Bohdalková, & Okie, 2018). In addition, Miranda-Urbina, Thiel, and Luna-Jorquera (2015) reported higher seabird abundances around Juan Fernández than around Rapa Nui, while our results indicate the inverse pattern for species richness. Thus, we conclude that oceanographic variables have little effect in determining the number of species nesting on islands of the south-eastern Pacific.

Even though the island area's effect is consistent with the predictions of island biogeography theory (Whittaker et al., 2008), the lack of effect of elevation is somewhat counter-intuitive. It would be expected that increased island elevation would increase the diversity of nesting habitats (Furness & Monaghan, 1987), thereby facilitating the establishment of nesting colonies of multiple species. This could be attributed to an interaction between physiographic variables, in which coastal islands are typically small and flat while more distant islands are large and high (Figure S2). It could also be an artifact of the low number of high islands observed in our study area. For example, the island of Alejandro Selkirk (Juan Fernández) is the highest in our study (1,650 m) but has a small number of nesting seabird species (two). Furthermore, the high islands of our study have permanent human populations that impose significant pressure on nesting seabird populations (Appendix S1). However, we found no significant effects of human population density on species richness, which suggests that seabird colonies are more sensitive to specific human impacts, such as habitat destruction and the introduction of

TABLE 4 Summary of the CAP results describing changes in species composition of nesting seabird assemblages across islands of the south-eastern Pacific Ocean

	CAP1	CAP2
Importance of components		
Eigenvalue	3.90	2.31
Proportion explained	0.22	0.13
Cumulative proportion	0.22	0.36
Vector scores		
Area	-0.43	0.48
Elevation	-0.44	0.32
Distance	-0.86	-0.33
Human density	0.02	-0.06
Temperature	-0.94	0.22
Salinity	-0.29	-0.65
Primary prod.	0.78	0.58

predators (Bourne, Brooke, Clark, & Stone, 1992; Thiel et al., 2018; Varela, Luna, & Luna-Jorquera, 2018; Wragg, 1995) than human population density per se.

Although the distance from the continent had a significant positive effect on seabird species richness, we failed to detect any effect of oceanographic variables on richness. This lack of a pattern may be driven by the Galápagos archipelago, which possesses high species richness and warmer and more productive waters than the other oceanic archipelagos considered in our study. When excluding Galápagos, we observed a marked increase in species richness from the Chilean coastal islands to the distant Pitcairn and Rapa Nui archipelagos. This increasing trend possibly reflects the proximity of major source populations within the Polynesian islands. The Polynesian islands host a diverse seabird assemblage that includes approximately 29 breeding seabird species (Thibault & Cibois, 2017). Except for the Henderson petrel (*Pterodroma atrata*) and the black-winged petrel (*Pterodroma nigripennis*), all nesting species of the Rapa Nui and Pitcairn archipelagos have nesting populations on other Polynesian islands (Thibault & Cibois, 2017). The distance to species-rich zones within the same ecoregion is known to be a driving factor for local species richness in sparsely distributed marine ecosystems (Parravicini et al., 2013). If the oceanic islands of the south-eastern Pacific share a common seabird species pool with Polynesia, then the eastward decrease in seabird species richness would reflect weakening connectivity between the most distant communities (i.e., Desventuradas and Juan Fernández) and the other components of the Polynesian metacommunity.

4.2 | Seabird β -diversity

The triangle formed by the distribution of islands in the CAP ordination of changes in seabird species composition reflects the different biogeographical realms proposed by Spalding et al. (2007)

and later by Costello et al. (2017). Spalding et al. (2007) placed the Galápagos Archipelago in the Tropical Eastern Pacific realm, Pitcairn and Rapa Nui in the Eastern Indo-Pacific realm, and the eastern Chilean islands in the Temperate South American realm. In our study, the Desventuradas and Juan Fernández are grouped with the Polynesian islands and separated from Chilean coastal islands. These differences are reflected in the results of the β -diversity components. The nestedness component was dominant at small distances (within archipelagos), possibly reflecting changes in species richness driven by differences in the physiography and conservation of the islands within each archipelago. The dominance of species turnover increased with increasing distances, reflecting the major gradients in environmental conditions that impose filters for species dispersion. In summary, the species assemblages with the greatest contrasts (i.e., the Galápagos Archipelago, the Chilean coastal islands and the Polynesian islands) were also the most distant in both geographical and environmental terms, indicating three different species pools.

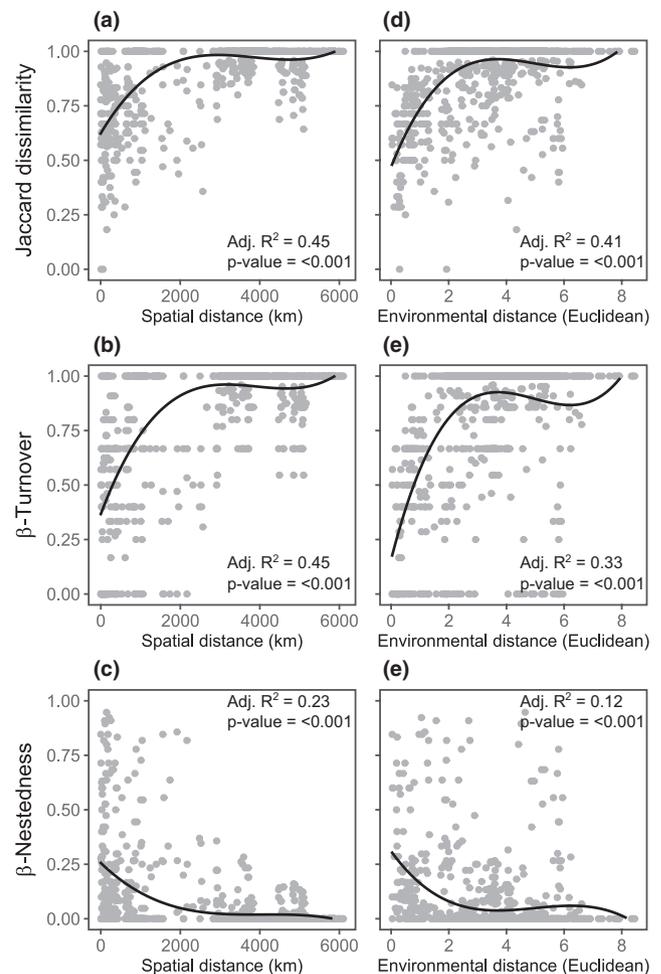


FIGURE 5 Model fits that describe how increasing spatial (a–c) and environmental (d–f) distances across islands of the south-eastern Pacific Ocean affect seabird β -diversity, expressed as β -total (Jaccard dissimilarities, a and d), β -turnover (b and e) and β -nestedness (c and f). Models are based on a third-degree polynomial fit. General results of the models (adjusted R^2 and p -values) are shown



Although we did not evaluate the importance of evolutionary processes, these are suggested by the analysis of β -diversity partitioning. The lack of nestedness in our analysis may reflect the multiple evolutionary origins of seabirds in our study area. In contrast, seabird species composition in the Southern Ocean shows a high degree of nestedness, suggesting a single evolutionary origin (Greve et al., 2005). The biogeographical control of species composition seems to be maintained by both physiographic and oceanographic variables (except salinity). However, the total variance explained by the model was relatively low, suggesting that other factors may be relevant to explain changes in species composition at the mesoscale, that is within the same biogeographical area. Indeed, environmental predictors explain much less variability in species dissimilarity than geographical distance alone (Figure 5). Additional environmental predictors, such as the presence/abundance of invasive species (Bellard et al., 2017) and past connections with other islands (Whittaker et al., 2008), are needed to test the relative importance of ecological and evolutionary drivers on the observed patterns of seabird species diversity.

4.3 | The macroecology of nesting assemblages

Given that island area is a significant predictor for both α - and β -diversities of nesting seabirds on islands, past climatic changes that affected sea level, such as glaciation and deglaciation processes, certainly drove current patterns of seabird assemblage structure. As sea level changed multiple times in the past millennia (Hansen, Sato, Russell, & Kharecha, 2013), the number and area of oceanic islands changed accordingly (Fernández-Palacios, 2016). These changes affected the connectivity of island communities over time, increasing the species interchange during periods in which shallow seamounts were islands and the area of current oceanic islands was larger, thereby creating corridors of 'stepping stones' for species dispersion (Weigelt, Steinbauer, Cabral, & Kreft, 2016). Past connections between Polynesia and eastern Pacific islands, such as the Desventuradas, possibly explain why our analyses indicated that their species assemblages have affinities. Indeed, there is a chain of seamounts between Rapa Nui and Desventuradas which is part of the Sala y Gómez and Nazca submarine ridges. Although the Juan Fernández Archipelago also showed some affinity with Polynesian islands, it has a relatively high number of endemic species. It suggests some degree of isolation from the other archipelagos of the south-eastern Pacific. The fact that there is no chain of seamounts between Juan Fernández and the other archipelagos possibly kept this archipelago relatively isolated even during periods of low sea levels. The highly clustered points that depict Chilean coastal islands indicate little variation in species composition within this archipelago, possibly reflecting the particular geological history of these islands. Unlike oceanic islands, Chilean coastal islands are on the South American continental platform, which is topographically irregular and includes many rocky reefs. This means that sea level changes affected the local seabirds differently when compared with

seabirds on oceanic islands. During glaciation periods, some coastal islands were connected with the mainland, while new islands were created as rocky reefs were exposed. As a result, nesting habitats and the connectivity among colonies on continental islands were not affected by changes in sea levels to the same degree as on oceanic islands.

5 | CONCLUSION

This study showed that physiographic and oceanographic conditions help to explain the species diversity of seabird assemblages in islands of the south-eastern Pacific. Variation in species composition reflects gradients observed across three different marine biogeographical realms: Temperate South American (Desventuradas, Juan Fernández and Chilean coastal islands), Eastern Indo-Pacific (Pitcairn and Rapa Nui) and Tropical Eastern Pacific (Galápagos). The relative differences in species richness and composition across archipelagos also highlight the vulnerability of specific seabird assemblages in the region. In our study, the Juan Fernández Archipelago possessed the most vulnerable seabird assemblages due to the small size of the archipelago and the relatively high proportion of endemic breeders (20%; *Pterodroma longirostris* and *Pterodroma externa*). This result is consistent with the conclusions of a study that classified the reef fish community of Juan Fernández as highly vulnerable (Parravicini et al., 2014). Our results suggest that even though oceanographic variables do not affect island species richness, they have significant impacts on seabird species composition, highlighting the potential vulnerability of local seabird assemblages to the effects of climate change.

ACKNOWLEDGEMENTS

This study was funded by the Millennium Nucleus for Ecology and Sustainable Management of Oceanic Islands ESMOI. For this study it was not necessary to process permits of any kind. We are grateful to Dr. André Menegotto for his valuable comments on the data analysis. We would like to thank Peter Hodum for English language editing. We also thank all referees for helpful reviews of the manuscript. Our thanks to Leo Joseph for his assistance in the final phase of writing the manuscript.

DATA AVAILABILITY STATEMENT

All data used in this work are available and may be found in the online version of this article.

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REFERENCES

Anderson, M. J., & Willis, T. J. (2003). Canonical analysis of principal coordinates: A useful method of constrained ordination

- for ecology. *Ecology*, 84(2), 511–525. [https://doi.org/10.1890/0012-9658\(2003\)084\[0511:CAOPCA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2)
- Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, 27, 277–284. <https://doi.org/10.1111/geb.12693>
- Ballance, L. T., Ainley, D. G., Ballard, G., & Barton, K. (2009). An energetic correlate between colony size and foraging effort in seabirds, an example of the adélie penguin *Pygoscelis adeliae*. *Journal of Avian Biology*, 40, 279–288. <https://doi.org/10.1111/j.1600-048X.2008.04538.x>
- Barton, K. (2018). MuMIn: Multi-model inference. Retrieved from <https://cran.r-project.org/package=MuMIn>
- Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Bellard, C., Rysman, J.-F., Leroy, B., Claud, C., & Mace, G. M. (2017). A global picture of biological invasion threat on islands. *Nature Ecology & Evolution*, 1, 1862–1869. <https://doi.org/10.1038/s41559-017-0365-6>
- Bjornstad, O. N., & Cai, J. (2018). ncf: Spatial covariance functions. Retrieved from <http://ento.psu.edu/directory/onb1>
- Bolton, M., Stanbury, A., Baylis, A. M. M., & Cuthbert, R. (2014). Impact of introduced house mice (*Mus musculus*) on burrowing seabirds on Steeple Jason and Grand Jason Islands, Falklands, South Atlantic. *Polar Biology*, 37(11), 1659–1668. <https://doi.org/10.1007/s00300-0-014-1554-2>
- Bost, C. A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., ... Weimerskirch, H. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, 78(3), 363–376. <https://doi.org/10.1016/j.jmarsys.2008.11.022>
- Bourne, W. R. P., de Brooke, M. L., Clark, G. S., & Stone, T. (1992). Wildlife conservation problems in the Juan Fernandez Archipelago, Chile. *Oryx*, 26(1), 43–51. <https://doi.org/10.1017/S003060530002322X>
- Chown, S. L., & Gaston, K. J. (1999). Patterns in procellariiform diversity as a test of species-energy theory in marine systems. *Evolutionary Ecology Research*, 1, 365–373.
- Chown, S. L., Gremmen, N. J. M., & Gaston, K. J. (1998). Ecological biogeography of southern ocean islands: Species-area relationships, human impacts, and conservation. *The American Naturalist*, 152(4), 562–575. <https://doi.org/10.2307/2463357>
- Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., & Chaudhary, C. (2017). Marine biogeographic realms and species endemicity. *Nature Communications*, 8(1), 1–9. <https://doi.org/10.1038/s41467-017-01121-2>
- Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International*, 22, 1–34. <https://doi.org/10.1017/S0959270912000020>
- Davies, R. G., Irlich, U. M., Chown, S. L., & Gaston, K. J. (2010). Ambient, productive and wind energy, and ocean extent predict global species richness of procellariiform seabirds. *Global Ecology and Biogeography*, 19(1), 98–110. <https://doi.org/10.1111/j.1466-8238.2009.00498.x>
- Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22(4), 1–20.
- Fernández-Palacios, J. M. (2016). Island biogeography: Shaped by sea-level shifts. *Nature*, 532, 42–43. <https://doi.org/10.1038/nature17880>
- Furness, R. W., & Monaghan, P. (1987). *Seabird ecology*. New York, USA: Chapman and Hall. <https://doi.org/10.1007/978-1-4613-2093-7>
- Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., ... Williams, G. J. (2016). Near-island biological hotspots in barren ocean basins. *Nature Communications*, 7(1), 1–9. <https://doi.org/10.1038/ncomms10581>
- Greve, M., Gremmen, N. J. M., Gaston, K. J., & Chown, S. L. (2005). Nestedness of Southern Ocean island biotas: Ecological perspectives on a biogeographical conundrum. *Journal of Biogeography*, 32, 155–168. <https://doi.org/10.1111/j.1365-2699.2004.01169.x>
- Hansen, J., Sato, M., Russell, G., & Kharecha, P. (2013). Climate sensitivity, sea level and atmospheric carbon dioxide. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 371(2001). <https://doi.org/10.1098/rsta.2012.0294>
- Harrison, S., Ross, S. J., & Lawton, J. H. (1992). Beta diversity on geographic gradients in Britain. *The Journal of Animal Ecology*, 61(1), 151–158. <https://doi.org/10.2307/5518>
- Hasegawa, D., Lewis, M. R., & Gangopadhyay, A. (2009). How islands cause phytoplankton to bloom in their wakes. *Geophysical Research Letters*, 36(20), 2–5. <https://doi.org/10.1029/2009GL039743>
- Hashmi, D., & Causey, D. (2008). A system in which available energy per se controls alpha diversity: Marine pelagic birds. *The American Naturalist*, 171(4), 419–429. <https://doi.org/10.1086/528997>
- Hijmans, R. J. (2017). geosphere: Spherical trigonometry. Retrieved from <https://cran.r-project.org/package=geosphere>
- Jenkins, C. N., & Van Houtan, K. S. (2016). Global and regional priorities for marine biodiversity protection. *Biological Conservation*, 204, 333–339. <https://doi.org/10.1016/j.biocon.2016.10.005>
- Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., & Howald, G. R. (2008). Severity of the effects of invasive rats on seabirds: A global review. *Conservation Biology*, 22(1), 16–26. <https://doi.org/10.1111/j.1523-1739.2007.00859.x>
- Legendre, P., & Andersson, M. J. (1999). Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, 69(1), 1–24. [https://doi.org/10.1890/0012-9615\(1999\)069\[0001:DBRATM\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2)
- Luna-Jorquera, G., Fernández, C. E., & Rivadeneira, M. M. (2012). Determinants of the diversity of plants, birds and mammals of coastal islands of the Humboldt current systems: Implications for conservation. *Biodiversity and Conservation*, 21, 13–32. <https://doi.org/10.1007/s10531-011-0157-2>
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17(4), 373–387. <https://doi.org/10.2307/2407089>
- McCauley, D. J., DeSalles, P. A., Young, H. S., Dunbar, R. B., Dirzo, R., Mills, M. M., & Micheli, F. (2012). From wing to wing: The persistence of long ecological interaction chains in less-disturbed ecosystems. *Scientific Reports*, 2, 409. <https://doi.org/10.1038/srep00409>
- Melo, A. S., Rangel, T. F. L. V. B., & Diniz-Filho, J. A. F. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, 32(2), 226–236. <https://doi.org/10.1111/j.1600-0587.2008.05502.x>
- Miranda-Urbina, D., Thiel, M., & Luna-Jorquera, G. (2015). Litter and seabirds found across a longitudinal gradient in the South Pacific Ocean. *Marine Pollution Bulletin*, 96(1–2), 235–244. <https://doi.org/10.1016/j.marpolbul.2015.05.021>
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation*, 70, 265–276. [https://doi.org/10.1016/0006-3207\(94\)90172-4](https://doi.org/10.1016/0006-3207(94)90172-4)
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., ... Wagner, H. (2009). vegan: Community ecology package. Retrieved from <https://cran.r-project.org/web/packages/vegan>
- Otero, X. L., La Peña-Iastra, S. D., Pérez-alberti, A., Ferreira, T. O., & Huerta-díaz, M. A. (2018). Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. *Nature Communications*, 9, 1–8. <https://doi.org/10.1038/s41467-017-02446-8>
- Pakhomov, E. A., & McQuaid, C. D. (1996). Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biology*, 16(4), 271–286. <https://doi.org/10.1007/s0030000050054>
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289–290. <https://doi.org/10.1093/bioinformatics/btg412>

- Parravicini, V., Kulbicki, M., Bellwood, D. R., Friedlander, A. M., Arias-Gonzalez, J. E., Chabanet, P., ... Mouillot, D. (2013). Global patterns and predictors of tropical reef fish species richness. *Ecography*, 36, 1254–1262. <https://doi.org/10.1111/j.1600-0587.2013.00291.x>
- Parravicini, V., Villéger, S., McClanahan, T. R., Arias-González, J. E., Bellwood, D. R., Belmaker, J., ... Mouillot, D. (2014). Global mismatch between species richness and vulnerability of reef fish assemblages. *Ecology Letters*, 17, 1101–1110. <https://doi.org/10.1111/ele.12316>
- Pöysä, H., & Pöysä, S. (2002). Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: Implications for the management of cavity-nesting birds. *Journal of Applied Ecology*, 39(3), 502–510. <https://doi.org/10.1046/j.1365-2664.2002.00726.x>
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org>
- Schneider, D. C. (1991). The role of fluid dynamics in the ecology of marine birds. *Oceanography and Marine Biology*, 29, 487–521.
- Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, 21(8), 464–471. <https://doi.org/10.1016/j.tree.2006.05.007>
- Serratos, J., Hyrenbach, K. D., Miranda-Urbina, D., Portflitt-Toro, M., Luna, N., & Luna-Jorquera, G. (2020). Environmental drivers of seabird at-sea distribution in the Eastern South Pacific Ocean: Assemblage composition across a longitudinal productivity gradient. *Frontiers in Marine Science*, 6, 1–13. <https://doi.org/10.3389/fmars.2019.00838>
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., ... Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, 57(7), 573–583. <https://doi.org/10.1641/B570707>
- Spatz, D. R., Newton, K. M., Heinz, R., Tershy, B., Holmes, N. D., Butchart, S. H. M., & Croll, D. A. (2014). The biogeography of globally threatened seabirds and island conservation opportunities. *Conservation Biology*, 28(5), 1282–1290. <https://doi.org/10.1111/cobi.12279>
- Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, 21(6), 920–937. <https://doi.org/10.1111/ele.12941>
- Thibault, J.-C., & Cibois, A. (2017). *Birds of Eastern Polynesia: A biogeographic atlas*. Barcelona: Lynx Edicions.
- Thiel, M., Luna-Jorquera, G., Álvarez-Varas, R., Gallardo, C., Hinojosa, I. A., Luna, N., ... Zavalaga, C. (2018). Impacts of marine plastic pollution from continental coasts to subtropical gyres – Fish, seabirds, and other vertebrates in the SE Pacific. *Frontiers in Marine Science*, 5, 1–16. <https://doi.org/10.3389/fmars.2018.00238>
- Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, 21, 272–281. <https://doi.org/10.1111/j.1466-8238.2011.00656.x>
- Varela, A. I., Luna, N., & Luna-Jorquera, G. (2018). Assessing potential Argentine Ant recruitment to pipping eggs in the Red-tailed Tropicbird on Rapa Nui (Easter Island). *Emu - Austral Ornithology*, 118(4), 381–385. <https://doi.org/10.1080/01584197.2018.1464372>
- Veech, J. A., & Crist, T. O. (2007). Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Global Ecology and Biogeography*, 16(5), 650–656. <https://doi.org/10.1111/j.1466-8238.2007.00315.x>
- Wahl, T. R., Ainley, D. G., Benedict, A. H., & DeGange, A. R. (1989). Associations between seabirds and water-masses in the northern Pacific Ocean in summer. *Marine Biology*, 103(1), 1–11. <https://doi.org/10.1007/BF00391059>
- Wang, Y., Naumann, U., Wright, S. T., & Warton, D. I. (2012). mvabund – An R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, 3, 471–474. <https://doi.org/10.1111/j.2041-210X.2012.00190.x>
- Warham, J. (1996). *The behaviour, population biology and physiology of petrels*. London, UK: Academic Press.
- Webb, T. J., & Mindel, B. L. (2015). Global patterns of extinction risk in marine and non-marine systems. *Current Biology*, 25(4), 506–511. <https://doi.org/10.1016/j.cub.2014.12.023>
- Weichler, T., Garthe, S., Luna-Jorquera, G., & Moraga, J. (2004). Seabird distribution on the Humboldt Current in northern Chile in relation to hydrography, productivity, and fisheries. *ICES Journal of Marine Science*, 61, 148–154. <https://doi.org/10.1016/j.icesjms.2003.07.001>
- Weigelt, P., Steinbauer, M. J., Cabral, J. S., & Kreft, H. (2016). Late Quaternary climate change shapes island biodiversity. *Nature*, 532, 99–102. <https://doi.org/10.1038/nature17443>
- Weimerskirch, H., Ancel, A., Caloin, M., Zahariev, A., Spaggiari, J., Kersten, M., & Chastel, O. (2003). Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Journal of Animal Ecology*, 72, 500–508. <https://doi.org/10.1046/j.1365-2656.2002.00720.x>
- Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, 35, 977–994. <https://doi.org/10.1111/j.1365-2699.2008.01892.x>
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer. <https://doi.org/10.1007/978-0-387-98141-3>
- Wragg, G. M. (1995). The fossil birds of Henderson Island, Pitcairn Group: Natural turnover and human impact, a synopsis. *Biological Journal of the Linnean Society*, 56, 405–414. <https://doi.org/10.1111/j.1095-8312.1995.tb01100.x>

BIOSKETCH

Joao B. Gusmao is a marine biologist broadly interested in the ecology of marine organisms. This work represents a component of his postdoctoral work at ESMOI on the biogeography of marine organisms in the Pacific Ocean.

Author contributions: GL-J conceived the study; JBG directed the study, analysed the data and drafted several versions of the manuscript; CF, NL, PP, MP-T, JS, PN and AIV conducted fieldwork and collected and analysed data. MMR contributed to the development of the idea for the study, analysis and interpretation of results. JBG, GL-J and MMR drafted the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Gusmao JB, Luna-Jorquera G, Fernández C, et al. The role of island physiography and oceanographic factors in shaping species richness and turnover of nesting seabird assemblages on islands across the south-eastern Pacific. *J Biogeogr.* 2020;00:1–11. <https://doi.org/10.1111/jbi.13973>