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Human visitation disrupts natural determinants of breeding seabird communities on coral reef islands

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ABSTRACT

Coral Reef Islands (CRIs) support key colonies of tropical seabirds, whose long-term sustainability is under growing threat from climate change and small-scale, island-specific pressures such as invasive species or human disturbance. Unlike most compartments of reef ecosystems, CRI seabirds have been poorly studied from a biogeographical perspective, which questions the relevance of existing conservation policies. Here, we investigate the effects of ecological, geographical and anthropogenic drivers on the diversity and abundance of CRI seabird communities, using survey data acquired over the 2000–2023 period in 100 CRIs of New Caledonia, South-western Pacific. Our results show that the diversity and biomass of breeding communities are mostly constrained by the availability of breeding habitat and by the characteristics of neighboring marine environments. We observe a negative effect of human visitation on both diversity and biomass, indicating that the mitigation of human disturbance combined with habitat maintenance are key for sustaining seabird colonies on CRIs. Our findings highlight the complementary roles of remote and coastal islands, which host distinct species assemblages, and demonstrate that although isolated islands are often seen as optimal conservation targets, they only host part of the diversity of CRI seabirds. This study emphasizes the importance of combining species and site monitoring for assessing the ability of managers to effectively restore the state of seabird communities and contribute to the health of adjacent reef ecosystems. In addition to local policies, we also underline that future management of CRI-dependent seabird communities must integrate multi-scale, long-term assessments of reef decline and coastal erosion.

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1. Introduction

The conservation of reef ecosystems faces ever-increasing challenges, that threaten the long-term sustainability of reef-dependent processes and services (Bellwood et al., 2019, 2004). While reef management has historically targeted subaquatic communities (e.g., Mumby and Steneck, 2008), recent evidence has emphasized the importance of island-ocean connections for developing holistic conservation policies (Sandin et al., 2022). Due to their dual dependency to terrestrial (breeding) and marine (foraging, dispersal) environments, seabirds stand at the core of the island-ocean interface, especially for species that breed on coral reef islands (CRIs) (Berr et al., 2023). CRIs are sedimentary structures formed by the accumulation of carbonated materials (coral debris, invertebrate shells) in shallow waters adjacent to reef ecosystems (Perry et al., 2011). They are found throughout the intertropical area in diverse shapes and sizes and exhibit a highly dynamic geomorphology (Kench and Mann, 2017). Most of the several thousands of existing CRIs are under some degree of human influence and many are permanently inhabited (e.g., French Polynesia (Duvat et al., 2017)). All are low-level structures, which makes them vulnerable to coastal erosion and flooding (Perry et al., 2011). Indeed, while CRIs may accommodate moderate sea level rise through vertical accretion (Masselink et al., 2020), the projected magnitude of reef decline in coming decades will likely alter the sedimentary processes at the core of their long-term sustenance (Cornwall et al., 2021; Kane and Fletcher, 2020). Overall, this puts into question the future of seabird colonies that depend on CRIs for breeding and the sustainability of associated ecological processes (Berr et al., 2023). CRI seabirds indeed provide important contributions to ecosystems and people, in addition to usual (e.g. trophic regulation, bio-indication) seabird roles: through guano deposition their colonies increase the productivity of neighboring reef ecosystems and indirectly support reef-dependent services (e.g., fishing resources, protection against coastal erosion) (Lorrain et al., 2017; Savage, 2019). As such, preserving seabird colonies on CRIs might yield cascading positive effects due to the mutually beneficial interaction between seabirds and reefs (Benkwitt et al., 2021).

Unlike corals (Obura, 2012) or reef fishes (Parravicini et al., 2013), CRIs and CRI-dependent seabirds have been poorly studied from a biogeographical perspective. Existing studies on CRIs are mostly dedicated to geomorphology (Woodroffe, 2008), but they rarely include information on CRI-dependent communities beyond human populations. Similarly, studies on CRI seabirds are generally accounts of seabird censuses and trends (e.g. (Borsa et al., 2010; Woodworth et al., 2021)), that offer limited insight into the links between seabird colonies and the characteristics of their breeding sites. Finally, existing assessments of seabird biogeography focus on at-sea distribution (Mendez et al., 2017) or are restricted to threatened species (Spatz et al., 2014). Consequently, little information currently exists on the spatial distribution of CRI-dependent seabirds or on its underlying determinants. Understanding how breeding communities are spatially structured on CRIs and how they respond to environmental constraints is however a key step for developing adequate protection or restoration measures (Berr et al., 2023).

Using New Caledonia, South Pacific (21.2° S, 165.9° E) as a study area, we take advantage of multiple survey campaigns conducted between 2002 and 2023 to characterize breeding seabird communities (species richness, biomass and assemblages) on a set of 100 CRIs spread across a 1.45 M km² area. Our aim is to assess the relative effects of natural (site geomorphology, habitat, neighboring geographical and marine features) and anthropogenic (human visitation, invasive species) drivers on community metrics. We notably test whether habitat diversity increases species richness, as suggested by studies of habitat selection in CRI seabirds (Batianoff, 2000; Carr et al., 2021), and whether high levels of human visitation alters species richness and biomass – as observed in reef fishes (D'Agata et al., 2014; Cinner et al., 2018). We then discuss the implications of our findings for the conservation of CRI seabirds in a context of expected reef decline and suggest leads for addressing current knowledge gaps in the global vulnerability of CRI seabirds.

2. Materials and methods

2.1. Study site

2.1.1. Geography

New Caledonia is located approximately 1300 km east of Australia and 1000 km west of Fiji. It forms the eastern boundary of the Coral Sea, along with the neighboring islands of Vanuatu and covers an Exclusive Economic Zone of 1.45 M km². New Caledonia is an archipelago with four main islands: “Grande Terre” (hereafter mainland) that concentrates most of the human population (~270 000 inhabitants), and the three Loyalty islands, Ouvéa, Maré & Lifou. It also includes 700–800 smaller islands (0.1–15 000 ha), among which approximately 160 CRIs – whose exact census is hampered by the existence of very small, unsurveyed cays that cannot be differentiated from periodically immersed sand banks (DTSI Nouvelle Calédonie, 2023) (Figs. 1 and 2). Both CRIs and rocky islands are mostly concentrated within the lagoon surrounding the mainland, yet two remote CRI archipelagos exist in the west (Chesterfield-Bampton) and north (d'Entrecasteaux reefs) of the EEZ (Fig. 1A, B).

2.1.2. Historical uses of CRIs

New Caledonian CRIs have never hosted long-term human settlements, which differentiates them from other insular territories (e.g. Maldives, Tuamotu, Cayman Islands). Prior to European colonization, CRIs close to the mainland likely received occasional visitation by fishermen, which may have favored the spread of Polynesian rats (*Rattus exulans*) across islands (Bell, 1998). Throughout the 19th century – and until the late 1920 s – remote islands from the Chesterfield and d'Entrecasteaux archipelagos were exploited for guano extraction and, to a lesser extent, whaling (Borsa and Vidal, 2018; Garrigue et al., 2018). This temporary human presence led to the introduction of invasive rodents (black rat *Rattus rattus*, house mouse *Mus musculus*) and plants on several CRIs (Borsa et al., 2010; Butaud and Jacq, 2015; Philippe-Lesaffre et al., 2023). Nowadays, all CRIs within the mainland's lagoon receive some degree of recreational human visitation (Gonson et al., 2016), whereas most remote CRIs are closed to visitors.

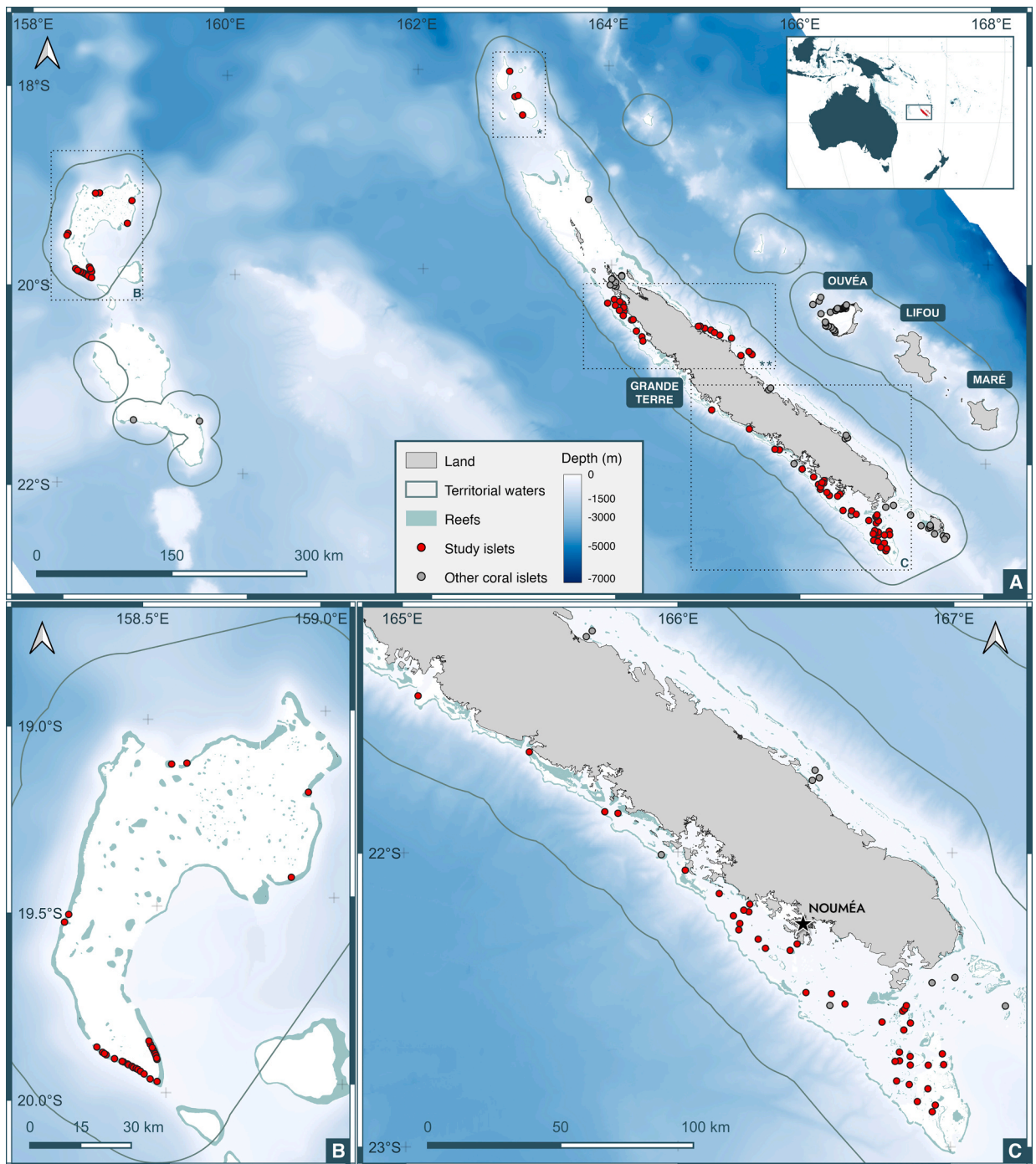


Fig. 1. Geographical distribution of study sites within New Caledonia waters. A: general overview of the 100 selected coral reef islets (red dots), separated across four sub-regions: B – Chesterfield-Bampton archipelago (32); C – Southwestern lagoon (39); * – d’Entrecasteaux reefs (4); ** – Northern lagoon (25). See Fig. A3 for maps of *, **. Coral islets that were not included in the study due to lack of survey data (60 sites) appear as grey circles. Bathymetry & administrative boundaries © Direction des Technologies et des Services de l’Information de Nouvelle-Calédonie, 2023.

2.1.3. Seabird populations and threats

Twenty-seven different seabird species have confirmed breeding records in New Caledonia (Bretagnolle et al., 2022; Spaggiari



Fig. 2. Examples of study sites. A, B: Carrey (0.6 ha) & Ouanne (2.4 ha) islets, Northern lagoon of New Caledonia. C: Surprise islet (19.9 ha), d'Entrecasteaux reefs. Grey shapes indicate picture orientation. D: relative sizes of the three islets.

et al., 2006) and at least 18 are known to breed on CRIs (5 different families; Table A1). The most abundant species include the wedge-tailed-shearwater *Ardenna pacifica* (WTS, 0.5–1 M breeding pairs), the sooty tern *Onychoprion fuscatus* (150–300k bp) and the black noddy *Anous minutus* (75–100k bp) (IFRECOR, 2007), all of which breed extensively on CRIs. Other species range from dozens of breeding pairs (e.g., red-tailed tropicbird *Phaethon rubricauda*) to several thousands (e.g., Brown booby *Sula leucogaster*). All species that breed on New Caledonia CRIs except the fairy tern *Sternula nereis* (VU) and the Tahiti petrel *Pseudobulweria rostrata* (NT) are currently classified as *Least Concern* in the IUCN Red List, however at least 9 of the 18 taxa exhibit declining population trends at the global scale (BirdLife International, 2023). Local threats to seabirds include invasive mammals (Palmas et al., 2017; Philippe-Lesaffre et al., 2023) and plants (Gargominy et al., 1996), human disturbance (Gonson et al., 2016), light pollution, occasional poaching, and plastic pollution (Berr et al., 2020).

2.1.4. CRI selection

This study considers 100 CRIs from New Caledonia separated across four geographical areas: southwestern lagoon (39), northern lagoon (25), Chesterfield archipelago (32), d'Entrecasteaux Reefs (4) (Fig. 1). The considered ensemble accounts for > 60% of all CRI in New Caledonia and was included in a survey conducted from 2017 to 2023, which aimed to analyze the spatial distribution of seabirds that breed on CRIs. Within all target areas, site selection was designed to include the highest possible number of CRIs regardless of seabird presence, in order to avoid under-sampling sites with few or no breeding species. All lagoon CRIs (64) are subject to human visitation, however only three sites are permanently inhabited. A detailed list and map of study sites are available in Appendix A2-A3.

2.2. Data collection

2.2.1. Data sources

The bulk of seabird census and CRI data used in this study was acquired over the 2017–2023 period through dedicated survey campaigns (2.2.2–4.). We gathered additional information on species abundance estimates and invasive rodents' presence from accounts of post-2000 surveys conducted in all four sub-regions. This includes published bibliography (e.g., Borsa et al., 2010; Philippe-Lesaffre et al., 2023), grey literature reports and survey accounts from provincial rangers (Table A4). Maps and GIS metadata from the New Caledonia-based website *Géorep.nc* (<https://georep.nc/>) were used as reference for GIS analysis (2.2.5–6).

2.2.2. Seabird census

We conducted successive boat campaigns concentrated in the austral summer (November–April) and winter (June–September) periods, during which most of the breeding activity of New Caledonia seabirds occur. We surveyed Lagoon CRIs in sequence, with main campaigns conducted in 2020 (northern lagoon), 2021 (western lagoon) and 2022–2023 (southern lagoon), that also included aerial imaging (2.2.3) and characterization of rodent populations (2.2.4). These campaigns were complemented by opportunistic surveys conducted across all target areas from 2018 to 2023, which primarily aimed to census species with low site fidelity and high inter-annual variation of colony size (most terns). For remote CRIs, we conducted respectively five and four survey campaigns in the Chesterfield-Bampton (April 2017, April 2019, January and June 2021, September 2022) and d'Entrecasteaux areas (March 2017, July 2019, February and July 2021) over the 2017–2022 period. Except for some isolated CRIs from the northern Chesterfield-Bampton archipelago, all study sites were surveyed at least twice during different breeding seasons.

We produced exhaustive counts of breeding pairs whenever possible and used indirect abundance assessments (point counts and subsequent extrapolation) only when the number of breeders induced a disproportionate survey duration. This mostly affected the census of the burrow-nesting WTS, whose colonies generally host several thousands of breeding pairs, and of black noddies. We counted as breeding pairs: (1) couples engaged in courtship or nest-building activity; (2) nests containing attended eggs or chicks (i.e., excluding abandoned nests), and (3) adult pairs displaying obvious breeding behavior (alarm calls, nest defence) for which the nest could not be directly observed. For WTS, we corrected abundance estimates by a burrow occupancy rate of 0.5, established from the observation by an endoscopic camera of 574 burrow contents from 18 different colonies (January–March 2022, 286/574 burrows with breeding activity, 0.50 ± 0.12 occupancy rate (mean \pm 1sd)).

2.2.3. Geographical extent of study sites & habitat characterization

The geographical extent of each surveyed CRI was delimited by aerial imagery. For 53 islets (Table A2), we produced original, high-resolution aerial maps using unmanned aircraft systems (DJI Phantom 4). For the remaining 47 islets, aerial imagery was obtained from freely available satellite data, with a minimum resolution of 0.6 m/px. We retained the high-tide mark (=shoreline) as the external boundary of each CRI's emerged area and set it as a reference for calculating CRI surface and perimeter. We then estimated the roundness of each site (Polsby-Popper score of shape compactness).

We characterized the composition and spatial distribution of seabird breeding habitat in 5x5m grids drawn upon each CRI. The use of gridded data was preferred to continuous habitat characterization (i.e. hand drawing of habitat polygons) as it was far less time-consuming, especially for sites with complex and/or patchy plant cover. We associated each square plot with one of 9 habitat types: 1-bare ground/coral; 2-low plant cover (<30 cm); 3-bay cedar bushes (*Suriana maritima*); 4-octopus bush trees (*Heliotropium foertherianum*); 5-Pisonia trees (*Pisonia grandis*); 6-prickly pear (*Opuntia* spp.); 7-other undifferentiated plant cover; 8-buildings; 9-miscellaneous (rubble, mangrove, etc.) (Appendix A5-A7). When one or more habitat types were present in a plot, the most abundant one was retained.

2.2.4. Invasive rodents

We assessed the presence or absence of invasive rodents (black rat *Rattus rattus*, Polynesian rat *R. exulans*, house mouse *Mus musculus*) on 59 sites by deploying snap-trap transects during surveys. Among the 41 other CRIs, we assumed that no permanent rodent populations were hosted on 18 small cays (<0.2 ha) with low or no plant cover, and derived information on rodent presence in the 23 remaining sites from existing bibliography and data sources. Since only 14 of the 100 study CRIs currently host rodents, all species (black rat, Polynesian rat, house mouse) were pooled together in a single presence/absence category for further analysis.

2.2.5. Human visitation

Direct data on the level of human visitation on CRIs (i.e., yearly numbers of visitors) were lacking. To address this gap we developed a proxy based on a CRI's proximity to human habitation and potential exposure, hereafter referred to as human visitation. We characterized each site's (1) accessibility (number of harbors within a 10 and 60 km radius, distance to the closest harbor and to Noumea), (2) exposure (number of inhabitants in source urban areas) and (3) level of anthropization (categorical assessment of tourist infrastructure and mitigation policies). A detailed description of numerical and categorical variables is shown in [Table A8](#).

2.2.6. Neighboring geographical and marine features

To evaluate the influence of a site's surroundings on the seabird community, we quantified the proportion of land, reef, lagoon or pelagic waters in eight buffers of varying size (0.5–200 km) drawn from the shoreline. The rationale for including these descriptors is that land masses act as obstacles to foraging, and that we expected lagoon- and pelagic-feeding seabird species to breed preferentially on sites in adequate distance of their respective foraging areas.

2.3. Data curation and variable treatment

2.3.1. Descriptors for the seabird community

We evaluated species richness for each CRI as the total number of breeding species recorded during the considered surveys (2.2.1). This includes species that exhibit high site fidelity (e.g., WTS, black noddy) and species with occasional breeding (e.g., black-naped tern *Sterna sumatrana*, greater crested terns *Thalasseus bergii*). We then averaged seabird counts to produce representative estimates of site-wise abundances, in breeding pairs. For species with high site fidelity and yearly breeding, abundance was calculated as the mean of available estimates (one value per breeding season during which the species was surveyed). For species with occasional presence, abundance was averaged across all surveys, including years without breeding activity. In both cases, we retained the highest seasonal estimate as a reference when multiple surveys were conducted within a single breeding season. Overall seabird biomass was then calculated as the sum of all individual species abundances multiplied by two and by the average adult weight of birds ([Tobias et al., 2022](#)).

We retained species richness, overall biomass and biomass without WTS as response variables in subsequent analysis. The latter response variable was used as WTS account for ~62% of overall biomass and we aimed to assess predictor contributions for the remaining set of species.

2.3.2. Explanatory factors

We considered five categories of drivers: site geomorphology (2 variables), habitat (9), geography (32), rodent presence (1) and human visitation (6). To reduce the overall number of predictors and avoid model overfitting, we performed principal component analyses (PCA) on the habitat and geography categories and a multi-factorial analysis (MFA) on the human visitation category. Similarly to PCA, MFA yields synthetic numerical dimensions (axes), however it can use a combination of both numerical and categorical variables. Prior to conducting the habitat PCA, the number of habitat types was reduced from 9 to 5, by lumping *Pisonia* and octopus bush trees together as they fulfil broadly equivalent roles and by creating an "other" category containing habitats that are not specifically used for breeding (e.g. prickly pear or building) ([Table A6](#)).

We retained the first two dimensions of each PCA or MFA as explanatory variables in subsequent model evaluation (hereafter *Habitat.1/2*, *Geography.1/2*, *Visit.1/2* (human visitation)). We followed the methodology of [D'agata et al. \(2014\)](#) to define the original variables characterizing each axis, by (1) estimating Pearson's correlation coefficient (R) between original quantitative variables and PCA/MFA axes and by (2) calculating the median, first and last quartile coordinates of MFA axes for the different modalities of qualitative original variables ([Figs. A9–10](#)).

2.4. Model design and selection

We evaluated predictor influence on species richness (generalized linear model, poisson) and both measures of biomass (gaussian linear model) by performing a two-step model selection. Model structure was designed to use geomorphology, habitat and geography drivers as basal predictors (6 explanatory factors). Anthropogenic drivers (rodent presence, *Visit.1 & 2*) were only used in interaction with these six drivers, yielding a total set of 24 (6 + 3 × 6) explanatory variables. Finally, predictors with correlation coefficient > |0.7| were deemed mutually exclusive during model selection steps.

Conducting model selection with a high number of predictors using only corrected Akaike's Information Criterion (AICc) comparisons can have limited relevance to effectively detect significant predictor effects ([Wagenmakers and Farrell, 2004](#)). Indeed, the commonly accepted value of $\Delta AICc < 2$ for retaining equivalent models may yield large numbers of models with different sets of variables that exhibit close AICc. We thus performed a first evaluation of each predictor's importance by summing Akaike weights (i.e.,

the proportion of total predictive power associated with each model) of all models in which the corresponding predictor was retained (1783 models in total). This yielded a value within a range of 0–1, with 0 indicating no effect of the predictor on the response variable. In the absence of a reference threshold, we chose to retain predictors with an overall Akaike weight > 0.4 for a second step of model selection (Fig. A11).

We conducted a regular AICc comparison on the three sets of predictors retained after the previous step (one for each response variable). Models with $\Delta AICc < 2$ were kept, and the models with the lowest AICc were further used to discuss and illustrate the effect of predictors.

We tested the residuals of all three retained model for spatial autocorrelation (Moran's I), considering a 100 km distance threshold above which no correlation was expected. In all cases, we found no significant spatial autocorrelation (P-value > 0.05), which validated the use of generalized linear models instead of mixed-effects models with random sub-region effects.

All statistical analyses were conducted in R 4.2.2 (R Core Team, 2023), with particular use of the packages *FactoMineR* (PCA and MFA construction), *MuMIn* (model selection) and *sdep* (analysis of spatial autocorrelation) (Bartoń, 2023; Bivand et al., 2023; Husson et al., 2023). Descriptive statistics are presented as mean \pm 1 SD.

3. Results

3.1. Seabird distribution

Eighteen seabird species were recorded as breeding on at least one of the 100 considered CRIs (Table 1). WTS, black-naped tern and brown noddy *Anous stolidus* were the most widely distributed species, with respectively 59, 43 and 38 breeding sites (Table 2). Conversely, the red-tailed tropicbird, black-winged petrel *Pterodroma nigripennis* and Tahiti petrel had the least breeding sites, with respectively 3, 5 and 7 confirmed breeding locations. On average, species were present on 23.7 ± 14.4 CRIs (Fig. A12).

Remote and lagoon CRIs exhibited distinct species assemblages (Table 1, Fig. 3AB). The two species of frigatebirds native to New Caledonia (great and lesser frigatebird, *Fregata minor* and *F. ariel*) and the red-tailed tropicbird exclusively bred on remote CRIs, while the silver gull *Larus novaehollandiae* and both black-winged and Tahiti petrels were only found on lagoon CRIs (Table 1). When summarizing the community matrix (100 sites \times 18 species) through PCA, the first two dimensions appeared respectively correlated to the species richness of remote (Pearson's r 95% CI: 0.90–0.96) and lagoon (0.85–0.93) CRIs, which highlights the segregation between the two communities (Fig. 3AB). Across all CRIs, the estimated values of species richness ranged from 0 (N = 10 sites) to 12 (Koko islet, Southern lagoon) confirmed breeding species, with an average of 4.3 ± 3 breeding species per site (Fig. A12). Typically,

Table 1
List of observed breeding species.

Order	Family	Name	Common name	Red List status	Number of breeding sites	# of lagoon / remote breeding sites	Combined population size on study sites (bp)	
CHARADRIIFORMES	<i>Laridae</i>	<i>Anous minutus</i>	Black noddy	LC	25	10/15	71 339	
		<i>Anous stolidus</i>	Brown noddy	LC	38	14/24	12 508	
		<i>Larus</i>	Silver gull	LC	34	34/0	255	
		<i>novaehollandiae</i>						
		<i>Onychoprion anaethetus</i>	Bridled tern	LC	27	25/2	707	
		<i>Onychoprion fuscatus</i>	Sooty tern	LC	15	4/11	139 116	
		<i>Sterna dougallii</i>	Roseate tern	LC	34	33/1	4 637	
		<i>Sterna sumatrana</i>	Black-naped tern	LC	43	34/9	772	
		<i>Sternula nereis</i>	Fairy tern	VU	21	18/3	161	
		<i>Thalasseus bergii</i>	Greater-crested tern	LC	29	23/6	1 674	
		PHAETHONTIFORMES	<i>Phaethontidae</i>	<i>Phaethon rubricauda</i>	Red-tailed tropicbird	LC	3	0/3
PROCELLARIIFORMES	<i>Procellariidae</i>	<i>Ardenna pacifica</i>	Wedge-tailed shearwater	LC	59	12	254 681	
		<i>Pseudobulweria rostrata</i>	Tahiti petrel	NT	7	7/0	12	
		<i>Pterodroma nigripennis</i>	Black-winged petrel	LC	5	5/0	24	
SULIFORMES	<i>Fregatidae</i>	<i>Fregata ariel</i>	Lesser frigatebird	LC	10	0/10	3 516	
		<i>Fregata minor</i>	Great frigatebird	LC	14	0/14	1 369	
		<i>Sulidae</i>	<i>Sula dactylatra</i>	Masked booby	LC	22	2/20	572
	<i>Sula leucogaster</i>	Brown booby	LC	23	2/21	4 309		
	<i>Sula sula</i>	Red-footed booby	LC	19	2/17	12 510		

Table 2

Coefficient estimates of retained models with species richness (Poisson generalized linear model) and biomass (standard linear model) as response variables.

Predictor	Estimate	95% CI
<i>Species richness</i>		
<i>Pseudo R² (Maximum Likelihood): 0.80</i>		
Intercept	0.834*	[0.026; 1.619]
Habitat.2	0.275***	[0.198; 0.352]
Habitat.2 ^{Visit.1}	-0.098***	[0.046; 0.150]
Geography.2	0.116***	[- 0.165; - 0.068]
log(Surface)	0.064 ·	[- 0.010; 0.140]
Roundness	-0.365 ·	[- 0.789; 0.07]
<i>Log (Biomass)</i>		
<i>Adjusted R²: 0.76</i>		
Intercept	-3.733***	[- 5.876; - 1.590]
log(Surface)	0.956***	[0.734; 1.178]
Habitat.2	0.666***	[0.344; 0.988]
Habitat.2 ^{Visit.1}	-0.499***	[0.287; 0.711]
log(Surface) ^{Visit.2}	0.092***	[0.053; 0.132]
log(Surface) ^{Visit.1}	0.034**	[- 0.059; - 0.010]
<i>Log (Biomass) (excluding WTS)</i>		
<i>Adjusted R²: 0.78</i>		
Intercept	4.154***	[3.250; 5.059]
Habitat.2	1.531***	[1.243; 1.818]
Habitat.2 ^{Visit.1}	-0.584***	[0.419; 0.748]
Geography.2	0.301***	[- 0.443; - 0.159]
log(Surface) ^{Visit.1}	-0.045***	[0.021; 0.070]
Roundness	-1.430 ·	[- 2.887; 0.028]

CI: Confidence interval. Significance thresholds: P-value < 0.1 (·); < 0.05 (*), < 0.01 (**), < 0.001 (***)

New Caledonia CRIs hosted 11–39% of the total seabird diversity.

Biomass estimates ranged from 0 to 36.0 (M'Ba islet, Southwestern lagoon) tons of breeding seabirds, with an average of 3.2 ± 5.4 tons per site. Overall biomass was highest in large CRIs among both remote and lagoon islands (Fig. 4). Correcting for CRI area, values ranged from 0 to 0.65 (Îlot du Sud-Est, Chesterfield) kg of biomass/m² (mean: 0.06 ± 0.11 kg/m²).

3.2. Site characteristics

CRI surface ranged from 0.0085 (Cay n°7, Chesterfield) to 31.9 ha (M'Ba islet), with an average islet surface of 4.6 ± 5.9 ha. Remote CRIs were near-entirely covered by habitats favorable to seabird breeding (bare ground/low plant cover/bay cedar/Pisonia or octopus bush trees) (Fig. 4, A13). Conversely, lagoon islets had more complex plant cover and CRIs close to the mainland often hosted forests that are unfavorable to epigeous or arboreal seabirds. The first dimension (*Habitat.1*, 32.5% of overall variance) of the corresponding habitat PCA was strongly correlated to log-transformed islet surface ($R = 0.66\text{--}0.83$): low values were associated with small unvegetated cays and higher with large, forest-covered CRIs. The second dimension (*Habitat.2*, 31.8%) was positively correlated to an increasing proportion of low plant cover and bush-like/arboreal plants favorable to seabird breeding (Fig. A9). Its highest values corresponded to CRIs whose entire emerged area were favorable to seabird reproduction, and as such it could be broadly approximated as a measure of habitat availability.

Remote and lagoon CRIs were strongly discriminated by the first dimension of the geography PCA (*Geography.1*, 42.8%), which effectively separated islets depending on the presence of land in a 200 km radius around them (Fig. 3B). The second dimension (*Geography.2*, 20.1%) was maximal for CRIs with high proportion of lagoon and reefs up to 50 km from the shoreline and high proportion of pelagic waters beyond (50–200 km). Conversely, islets with higher proportions of reefs and lagoon up to 200 km exhibited low values (Fig. A9).

CRIs close to New Caledonia's capital city Noumea were clearly segregated from remote CRIs along the first MFA axis (*Visit.1*, 47.8%), as the former have the highest accessibility and exposure to human visitation (Fig. 3B). CRIs along the mainland's coastline exhibited intermediate values. The two groups of remote islands were poorly discriminated from one another by all dimensions of the MFA, which underlined that both sub-regions receive comparably low levels of visitation. The presence of buildings on study sites was rare, as only seven CRIs in Nouméa's vicinity and three in the Northern province hosted permanent infrastructure. Only 14 sites hosted rodent populations, among which 5 hosted black rats, 3 domestic mice, 1 Polynesian rats, 1 both mice and Polynesian rats and the remaining 5 hosted unidentified species.

3.3. Assessment of predictor influence on community metrics

Habitat availability (*Habitat.2*) appeared as the most important driver of species richness (Fig. 5A), displaying a significant positive effect (Fig. 5B, Table 2). It was however negatively affected by human visitation (*Visit.1*), as the most accessible and exposed CRIs hosted fewer species than less visited sites with comparable habitats. Geography also had a significant influence, with islets on the higher end of the *Geography.2* dimension (high lagoon proportion up to 50 km) exhibiting the highest values of species richness (Fig. 5B). Roundness (negative effect) and islet surface (positive effect) marginally affected species richness (Table 2) but were retained

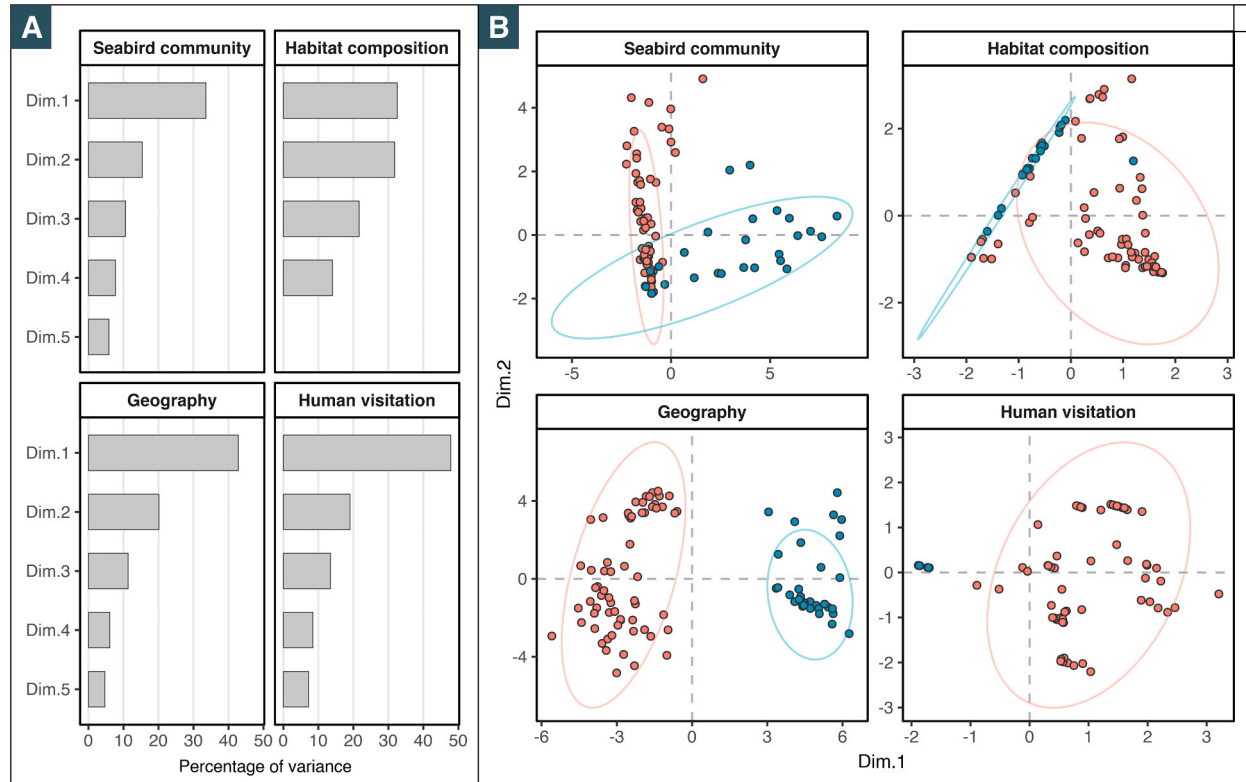


Fig. 3. A: percentage of variance explained by the first five Principal Component (seabird community, habitat composition and neighboring geographical features (= Geography)) or Multi-Factorial Analysis (Human visitation) axes used to summarize descriptive (seabird community) and explanatory variables (rest of the panels). B: two-dimensional scatterplots of the first two dimensions of each variable category. Blue: remote islands; Red: Lagoon islands.

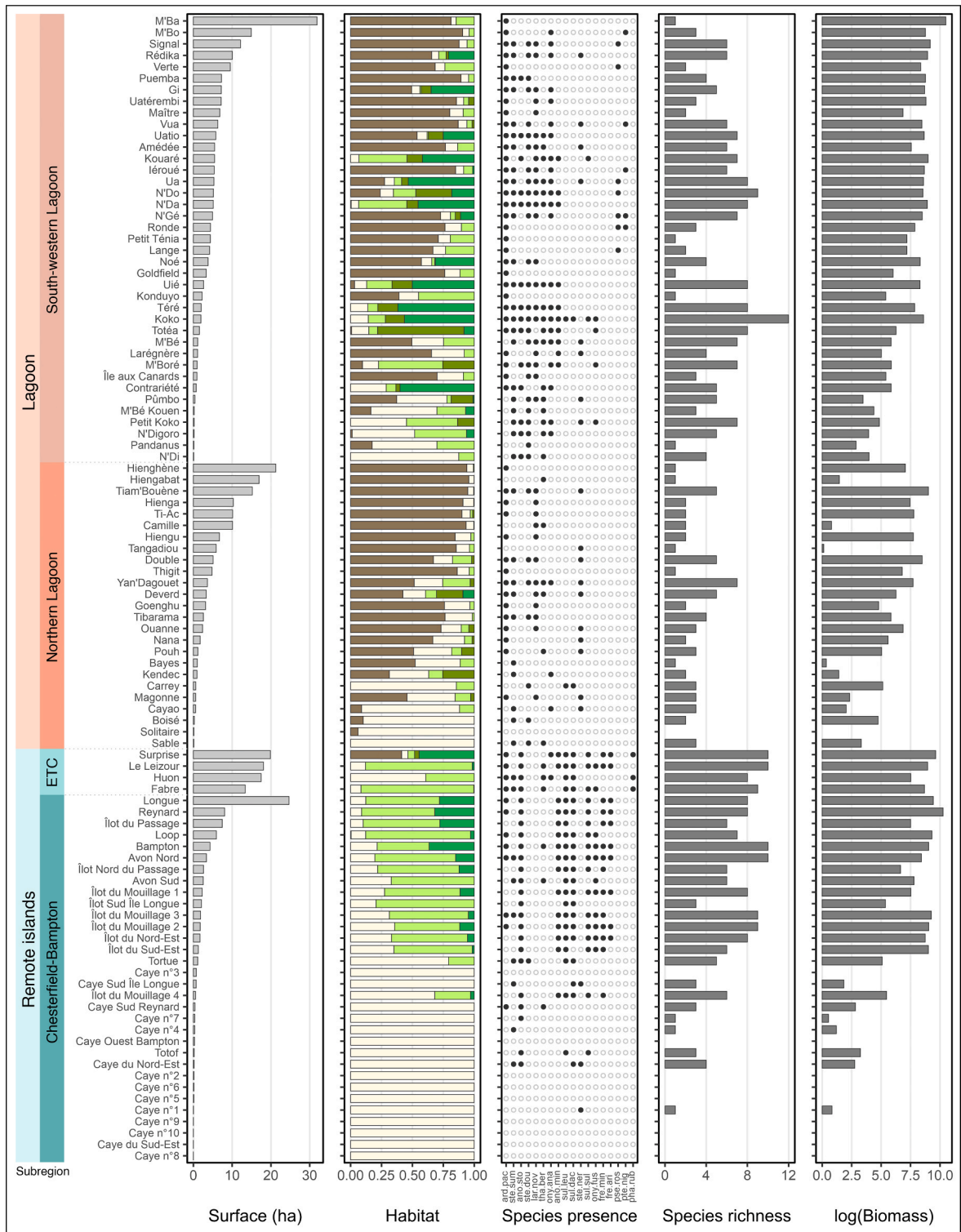


Fig. 4. Characteristics of study sites and associated breeding seabird communities. From left to right: **Island surface (ha)**; **Proportion of breeding habitats** (beige: bare coral/ground; lightgreen: low plant cover, kaki: *Suriana maritima* bushes, green: arboreal patches of *Pisonia grandis* or *Heliotropium foertherianum*, brown: other); **Species presence** (black dots: breeding observed on the corresponding site over the study period, white: no breeding observation); **Species richness**; **log-transformed Biomass** (originally in kg).

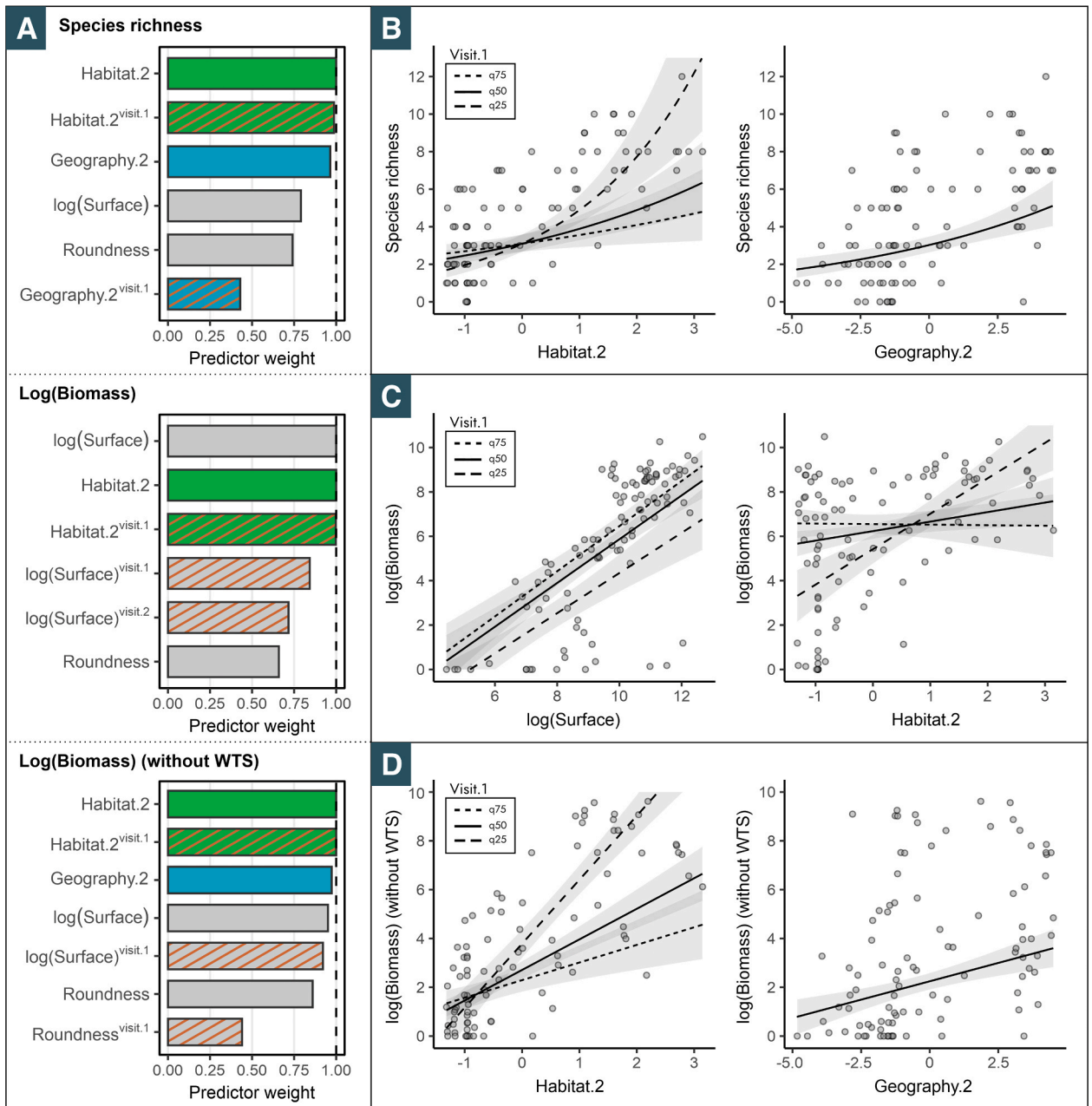


Fig. 5. A: Cumulative AICc weights of evaluated predictors with Species richness (top), log-transformed Biomass (middle), and log-transformed Biomass excluding Wedge-tailed shearwaters (without WTS) (bottom) as response variables. Superscript text (e.g. ^{visit.1}) and dashed bars indicate interaction with anthropogenic covariates. Numbers next to predictors indicate the corresponding dimensions of respective Principal Component (Habitat, Geography) or Multi-Factorial (Human visitation) Analyses. Only predictors with an inferred weight > 0.4 are shown. B, C, D: observed (dots) and predicted values (line) of species richness, log-transformed Biomass, and log-transformed Biomass excluding Wedge-tailed Shearwater (without WTS) with Habitat.2 and Geography.2, (B) log-transformed Surface and Habitat.2 (C), and Habitat.2 and Geography.2 (D) as respective predictors. Grey ribbons indicate 95% confidence intervals. For each graph, predictions were obtained from the models described in Table 3, with all variables except the one being tested assumed constant at their median values. When statistically significant, multiplicative effects of human visitation are shown (0.25 (high visitation), 0.5 (median visitation) and 0.75 (low visitation) quantiles of the Visit.1 predictor).

in the model with the lowest AIC after the second selection step (2.4.). We found no significant effect of remoteness (*Geography.1*) on species richness, and the absence of residual spatial autocorrelation suggested that similar drivers influence species diversity on both lagoon and remote islets regardless of species assemblages.

Overall biomass was mostly determined by log-transformed islet surface and habitat availability (*Habitat.2*), both of which exerted

a positive influence (Fig. 5A, Table 2). Contrary to species richness, sites that receive more human visitation were associated with higher seabird biomass (Fig. 5C). This effect disappeared when excluding WTS, which diminished the influence of islet surface and revealed an expected negative impact of human visitation on biomass (Fig. 5D). Predictor influence on biomass without WTS was broadly similar to that for species richness (Fig. 5A), with habitat availability (*Habitat.2*) and geography (*Geography.2*) displaying the most important contributions. However, islet surface retained a significant positive influence, also lowered by human visitation (Table 2).

4. Discussion

Overall, we established that habitat and resource diversity, as well as island size, positively contributed to species richness and biomass. Conversely, high levels of human visitation had a negative influence on both metrics, except when wedge-tailed shearwaters were included in the biomass estimates. This may reflect a limited impact of visitation on burrow-nesting species, as well as a concentration of WTS colonies on optimal (i.e. forest-covered) breeding sites near the mainland.

4.1. Habitat and resource availability shape seabird communities on CRI

Although remote islands may be seen as optimal conservation targets as they receive minimal anthropogenic influence, they only host part of CRI diversity at the considered scale. Islets located within the mainland's lagoon specifically host short-range foragers (gulls, terns) that generally feed within a 1–50 km kilometer radius from their breeding sites (McLeay et al., 2010), while remote islets mostly host mid-range (<150 km) foragers (boobies, frigatebirds, sooty terns) (Mendez et al., 2017). Resource availability in the vicinity of breeding sites might constrain the composition of seabird communities, which is further validated by WTS being abundant throughout the entire area and exhibiting greater foraging distances that limit the influence of the immediate surroundings of their colonies (Weimerskirch et al., 2020). Counter-intuitively, site remoteness (*Geography.1*) did not seem to alter values of species richness and biomass, even though lagoon and remote islands host dissimilar seabird assemblages. Therefore, predictor influence on these two community traits was consistent across geographical areas, regardless of species composition. This may reflect the lesser impact of anthropogenic activities in the New Caledonian lagoon compared to other CRI archipelagos (e.g. Maldives, Cayman islands) (Cinner et al., 2018).

The influence of habitat availability on both species richness and biomass is the most significant among all predictors, highlighting that the primary constraint on species presence is, as expected, the possibility for a given species to nest on the considered site, in accordance with Batianoff (2000) and Carr et al. (2021). Combined with CRI surface, habitat diversity provides a proxy of a site's carrying capacity: the former constrains biomass and the latter species richness, respectively. The influence of *Geography.2* can be interpreted as a measure of resource diversity around a CRI, with a high proportion of lagoon up to 50 km from the shoreline and pelagic waters beyond, thereby providing potential environmental conditions to support seabird species requiring neritic and/or pelagic foraging environments (Fig. A9). While CRIs are present throughout the intertropical area and host important colonies of seabirds (Berr, 2023, BirdLife International, 2023), we found no published study with comparable scope, consequently the discussion of these particular results cannot include direct comparisons with prior examples.

The limited monitoring of study sites induces a possible overlook of cryptic species or species with rare breeding occurrence, meaning that species richness may occasionally be underestimated. The small number of surveys per site and breeding season did not allow us to correct species abundance for phenological bias (i.e., census not conducted during the breeding peak or succession of successive cohorts of breeders), and the use of averaged counts may not be the most appropriate for all species, as it could be inferred that the maximum reported number of breeders is more representative of a site's carrying capacity. However, the influence of possible biases in biomass estimates is reduced by the use of log-transformed values, as differences between real and estimated biomass are scaled down (for example, if a population estimated at 8000 bp is underestimated by 50%, the resulting difference in log-transformed estimates is 4.3%). We thus consider that such bias would only marginally affect the study's conclusions.

4.2. Human visitation reduces site suitability

High human visitation lowered both species richness and biomass, which may reflect multiple anthropogenic influences such as habitat modification, disturbance and presence of invasive species (e.g., mice and rats) (Carlberg et al., 2022; Devney and Congdon, 2009; Philippe-Lesaffre et al., 2023; Thibault et al., 2020). All these possibly co-occurring effects contribute to reducing a site's suitability for seabirds, either by altering the carrying capacity of the site or breeding success. A similar, negative influence of visitation on species richness and biomass was mentioned in a previous study conducted in the Southern lagoon of New Caledonia, although with less study sites and a simpler set of predictors (Benoit and Bretagnolle, 2002). This observation also echoes prior assessments of distribution patterns conducted on reef fishes that showed highly visited reefs hosted fewer species and reduced biomass, although the underlying mechanisms (e.g., fishing pressure) differ slightly (Cinner et al., 2018; D'agata et al., 2014).

The seemingly positive effect of visitation observed in the overall biomass model is an artefact due to WTS having higher densities in islets close to the mainland, which likely host slightly more favorable habitats (the presence of forests yields thicker soil that may be more adapted to burrow-nesting birds). We were however unable to demonstrate this quantitatively since our characterization of CRIs lacked information on substrate, as it cannot be inferred from aerial imagery. Optimal WTS breeding sites may therefore be more exposed to anthropogenic pressure, even though burrow nesting likely reduces the species' vulnerability to direct disturbance.

4.3. New leads for evidence-based conservation

Species of conservation concern (Tahiti petrel, Fairy tern) accounted for only 0.01% of the total biomass of seabirds that breed on the considered 100 CRIs. Such a pattern is consistent with the observation that CRI seabirds currently exhibit more favorable conservation status than other seabirds (Berr et al., 2023). This peculiarity may partly explain the limited amount of studies dedicated to CRI seabirds, as large-scale conservation approaches mostly target species with established threatened status (Dias et al., 2019; Spatz et al., 2014). We may nevertheless infer that the ecological processes and ecosystem services associated with CRI seabirds (e.g., guano supply, trophic regulation) are essentially driven by abundant species (WTS, noddies, boobies). Effectively preserving these processes therefore requires conservation strategies to also include species that are currently not identified as threatened but are already declining at the local (e.g., Woodworth et al., 2021 for Great Barrier Reef CRIs) or global scale (9 of the 18 considered taxa – BirdLife International, 2023).

Our study highlights the importance of (1) CRIs with diverse breeding habitats that have the potential to host higher diversity and (2) large CRIs or CRIs whose surface is entirely usable for breeding that host a higher biomass of breeders. Consequently, habitat management should be considered a key conservation focus when targeting CRI seabird communities. Indeed, the restoration of a site's native plant cover coupled with social attraction increases breeder density (Feare et al., 2015) and can facilitate the return of previously extirpated species (Carr et al., 2021). Future translocation opportunities for communities threatened by CRI erosion will be directly constrained by the availability of suitable breeding sites (Reynolds et al., 2015), and therefore by the ability of managers to restore CRIs that currently host degraded habitats. Thus, while access restrictions (Devney and Congdon, 2009) and species eradication (Philippe-Lesaffre et al., 2023) hold valuable and demonstrated conservation potential, their use must be adjacent to the assessment of long-term prospects of CRI durability: the future, joint monitoring of both breeding sites and colonies appears especially relevant here, as habitat alterations directly influence seabird presence. Predictions of upcoming erosion dynamics will contribute to site prioritization, which requires building interdisciplinary approaches that combine geomorphological and biological information (Andréfouët et al., 2015; Garcin et al., 2016).

Local monitoring must fuel wider, large-scale assessments of (1) seabird distribution, (2) CRI characteristics, (3) current and future seabird threats, and (4) current and future CRI threats. Indeed, many CRI-dependent species have pantropical distribution (Berr, 2023, this study), thus their conservation must include both local, regional and global assessments of population traits (trends, size, connectivity) and vulnerability. Similar approaches were successfully developed for reef fishes and corals, and have produced multiple assessment of community vulnerability and hierarchization of natural vs anthropogenic impacts on target communities (Cinner et al., 2018; D'agata et al., 2014). The challenge here is that there does not currently exist data exchange networks on CRI seabirds, that would facilitate such analyses.

5. Conclusion

The use of community metrics to highlight conservation priorities is routinely applied in conservation science, however there has been little focus on CRI seabirds despite seabirds (as a species group) being widely studied worldwide. This gap may be seen as a consequence of seabirds having only recently been shown to contribute to reef processes and to reef conservation having historically been focused on aquatic communities. Furthermore, CRI-dependent seabirds currently have better conservation status than other species, despite facing pervasive, global impacts of climate change in coming decades.

While the observed influence of habitat, geography and anthropogenic pressures on seabird communities does not come as a surprise, as it obeys widely accepted biogeography hypotheses, the absence of prior studies and literature is remarkable. It may seem an oddity that the conservation of CRI seabirds has produced no global, dedicated initiative so far, and we hope that this type of study will emphasize the need for more cooperation to fill this gap and contribute to the conservation of reef ecosystems as a whole.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02732](https://doi.org/10.1016/j.gecco.2023.e02732).

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