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Temporal changes in seabird assemblage structure and trait diversity in the Rapa Nui (Easter Island) multiple-use marine protected area

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Abstract

1. For Rapa Nui (Easter Island) and its largest islet, Motu Nui, the change of the species assemblage over time was analysed, and a trait-based approach to evaluate the potential losses in seabird function across the past centuries was applied. At a finer scale, the seasonal changes in seabird species composition in the current seabird assemblage was assessed to better understand the dynamics of the long-term inferred patterns.

2. For Rapa Nui, the composition of the seabird assemblage between the prehistorical, historical, and current time has changed significantly. The most critical change, probably associated with human colonization, was observed between prehistoric and current times. The current diminished number of nesting seabird species was probably the result of local extirpation without evidence of colonization by new species.

3. For Motu Nui, changes in species composition were also followed by changes in trait structure, which were smaller than observed in Rapa Nui. This is probably due to the presence of a relatively high number of related species (i.e. Procellariids) with high similarities in their foraging behaviour.

4. The nesting seabird assemblages in Rapa Nui and Motu Nui differ in exposure to risk; thus, conservation strategies applied to the islands should be planned on a fine spatial scale. For Rapa Nui, which is an urban wildlife area with several invasive species and a low number of remaining native seabird species, management should focus on fencing and pets control. For Motu Nui, management should instead focus on the establishment of quarantine and other biosecurity tools to avoid both the entry and proliferation of new invasive species.

KEYWORDS
birds, island, marine protected area, taxon richness

1 | INTRODUCTION

Archaeological records from the Holocene period in the Polynesian islands reveal widespread extinction of numerous bird species, as well as local extirpation of seabird populations (Steadman, 1989; Steadman & Martin, 2003). Massive extinction of insular biota during the Holocene has been associated with hunting by the first wave of human colonization from South-East Asia to the islands of the South-

East Pacific (e.g. Dye & Steadman, 1990; Olson, 1989; Steadman, 1989, 2006; Steadman & Martin, 2003). Later, the European colonization of the islands caused additional extinctions. Species presence in this period are documented as museum specimens, paintings, or written records (Steadman, 1989). Comparison among the archaeological and current record from some Polynesian islands suggests that human-driven disturbances caused a decline in bird species richness and the reduction and fragmentation of the distribution range of many species of seabirds (Steadman, 1995, 2006; Steadman & Olson, 1985).

Rapa Nui (or Easter Island, 27° 8′S, 109° 20′W) is an outlier of Eastern Polynesia, with an area of 162 km^2 (Figure 1). On the island, geographic isolation, climatic and ecological change (see Rull et al., 2018), anthropogenic landscape degradation, and human hunting may have had a synergistic effect leading to the extinction/extirpation of birds in the past (Rull et al., 2016; Steadman, 2006). Archaeological studies described at least 22 seabird species inhabiting Rapa Nui (including terns (Sterninae), storm petrels (Hydrobatidae), and petrels (Procellariidae)) and six terrestrial bird species (including parrots (Psittaciformes), rails (Rallidae), and herons (Ardeidae)) (Steadman, 1995, 2006). Today, all the native terrestrial birds of Rapa Nui are extinct, and only five species of seabirds still nest there: the red-tailed tropicbird (*Phaethon rubricaudra*), the white-tailed tropicbird (*Phaethon lepturus*), the brown noddy (*Anous stolidus*), the grey noddy (*Anous albivitta*), and the great frigatebird (*Fregata minor*) (Lazo, 2011;

P. Lazo, personal communication, July 2015). However, 12 additional seabird species nest on three islets, called *Motus*, located on the south-west side of Rapa Nui. Among these islets, Motu Nui is the largest and provides most of breeding seabird species records (Flores, Schlatter, & Hucke-Gaete, 2014; Jaramillo, Johnson, Rothfels, & Johnson, 2008; Johnson, Millie, & Moffett, 1970).

The effects of human perturbation on biodiversity are manifold. Recently, trait-based approaches have been applied to different systems to assess the effects of human-driven disturbances on ecosystem function (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). This approach focuses on the diversity of biological traits instead of species diversity to characterize assemblage structure. Biological traits, also known as biological attributes, are any organismal characteristics that can be measured at the individual level. A biological trait is considered as functional when it somehow affects the organism's performance (individual fitness), and traits are related to a particular ecosystem factor or process (Mlambo, 2014; Violle et al., 2007). For instance, morphological traits, such as wingspan, body size, and body length, reflect the ways seabird species exploit resources, reflecting their trophic role in the marine food web (Furness & Monaghan, 1987; Schreiber & Burger, 2001). Trait diversity is a measure of functional diversity and has been linked to increased ecosystem functioning (Petchey & Gaston, 2006). Examination of trait diversity in the seabird assemblages of Polynesian islands may reveal valuable information about the human-driven disturbances in this insular habitat
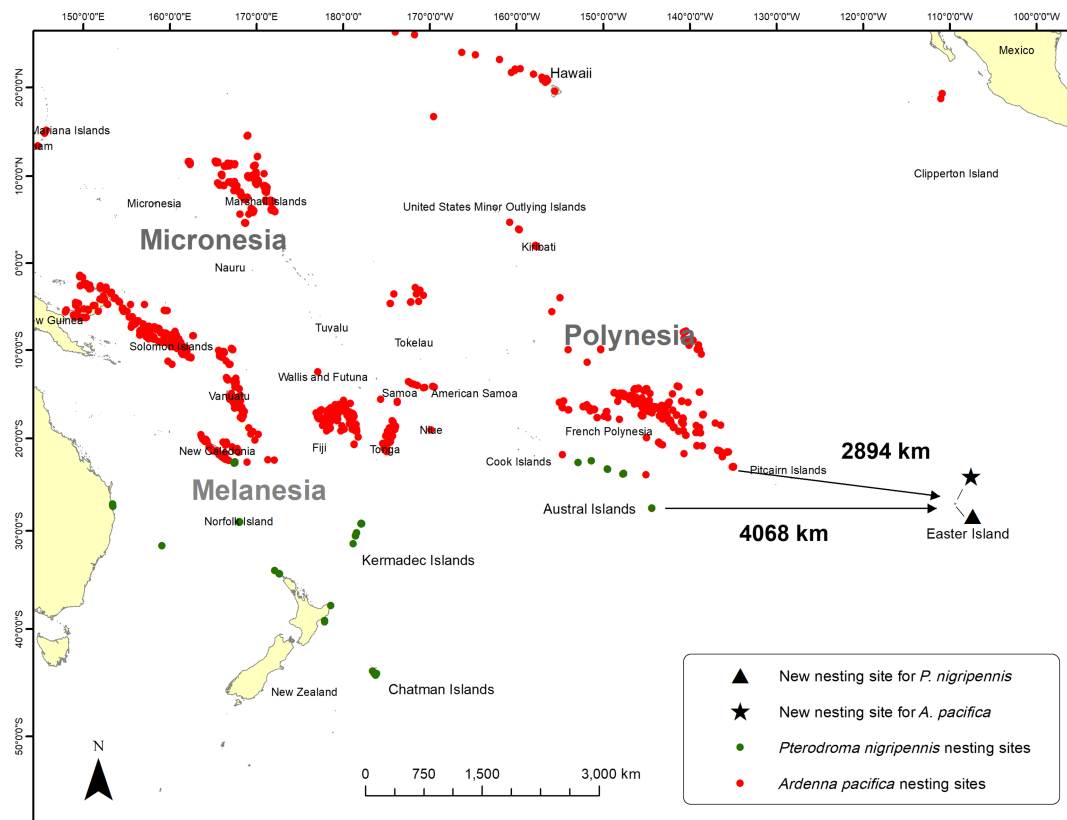
FIGURE 1 Breeding distribution of the black-winged petrel (*Pterodroma nigripennis*), and the wedge-tailed shearwater (*Ardenna pacifica*). These species are recent records for Rapa Nui (Easter Island), Chile. Arrows and numbers indicate direction and distance to nearest nesting site. Data of breeding reports are from Onley and Scofield (2007) and BirdLife International and NatureServe (2015)

(Steadman, 1995, 2006). For Rapa Nui and nearby islets, the change of the species assemblage over time was analysed, and a trait-based approach to evaluate the potential losses in seabird function across the past centuries was applied. Finally, at a finer scale, the seasonal changes in seabird species composition in the current seabird assemblage were assessed to better understand the dynamics of the inferred long-term patterns.

2 | METHODS

2.1 | Data compilation

Information on seabird assemblages on Rapa Nui and Motu Nui (Table 1), during the prehistoric (900–650 BP) and the historical time periods (20th century), were compiled from the existing literature. For the prehistoric time period, studies are based on archaeological data collected from different locations on Rapa Nui (Ayres, 1985; Carr, 1980; Steadman, 1995; Steadman, Casanova, & Ferrando, 1994). Only records of seabird at the species level were included, with records at lower taxonomic resolution excluded. For historical times (i.e. post-European contact), the studies of Fuentes (1914), Johnson et al. (1970), and Harrisson (1971) were used. For current species composition, our records were supplemented with information from Flores et al. (2014), Jaramillo et al. (2008), Marin and Cáceres (2010), and Thibault and Cibois (2017).

2.2 | Species change over time

The temporal β-diversities of seabird assemblages were used to describe changes in species composition through time. The framework proposed by Baselga (2010) was used to estimate whether changes in species composition across time periods were mostly related to species extinction or to species replacement. This framework allows the partitioning of β-diversity into two components: β-nestedness, describes how much of the variation is related to species loss (or gain), which makes a certain time period an impoverished subset of the richest one (a nested pattern); and β-turnover, which describes how much of the variation is related to species substitution from one-time period to another. The sum of nestedness and turnover components is the β-total, which describes the total change in species composition across time. These β-diversity components were calculated using the R package betapart (Baselga & Orme, 2012). The calculations were based on pairwise Jaccard dissimilarities on species occurrences (i.e. presence and absence).

2.3 | Traits diversity change over time

Seabirds from different time periods were compared by analysing changes in the functional trait space. The chosen traits were wingspan (in centimetres), body size (in kilograms), and body length (in centimetres). These traits are related to how species interact and exploit resources within their environment. For tropical seabirds, a greater wingspan is associated with an advantage in using winds to find food over broader ocean areas (Furness & Monaghan, 1987; Schealer, 2001; Schreiber & Burger, 2001). Since morphometric measures can be collinear (i.e. large animals tend to present longer lengths and wings), the relative morphometries of each trait, the ratios wingspan:body mass, body length:body mass, and wingspan:body length were used. The functional trait space constructed from these traits was represented in a principal component analysis (PCA), for which traits were transformed to $\ln(x + 1)$, scaled, and centred. The PCA was performed using the rda routine of the R package vegan (Oksanen et al., 2009).

The trait extension of each time period was estimated using the area of the convex hulls in the first two axes of the PCA. The convex hull area of a functional trait space is a known metric of functional trait diversity, frequently referred to as functional richness (Mason, Mouillot, Lee, & Wilson, 2005; Villéger, Mason, & Mouillot, 2008). Since the dimensionality of the trait space was reduced to the first two axes of the PCA, trait diversity was estimated as the convex hull area by applying the polyarea routine of the R package geometry (Habel, Grasman, Stahel, & Sterratt, 2015). Differences in the convex hulls' area across time periods were tested by applying non-parametric random permutation tests ($\alpha = 0.05$).

The change in species over time was analysed using all nesting and non-nesting species recorded for Rapa Nui. Only species with breeding areas also reported for tropical and subtropical islands were used for analysing the traits' diversities over time.

2.4 | Field surveys on Motu Nui

Motu Nui is a small islet located 13 km off the Rano Kao crater on Rapa Nui, Chile (27° 20′S, 109° 45′W). Motu Nui has an exposed area of 38 ha and a maximum elevation of 56 m above the sea level. Two field surveys on Motu Nui in 2015 during austral summer (January, 10 days) and austral winter (July, five days) were conducted to record and estimate the abundance of breeding seabirds. During each visit, the whole islet was searched for active nests. To identify seabird species, we followed the classification of Onley and Scofield (2007), with a posteriori confirmation by a specialist (P. Harrison, personal communication, September 2015). For the genus Pterodroma, species identification was based on the coloration of wing primaries, secondaries, and coverts. Specifically, individuals with white primary shafts were recorded as Kermadec petrels (Pterodroma neglecta), and individuals with dark primary shafts were recorded as Herald petrels (Pterodroma heraldica) (see Figure 2). The birds were taken from their burrows to identify and photograph them for further confirmation of the species.

The number of breeding individuals was estimated through direct counts of well-constructed nests capable of holding eggs and occupied by at least one bird on or within touching distance to the nest (Bibby, Burgess, Hill, & Mustoe, 2000). To estimate the density of

TABLE 1 Presence (1) and absence (0) of seabird species in prehistoric time (P-H), historical time (H), and contemporary time (CT) nesting records (nes) and species occurrence records (rep)

Seabirds			Rapa Nui				Motu Nui			
Family/species	Common name	Code	P-H	H	CT-rep	CT-nes	H-rep	H-nes	CT-rep	CT-nes
Laridae										
Anous stolidus	Brown noddy	Ano.sto	1	1	1	1	1	1	1	1
Anous albivitta	Grey noddy	Pro.alb	1	1	1	1	1	0	1	1
Gygis alba	White tern	Gyg.alb	1	1	0	0	1	0	0	0
Gygis alba microrhyncha	Little white tern	Gyg.mic	1	0	0	0	0	0	0	0
Onychoprion fuscatus	Sooty tern	Ony.fus	1	1	0	0	1	1	0	0
Onychoprion lunatus	Spectacled tern	Ony.lun	0	1	0	0	1	0	0	0
Sterna paradisaea	Artic tern	Ste.par	1	1	0	0	1	1	0	0
Phaethontidae										
Phaethon lepturus	White-tailed tropicbird	Pha.lep	1	1	1	1	1	1	1	1
Phaethon rubricauda	Red-tailed tropicbird	Pha.rub	1	1	1	1	1	1	1	1
Diomedeidae										
Thalassarche cauta	Shy albatross	Tha.cau	1	0	0	0	0	0	0	0
Thalassarche melanophris	Black-browed albatross	Tha.mel	0	0	1	0	0	0	1	0
Oceanitidae										
Nesofregetta fuliginosa	Polynesian storm petrel	Nes.ful	1	0	0	0	0	0	0	0
Procellariidae										
Ardenna carneipes	Flesh-footed shearwater	Ard.car	1	0	0	0	0	0	0	0
Ardenna creatopus	Pink-footed shearwater	Ard.cre	1	0	0	0	0	0	0	0
Ardenna grisea	Sooty shearwater	Ard.gri	1	0	0	0	0	0	0	0
Ardenna pacifica	Wedged-tailed shearwater	Ard.pac	0	0	1	0	0	0	1	1
Daption capense	Cape petrel	Dap.cap	0	0	1	0	0	0	1	0
Fulmarus glacialoides	Southern fulmar	Ful.gla	1	0	0	0	0	0	0	0
Halobaena caerulea	Blue petrel	Hal.cae	1	0	0	0	0	0	0	0
Macronectes giganteus	Southern giant petrel	Mac.gig	0	1	1	0	1	1	1	0
Macronectes halli	Northern giant petrel	Mac.hal	0	0	1	0	0	0	1	0
Pachyptila turtur	Fairy prion	Pac.tur	1	0	0	0	0	0	0	0
Pachyptila vittata	Broad-billed prion	Pac.vit	1	0	0	0	0	0	0	0
Procellaria aequinoctialis	White-chinned petrel	Pro.aeq	0	0	1	0	0	0	1	0
Pterodroma alba	Phoenix petrel	Pte.alb	0	0	1	0	0	0	1	1
Pterodroma atrata	Henderson petrel	Pte.atr	0	0	1	0	0	0	1	1
Pterodroma externa	Juan Fernandez petrel	Pte.ext	1	0	1	0	0	0	1	0
Pterodroma heraldica	Herald petrel	Pte.her	0	0	1	0	1	1	1	1
Pterodroma lessonii	White-headed petrel	Pte.les	1	0	0	0	0	0	0	0
Pterodroma neglecta	Kermadec petrel	Pte.neg	0	0	1	0	1	1	1	1
Pterodroma nigripennis	Black-winged petrel	Pte.nig	0	0	1	0	0	0	1	1
Pterodroma ultima	Murphy's petrel	Pte.ult	1	0	1	0	0	0	1	1
Puffinus nativitatis	Christmas shearwater	Puf.nat	1	1	1	0	1	1	1	1
Fregatidae										
Fregata minor	Great frigatebird	Fre.min	1	1	1	1	1	0	1	1
Sulidae										
Sula dactylatra	Masked booby	Sul.dac	1	1	1	0	1	0	1	1
Sula leucogaster	Brown booby	Sul.leu	0	0	1	0	0	0	1	0
Sula sula	Red-footed booby	Sul.sul	0	0	1	0	0	0	1	0
Total			23	12	22	5	14	9	22	14

FIGURE 2 Primary shaft coloration patterns. (a, b) Kermadec petrel (*Pterodroma neglecta*), white shafts: (a) underparts; (b) upperparts. (c, d) Herald petrel (*Pterodroma heraldica*), dark shafts: (c) underparts; (d) upperparts
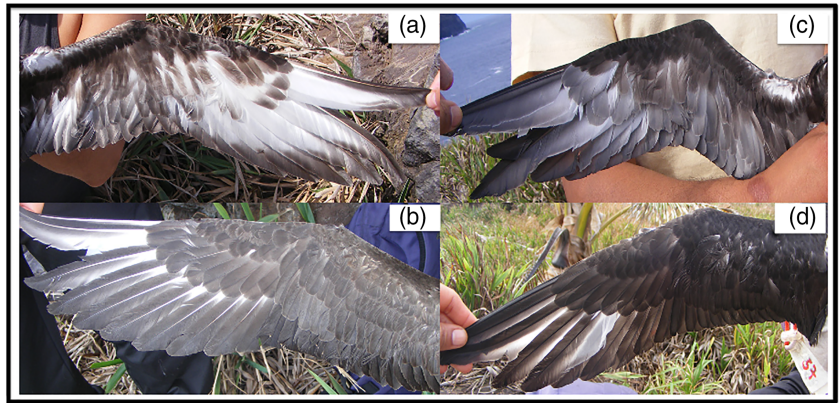
TABLE 2 The β-diversity components estimated for pairwise time periods comparisons based on Jaccard dissimilarities

	Rapa Nui			Motu Nui		
	P-H	H	CT-reported	H-reported	H-nesting	CT-reported
β-turnover						
H	0.29			0		
CT-reported	0.74	0.50		0.44	0.36	
CT-nesting	0	0	0	0.53	0.50	0
β-nestedness						
H	0.31			0.36		
CT-reported	0.01	0.19		0.17	0.34	
CT-nesting	0.78	0.58	0.77	0	0.15	0.36
β-total						
H	0.60			0.36		
CT-reported	0.75	0.69		0.62	0.71	
CT-nesting	0.78	0.58	0.77	0.53	0.65	0.36

β-turnover estimates the proportion of the total dissimilarity that is related to species substitution, β-nestedness is related to species extinction, and β-total is the sum of both components. CT: contemporary time; P-H: prehistoric time; H: historical time.

burrows, the periphery of each nest aggregation was recording with a GPS. A 10 m rope was randomly placed on the ground and the nests or burrows within 1 m on both sides of the rope were counted; and the number of nests per square metre for the whole nest aggregation was extrapolated. A burrow was considered as an occupied nest when feathers and guano were present. Table 3 reports only individuals that were present inside burrows. Seasonal changes in seabird abundance on Motu Nui were analysed with the Shannon–Wiener index, and species composition was analysed with the Jaccard index using the R package *vegan* (Oksanen et al., 2009).

3 | RESULTS

3.1 | Species change over time

For Rapa Nui, the major differences in total β-diversity were between the current nesting reports and the prehistoric time period (β-total = 0.78), which was explained by species loss (β-total = β-nestedness)—see Table 2 for a summary of the β-diversity indices. The high value of β-total was forced by the low number of nesting seabird species reported for Rapa Nui. Currently, five nesting species persist from prehistoric to present times; these belong to the orders Suliformes, Phaethontiformes, and Charadriiformes (Table 1). When comparing current species reports and reports from the prehistoric period, most of the β-total was associated with species turnover (β-turnover = 0.76), and only a small portion was related to species extinction (β-nestedness = 0.02).

For Motu Nui, most of the β-diversity between historical time periods and current time observations was related to species turnover. The most notable difference was between the current reports and historical reports of species nesting (β-total = 0.71; β-turnover = 0.36). This suggests that the current seabird assemblage on Motu Nui is not a simple impoverished subset of prehistoric and historical seabird assemblages but a different assemblage that includes six new Procellariids (Table 1). For example, *Pterodroma nigripennis* and *Ardenna pacifica* are extending their breeding ranges from the north west to Motu Nui in the south east of Polynesia (Figure 1).

3.2 | Trait diversity changes over time

The multivariate space projected from the traits of all seabird species ever reported at Rapa Nui and Motu Nui is presented in Figure 3. The first axis explained 64.8% of the total variation and was mostly related to the traits wingspan:body size and body length: body size. This axis separated Charadriiformes and Procellariiformes. The second axis explained 34.9% of the total variation and was mostly related to the trait wingspan:body length. This axis separates three species from the others: *Gygus alba microrhyncha* (characterized by high wingspan:body length ratio), *Phaethon lepturus*, and

Phaethon rubricauda (characterized by low wingspan:body length ratio). Changes in the trait structures of seabirds of assemblages across time are depicted in Figure 4.

In most cases, the non-parametric permutation tests were not sensitive enough to detect changes in the convex hull area across time (*P* > 0.05 under 1,000 permutations, Table 3). However, differences were detected in the functional trait space over time for both Rapa Nui and Motu Nui (Figure 4). For Rapa Nui, the prehistoric period presented the largest convex hull due to the presence of *G. alba microrhyncha*, a morphologically unique subspecies (Figure 4). The convex hull delimited by current nesting species is two times smaller than in the historical reports and three times smaller than in the prehistoric time period. The contemporary reports of non-nesting species expand the trait space delimited by seabirds in Rapa Nui, making it relatively similar to the historical reports. For Motu Nui, the trait space does not show major changes from historical to current periods. The trait space delimited by current nesting species was the smallest, followed by the trait space of historical breeding species.

FIGURE 3 Principal component analysis representing the trait space derived from the traits of all seabirds ever reported at Rapa Nui and Motu Nui. See Table 1 for the species' codes. Changes in the trait structure of seabird assemblages across time periods are shown in Figure 4

TABLE 3 Pairwise comparisons of the convex hull of different time periods for Rapa Nui and Motu Nui

Rapa Nui		Motu Nui	
Contrasts	*P*-value	Contrasts	*P*-value
H vs. CT-rep	0.4	H-nes vs. CT-rep	0.7
P-H vs. CT-rep	0.2	H-rep vs. CT-rep	0.5
CT-nes vs. CT-rep	0.5	CT-nes vs. CT-rep	0.7
H vs. P-H	<0.001	H-nes vs. His-rep	0.05
H vs. CT-nes	<0.01	H-nes vs. CT-nes	0.7
P-H vs. CT-nes	0.35	H-rep vs. CT-nes	0.6

Comparisons were based on 1,000 simulations. CT: contemporary time; P-H: prehistoric time; H: historical time; nes: nesting records; rep: species occurrence records.

FIGURE 4 Principal component analyses depicting the functional trait space of seabird communities of Rapa Nui. Individual points represent species. (a) Species that occur on Rapa Nui. (b) Species that only occur on the islet Motu Nui. Coloured polygons depict the convex hull of seabird assemblages of different time periods

3.3 | Species change between seasons on Motu Nui

In the field, we confirmed breeding of 10 seabird species on Motu Nui (Table 4). Procellariids accounted for eight of the species. In summer three species were observed in burrows under vegetation in two patches separated by nearly 14 metres: wedge-tailed shearwater (*A. pacifica*), black-winged petrel (*P. nigripennis*) and Christmas shearwater (*Puffinus nativitatis*). These patches were small, with 13 and 18 nests within areas of 40 m^2 and 45 m^2 respectively The Christmas shearwater was the most abundant species, with 46 individuals (83% of the seabird abundance in burrows). A third colony of black-winged petrels occurred a few metres to the south of the nesting Christmas shearwaters, with 15 dirt burrows in an area of 47 m^2. The Jaccard index of changes in species composition between seasons on Motu Nui was 0.54. Three of 10 species nested during both summer and winter: masked booby *Sula dactylatra*, Kermadec petrel, and Henderson petrel (*Pterodroma atrata*; see Table 4). Species diversity indicated that, in winter, no species was dominant, whereas masked booby was the dominant species in summer (Table 4).

4 | DISCUSSION

Because of the different data sources, particularly those from the historical period, the conclusions of this study should be considered with caution. The prehistoric information on seabird assemblages from Rapa Nui is derived from archaeological studies that do not provide information on nesting species or bird populations at the islands. The fragments of bird feathers and bones recovered from human artefacts are the only available information on the bird species that occurred on the island. Also, historical reports on species occurrences from Motu Nui are few and derived from occasional records that did not follow actual taxonomic criteria. Johnson et al. (1970) and Harrisson (1971) visited the islet for several days (between 8 and 12 days) in summer, but winter-breeding species may be underestimated as they did not visit the island in winter. Despite the limitations of archaeological and historical data, the change over time in the diversity of traits on Rapa Nui provides insight into the processes of change that explain current species richness and trait diversity. As suggested by Petchey and Gaston (2006), the diversity of traits is a measure of functional diversity and the related functional complexity of ecosystems. Thus, the approach used here to assess the degree of change in a relevant component of the marine ecosystems across time can provide valuable information on the variability of seabird assemblages useful for suggesting conservation measures for the island (Nogué et al., 2017).

On Rapa Nui, significant changes in the composition of the seabird assemblage between the prehistorical, historical, and current time periods were detected. The most important change was observed between the prehistoric and current periods. The number of nesting seabird species decreased due to local extirpation without evidence for colonization of species not recorded in the subfossil prehistoric record. Currently, only five nesting species persist from the prehistoric period or have successfully recolonized Rapa Nui. The red-tailed tropicbird, which since 2007 has maintained a small colony on Rano Raraku (Flores, Lazo, Campbell, & Simeone, 2017), appears to be most resistant to human impacts. Conversely, other species have been extirpated from the island; for example, the Polynesian storm petrel *Nesofregetta fuliginosa*. The persistence of this species on remote and uninhabited islands, like Salas y Gómez (Vilina & Gazitua, 1999), suggests it is likely to be highly sensitive to the presence of humans and alien species. In the current time, the low diversity of nesting seabird

TABLE 4 Numbers of breeding seabirds on nests in winter (W) and summer (S) on Motu Nui

Order	Genus	Species	Common name	Season	
				W	S
Suliformes	*Sula*	*dactylatra*	Masked booby	20	162
Phaethontiformes	*Phaethon*	*rubricauda*	Red-tailed tropicbird	4	0
Procellariiformes	*Pterodroma*	*neglecta*	Kermadec petrel	9	11
	Pterodroma	*heraldica*	Herald petrel	32	0
	Pterodroma	*atrata*	Henderson petrel	9	2
	Pterodroma	*ultima*	Murphy's petrel	7	0
	Pterodroma	*alba*	Phoenix petrel	4	0
	Pterodroma	*nigripennis*	Black-winged petrel	0	8
	Puffinus	*nativitatis*	Christmas shearwater	0	46
	Ardenna	*pacifica*	Wedge-tailed shearwater	0	1
Total	5	10		85	233
Shannon−Wiener				167	0.9
Jaccard				0.54	

species on Rapa Nui itself reflects the high degree of change in the landscape due to human activity and ecological changes (Hunt, 2007; Rull et al., 2016). Deforestation began with the arrival of Polynesians and was exacerbated by the introduction of ungulates (e.g. sheep, *Ovis aries*) and rats (Flenley et al., 1991; Rull et al., 2016). Additionally, other introduced predators must have had significant negative impacts on the original indigenous, now extinct, birdlife. For example, the small colony of the red-tailed tropicbird is currently under permanent attack from rats (brown rat, *Rattus norvegicus*, and Polynesian rat, *Rattus exulans*), dogs, cats, chimango caracaras (*Phalcoboenus chimango*), and Argentine ants (*Linepithema humile*) (Flores et al., 2017; Luna, Varela, Brokordt, & Luna-Jorquera, 2018; Varela, Luna, & Luna-Jorquera, 2018), probably limiting the development and growth of the colony.

On Motu Nui, the current nesting seabird assemblage comprises 'resident species' that remained or recolonized and 'colonizing species' that arrived recently. We suggest that the current composition is the result of a turnover process over time. Local extinction influenced by human action was followed by the gradual arrival of new colonizing seabird species that breed on the islet (see Tables 1 and 2). Murphy's petrel, *Pterodroma ultima*, which was present in the prehistoric records of Rapa Nui, has successfully recolonized Motu Nui during the last decade, but not Rapa Nui (Lazo, 2011). On the other hand, the black-winged petrel and the wedge-tailed shearwater may have colonized the Motu Nui area only recently, as they are absent from the archaeological and historical records (Ayres, 1985; Steadman, 1995). The nearest breeding sites for these species are the Austral and Pitcairn Islands respectively (Onley & Scofield, 2007; Thibault & Cibois, 2017); nesting on Motu Nui shows that these species extended their breeding range to south-eastern Polynesia (see Figure 1).

Two factors could explain the relatively high seabird species richness recorded on Motu Nu. The first, and perhaps most important, is the difficult access to the islet that limits human presence. Introduced mammalian predators, such as rats, dogs, and cats, are absent. The invasive Argentine ant has been detected recently, perhaps as the result of planting palm trees by local fishermen (Varela et al., 2018). In Hawaii, Argentine ants do not affect the reproductive success of burrow-nesting Hawaiian petrels (*Pterodroma hawaiiensis*), perhaps because burrows are too cold for ants to be active (Krushelnycky, Hodges, Medeiros, & Loope, 2001). A similar constraint may occur on Motu Nui, but this ant may be a problem for surface-nesting birds. The chimango caracara has been recorded flying over the Motu Nui islet but not nesting (unpublished data). The second factor is the geomorphology, characterized by porous substrates that prevent flooding during heavy rain. The vegetation is dominated by a native grass species, *Paspalum forterianum* (Dubois, Lenne, Nahoe, & Rauch Gonzalez, 2013). It offers sheltered rocky caves, scattered among large rocks of different sizes, ranging from centimetres (~10 cm high and 50 cm wide) to a few metres (~2 m high and 4 m wide; Englert, 2014). Thus, the combination of suitable nesting sites without introduced mammals, the vacant niches available on the islet, and the high dispersal abilities of seabirds (Dunlop & Wooller, 1986; Hutton & Priddel, 2002) probably favour the colonization of Motu Nui.

Overall, this study showed that changes in seabird species composition over time were followed by a notable restructuring of the assemblage trait space. The nesting seabird assemblage of Rapa Nui has diminished compared with historical and prehistoric records, suggesting that seabird-related functions in the area were dramatically affected by human-driven extirpation of seabird populations on the island. For Motu Nui, changes in species composition were also followed by changes in trait structure; however, these changes are not as dramatic as for Rapa Nui, since Motu Nui has a relatively high number of nesting species. These changes were mostly driven by the loss of species with unique morphological traits, such as a subspecies of the white tern (*G. alba microrhyncha*) that has a high wingspan to body length ratio, due to its small size (23 cm; del Hoyo, Collar, & Kirwan, 2019). Very little is known about the feeding ecology of *G. alba microrhyncha*, although its trophic niche is assumed to be similar to the white tern *Gygis alba*, which feeds in the inshore pelagic zone on small prey (20–40 mm) **such as pelagic planktivorous fishes** (e.g. Mullidae and Exocoetidae; Ashmole & Ashmole, 1967; Catry et al., 2009). The loss of species with unique trait values and the potential reduction in seabird populations in the zone certainly affected the structure of local food webs. However, the potential for top-down effects on the local marine food webs due to changes in seabird assemblages in East Polynesia is unknown.

Our results on trait diversity might sound counter-intuitive, because they describe a temporal decrease in trait diversity even though species richness increased. Indeed, the more species that are added in an assemblage, the more likely that the increase comes from other taxonomic groups with different traits (Mouchet, Villéger, Mason, & Mouillot, 2010). However, in some cases, particular niches might be no longer available when disturbances cause permanent changes in the system, imposing environmental constraints on colonizing species (Devictor et al., 2008). The introduction of new interacting species, such as new predators and superior competitors, can also hinder the establishment of species with specific traits (Mouillot et al., 2013). These limiting factors can result in a colonizing process in which the increasing number of species is not followed by an increase in trait diversity, indicating that species with certain traits are being excluded (Gerisch, Agostinelli, Henle, & Dziock, 2012). In our study case, if particular habitats are no longer available for nesting, specialist seabird species that rely on such resources might no longer be able to use Rapa Nui as nesting grounds, which explains the shrunken trait space. If this is true, then the trait diversity of the island would reflect a decrease in environmental quality. Only long-term monitoring efforts could assess the significance of the changes in Rapa Nui and to what extent the former nesting seabird assemblages can be recovered.

There is no information on how stable prehistorical seabird assemblages were through large time scales (i.e. from decades to centuries). However, the observations on the nesting seabird assemblages in Motu Nui indicate that notable changes can be observed even over short periods (i.e. across seasons within a year). These notable short-term changes in assemblage composition from winter to summer possibly indicate the seasonal breeding of local populations. Three

species, the masked booby, the Kermadec petrel, and the Henderson petrel, breed during both winter and summer on Motu Nui, as described for other islands in the Pacific and Indian oceans (Brooke, 1995; Brown et al., 2010, 2011; Schreiber & Ashmole, 1970). In contrast, the Christmas shearwater and the Phoenix petrel (*Pterodroma alba*) breed in a single season on Motu Nui, a pattern that differs from other islands, like Christmas Island, where breeding occurs throughout most of the year (Schreiber & Ashmole, 1970). Temporal segregation of breeding habitat has been reported for other seabird species as a mechanism to avoid competition for breeding habitats and food resources (Bretagnolle, Zotier, & Jouventin, 1990; Monteiro & Furness, 1998). Differences in breeding phenology among seabirds on Motu Nui could be a way of sharing limited resources, such as nesting burrows.

Conservation programmes on islands require scientific knowledge about patterns, processes, and threats that determine species richness and composition (Luna-Jorquera, Fernández, & Rivadeneira, 2012). A long-term monitoring programme is needed for Rapa Nui and their *Motus* to determine changes in the seabird abundance and to provide information on how species composition and functional diversity change across short and long temporal scales. Nevertheless, reliable preservation and restoration programmes for Motu Nui and Rapa Nui respectively are urgently needed to ensure both the viability of seabird assemblages and their functional diversity.

Because seabirds nesting on Rapa Nui and Motu Nui face different threats, conservation measures must be specific to each island. For Rapa Nui, which is an urban wildlife area with invasive species that include Argentine ants, rats, cattle, horses, dogs, and cats (see Luna et al., 2018), eradication of invasive mammals may not be feasible. Domestic mammals have owners that may oppose an eradication campaign because of perceived benefits (Oppel, Beaven, Bolton, Vickery, & Bodey, 2011). However, a high number of domestic and pet mammals are free-ranging and hamper the nesting of seabirds. Fencing and local control would be practical measures to protect seabird nesting sites on Rapa Nui. Fencing Rano Raraku could prevent mammals from disrupting the nesting attempts of the red-tailed tropicbird and *Pterodroma* species (Lazo, 2011; Marin & Cáceres, 2010). For domestic pets (cats and dogs), control should be accompanied by collaborative work with the local community to design a responsible ownership plan to eliminate free-ranging pets. For the three species of rats on Rapa Nui (Luna et al., 2018), chemical deterrents (Latorre, Larrinaga, & Santamaría, 2013), accompanied by better disposal of domestic waste, may be suitable measures.

Motu Nui islet should be a no-take area dedicated to the preservation of the biodiversity. The management actions should focus on the establishment of quarantine and other biosecurity tools to avoid both the entry and proliferation of new invasive species. A monitoring programme should be implemented, both for the early detection of new invasive species and for determining the potentially harmful effects of Argentine ants on the post-fledging survival rate of the birds breeding on Motu Nui (Varela et al., 2018). Efforts at both sites could contribute to the perpetuation and growth of this geographically important seabird community.

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