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RESEARCH ARTICLE

# Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication

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**On many Pacific and Indian Ocean islands, colonization by humans brought invasive species, native vegetation destruction, and coconut plantations, leading to the decimation of seabird populations. The coconut industry on oceanic islands has since crashed, leaving the legacy of altered, impoverished ecosystems. Many island restoration projects eradicate invasive species, particularly rats, with the goal of restoring seabird-driven ecosystems. However, in the absence of converting abandoned plantations to habitat conducive to breeding seabirds, seabird-driven ecosystems may not fully recover after rat eradication. Here we quantify and, by resource selection function, confirm seabird habitat selection within the Chagos Archipelago, before estimating the potential difference in breeding abundance following rat eradication with and without active management of abandoned plantations. Using Ile du Coin as our primary example, we estimate that following rat eradication, but without plantation conversion, this island could potentially support 4,306 (±93) pairs of breeding seabird; if restored to habitat representative of associated rat-free islands, 138,878 (±1,299) pairs. If 1 km$^2$ of plantation is converted to produce 0.5 km$^2$ each of native forest and savanna, it could theoretically support 319,762 (±2,279) breeding pairs—more than the entire archipelago at present. Our research indicates that when setting restoration goals in the Chagos Archipelago, at least 55% of the restored habitat should be composed of native forest and savanna in order to support a viable seabird community. Our research enhances the prospects of successfully restoring seabird islands across the tropical landscape with wider benefits to native biodiversity.**

**Key words:** Chagos Archipelago, invasive species, rat eradication, restoration, vegetation management

### Implications for Practice

- To restore tropical oceanic seabird islands that have been ecologically degraded due to introduced mammalian predators and native habitat destruction, eradicating the predator as a single intervention is unlikely to result in fully functional seabird-driven ecosystems.
- On degraded islands where invasive rats and abandoned coconut plantations exist together, to restore seabird-driven ecosystems rats must be eradicated, and the plantations converted to native habitat.
- Once predators have been eradicated, at least 55% of the habitat needs to be of rehabilitated native communities to restore seabird-driven ecosystems.
- Our research indicates that a whole ecosystem approach to recovery is likely to be more successful than just targeting invasive mammal removal.

## Introduction

Islands contribute disproportionally to global biodiversity relative to their comparatively small land mass (Whittaker 1998). With their high rates of endemism and relative isolation, they have incurred 61% of all documented extinctions and currently support 37% of all critically endangered species (Tershy et al. 2015). The conservation (and restoration) of islands and their associated biodiversity is therefore a global priority (CBD 2020).

Seabirds are key components of island ecosystems (Smith et al. 2011), transporting nutrients from the open ocean to islands, enhancing the productivity of island flora and fauna

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and surrounding marine ecosystems (Graham et al. 2018). Yet, seabird islands have been severely degraded by human activities worldwide (Mulder et al. 2011a) due in part to deforestation (Anderson & Mulder 2011), and the introduction of invasive species (Jones et al. 2016). Indeed, invasive species, particularly rats and cats, are the greatest threat to global seabird populations (Dias et al. 2019) as well as to island biodiversity generally (Millennium Ecosystem Assessment 2015).

Repairing damage to degraded seabird islands by eradicating invasive mammals has proven extremely effective (Jones et al. 2016). However, predator eradication may not necessarily lead to (re)colonization and ecosystem recovery because of ecological factors such as distances to source populations, metapopulation dynamics, philopatry strength, reproductive rates, and competition with other colonizers (Kappes & Jones 2014). Moreover, the recovery of a seabird island post-eradication is strongly influenced by the availability of suitable breeding habitat (Smith et al. 2011; Mulder et al. 2011a).

In the tropical Indian and Pacific oceans, many seabird islands became degraded following human colonization, the introduction of invasive mammals, and clearance of native vegetation for *Cocos nucifera* (coconut) plantations (Maunder et al. 1998; Samways et al. 2010; von Brandis 2012; Wenban-Smith & Carter 2017). With the demise of coconut farming on oceanic islands (Wenban-Smith & Carter 2017), many former plantations were abandoned and >50% of the 1.3 million trees on Pacific islands are classified as senile and unproductive (McGregor & Sheehy 2017). These abandoned plantations are considered invasive (Young et al. 2017), break natural ecological interactions (McCauley et al. 2012), reduce floristic diversity, and change soil characteristics (Young et al. 2010a; Mulder et al. 2011b), resulting in impoverished ecosystems that support few breeding seabirds (Young et al. 2010b; Carr et al. 2013). Therefore, even if invasive mammals are eradicated, seabird-driven ecosystems are unlikely to recover fully in the absence of vegetation management. Conversion of abandoned plantations to seabird breeding habitat is thus essential for ecological rehabilitation (Norton & Miller 2000), although more evidence is required to quantify such effects.

The Chagos Archipelago, central Indian Ocean (Fig. 1), formerly held seabird colonies at least an order of magnitude greater than today (Bourne 1886; Gardiner & Cooper 1907; Bourne 1971). The decline was due to invasive mammalian predators, harvesting, and clearance of native habitat for monospecific coconut plantations (Bourne 1971; Wenban-Smith & Carter 2017). Copra (coconut kernel for oil production) was so successful that by 1880 the archipelago was known as the Oil Islands (Scott 1961). Coconut farming ceased in the 1970s and except for a transient military population on one island (Diego Garcia), all islands are now uninhabited. Abandoned plantations are the dominant vegetation throughout the archipelago (Carr et al. 2013) and on all 30 islands where plantations were established, invasive *Rattus rattus* (ship/black rats—hereafter rat) are present (Harper et al. 2019).

However, islands not farmed for coconut ($n$ = 24) are in a near-natural vegetative state and rat-free (Scott 1961; Edis 2004; Wenban-Smith & Carter 2017; Harper et al. 2019) with seabird-

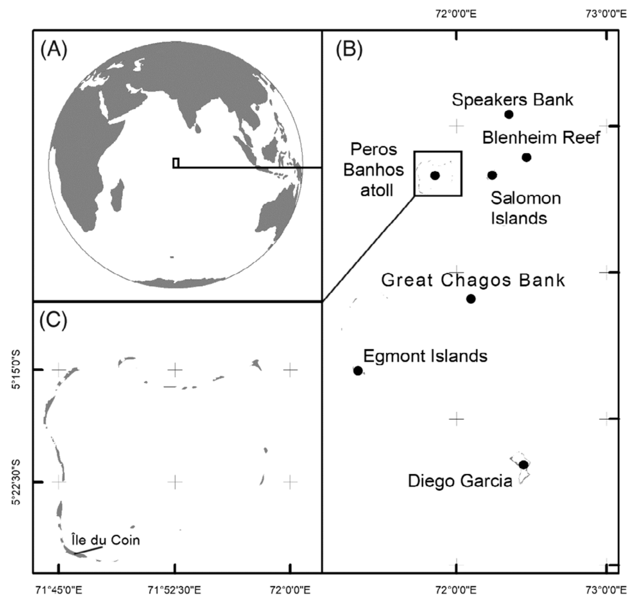


Figure 1. The Chagos Archipelago, (A) location within the Indian Ocean, (B) major reef, banks, and atolls, and (C) Ile du Coin within Peros Banhos atoll.

driven ecosystems (Graham et al. 2018; Benkwitt et al. 2019). Collectively, these 24 islands form a contemporaneous reference site (CTR) (Mulder et al. 2011a). CTRs are sites (here islands) that are used to set targets for island restoration projects, especially where historical data are lacking (Mulder et al. 2011a), such as in the Chagos Archipelago, as they represent present-day climatic and environmental regimes and have properties that can be explicitly measured to evaluate restoration progress against (Jones et al. 2011). The measured properties in this study's CTR are the six types of breeding habitat and the number of species and abundance of breeding seabirds in them. The numbers of breeding seabirds in the CTR are what the restored islands will be evaluated against.

Here, in the Chagos Archipelago, we quantify the hypothetical potential increase in breeding seabird numbers with and without conversion of abandoned coconut plantations to breeding seabird habitats, post rat eradication.

## Methods

### Overview

To estimate breeding seabird numbers, post-hypothetical rat eradication, and vegetation management, we first defined seabird breeding habitats ($n$ = 6) and measured their availability on every island. We recorded the number of different species of seabirds and their abundance breeding in each habitat and used resource selection modeling to identify species-specific preferred nesting habitats. Using the (rat-free) CTR breeding seabird data, we calculated population density (breeding pairs/km$^2$) for each species in each breeding habitat. We used these habitat-specific breeding seabird densities to estimate breeding seabird abundance on a former coconut plantation island (Ile

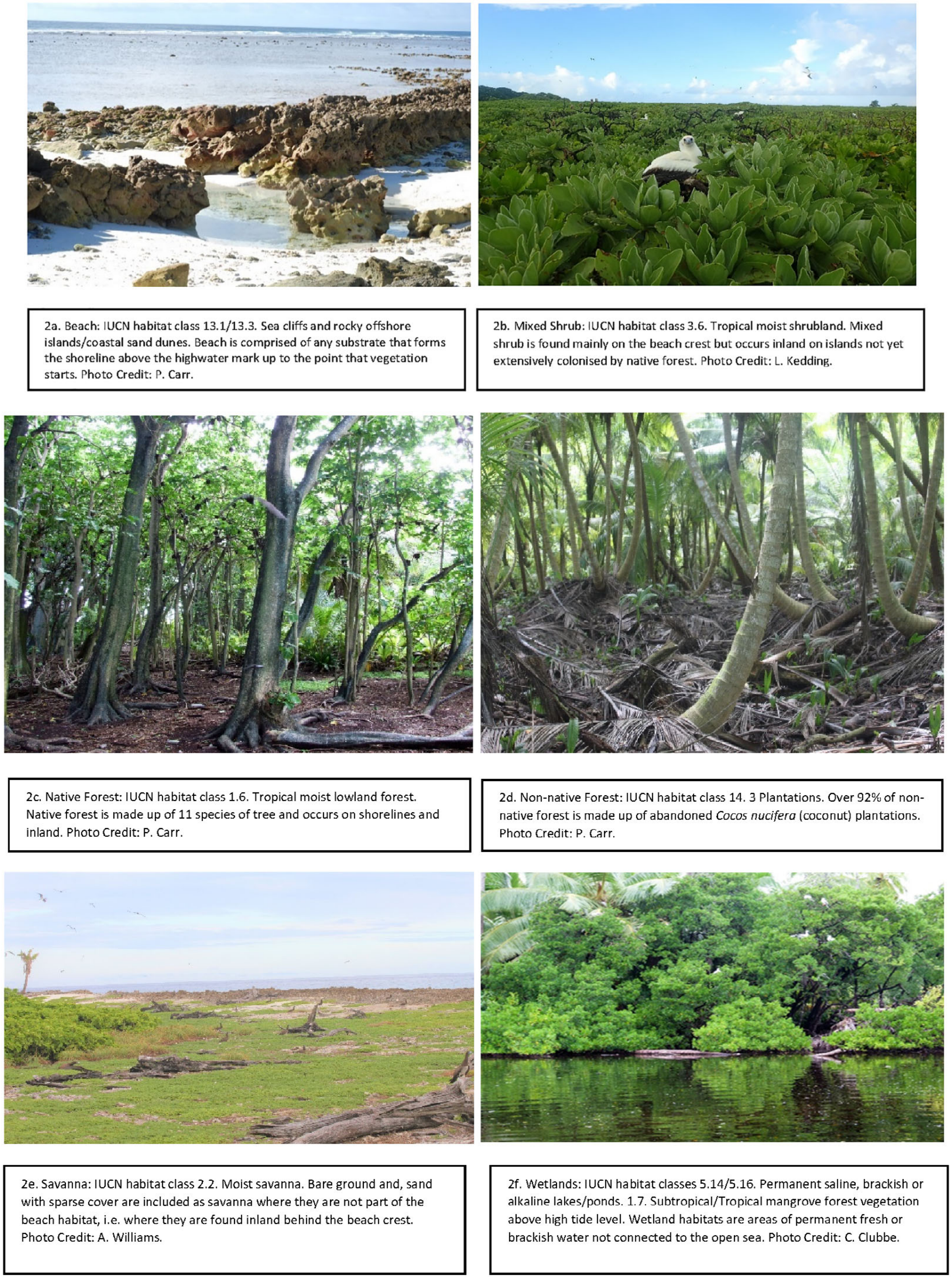


Figure 2. Tropical seabird breeding habitat classification in the Chagos Archipelago; adapted from Wilkinson (2017) and Bárrios and Wilkinson (2018). (A) Beach: IUCN habitat class 13.1/13.3. Sea cliffs and rocky offshore islands/coastal sand dunes. Beach is comprised of any substrate that forms the shoreline above the highwater mark up to the point that vegetation starts. Photo Credit: P. Carr. (B) Mixed Shrub: IUCN habitat class 3.6. Tropical moist shrubland. Mixed shrub is found mainly on the beach crest but occurs inland on islands not yet extensively colonized by native forest. Photo Credit: L. Kedding. (C) Native Forest: IUCN habitat class 1.6. Tropical moist lowland forest. Native forest is made up of 11 species of tree and occurs on shorelines and inland. Photo Credit: P. Carr. (D) Non-native Forest: IUCN habitat class 14.3. Plantations. Over 92% of non-native forest is made up of abandoned *Cocos nucifera* (coconut) plantations. Photo Credit: P. Carr. (E) Savanna: IUCN habitat class 2.2. Moist savanna. Bare ground and sand with sparse cover are included as savanna where they are not part of the beach habitat, i.e. where they are found inland behind the beach crest. Photo Credit: A. Williams. (F) Wetlands: IUCN habitat classes 5.14/5.16. Permanent saline, brackish, or alkaline lakes/ponds, 1.7. Subtropical/Tropical mangrove forest vegetation above high tide level. Wetland habitats are areas of permanent fresh or brackish water not connected to the open sea. Photo Credit: C. Clubbe.

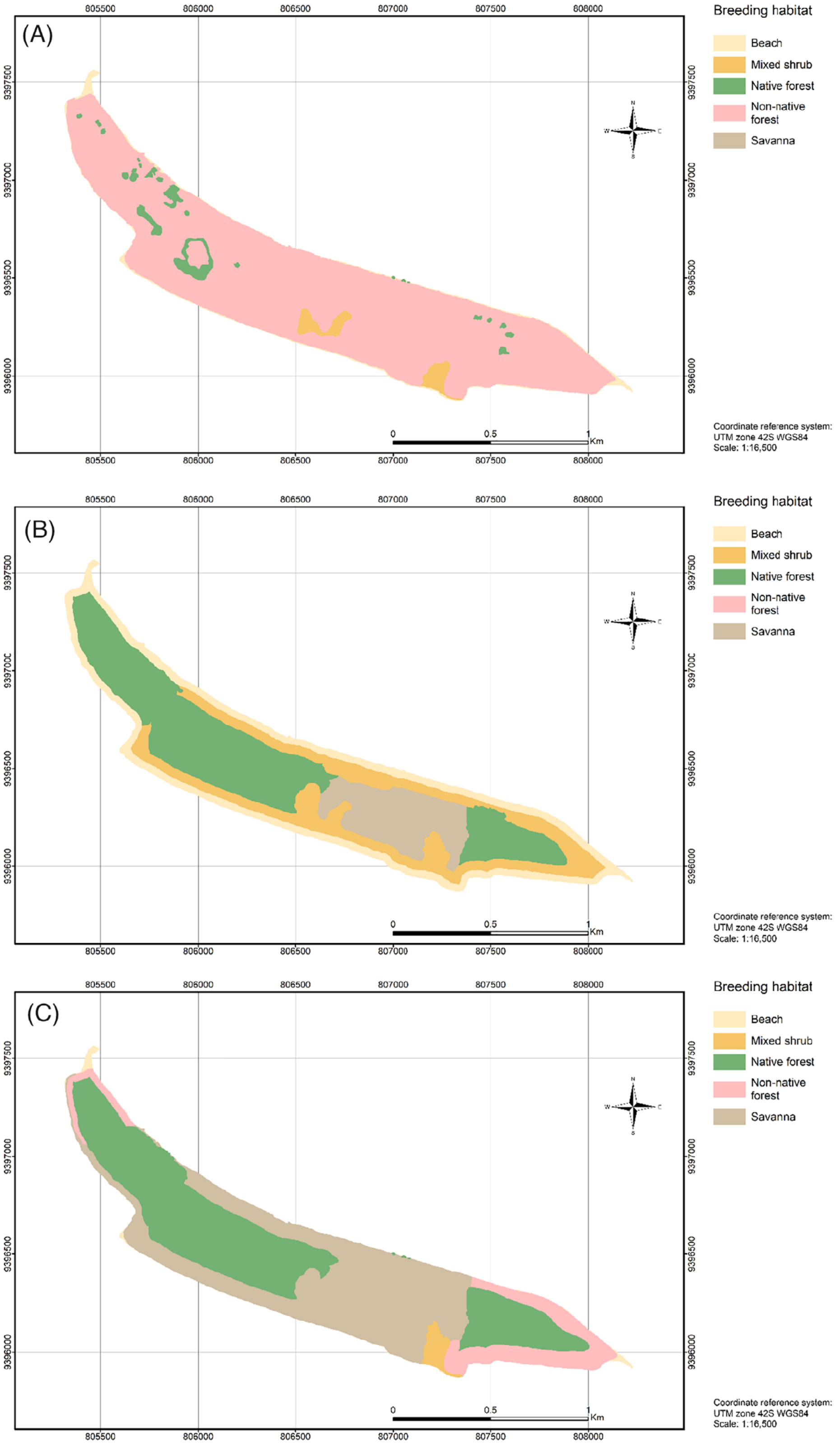


Figure 3. Ile du Coin, Peros Banhos atoll, Chagos Archipelago. (A) Extant vegetation cover; (B) vegetation cover after hypothetical conversion of *Cocos nucifera* (coconut) plantations to proportionately represent the extant vegetation cover on the contemporaneous reference site; and (C) after converting 1 km$^2$ of plantation to produce 0.5 km$^2$ each of native forest and savanna (adapted from Wilkinson 2017).

**Table 1.** The physical area and mean percentage area with standard deviation (SD) covered by six breeding habitats across the Chagos Archipelago; the actual number of breeding pairs and breeding pairs/km$^2$ per habitat and number of species breeding in a habitat, on rat-free (RF) and rat-infested (RI) islands. BEAC, beach; MISH, mixed shrub; NATF, native forest; NONF, non-native forest; SAVA, savanna; WETL, wetlands.

| | *Area (km$^2$)* | | *% Area/SD* | | | | *Breeding Pairs* | | *Breeding Pairs/km$^2$* | | *No. of Breeding Species in Habitat* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Habitat* | *RF* | *RI* | *RF* | | *RI* | | *RF* | *RI* | *RF* | *RI* | *RF* | *RI* |
| BEAC | 0.280 | 7.860 | 20.790 | 5.040 | 7.350 | 1.950 | 434 | 316 | 1,550 | 40 | 4 | 3 |
| MISH | 1.110 | 2.800 | 23.770 | 3.810 | 20.260 | 4.020 | 9,900 | 3,047 | 8,919 | 1,088 | 7 | 4 |
| NATF | 1.210 | 10.900 | 36.990 | 5.850 | 13.200 | 3.500 | 61,280 | 7,001 | 51,471 | 697 | 10 | 5 |
| NONF | 0.240 | 15.870 | 5.200 | 3.180 | 54.860 | 5.270 | 136 | 1,121 | 588 | 71 | 3 | 2 |
| SAVA | 0.340 | 1.200 | 12.930 | 2.990 | 3.360 | 1.290 | 197,409 | 0 | 580,615 | 0 | 6 | 0 |
| WETL | 0.004 | 0.300 | 0.330 | 0.310 | 0.980 | 0.440 | 55 | 450 | 13,750 | 1,500 | 1 | 1 |
| Totals | 3.184 | 38.930 | — | — | — | — | 269,214 | 11,935 | — | — | — | — |

du Coin, 1.26 km$^2$, hereafter Coin), following rat eradication, under three plantation conversion scenarios.

There are assumptions in the calculations that require consideration. It is assumed that throughout the data gathering period (2008–2018) the habitat remained constant and the breeding birds' selection of habitat remained consistent. It is also assumed that all breeding habitats were identified, and birds had access to these all the time. It is accepted that recolonization post-ecological intervention by tropical seabirds can be unpredictable with extenuating circumstances impacting (Jones et al. 2011), can take decades (Dunlop et al. 2015), and that the marine resources capable of supporting increased seabird populations must be extant (e.g. Danckwerts et al. 2014).

### Study Site

The Chagos Archipelago, central Indian Ocean (05°15′–07°27′S, 71°15′–72°30′E), holds 55 low-lying (1–3 m AMSL) porous, coralline islands sited on five atolls (Fig. 1). The southernmost island of Diego Garcia constitutes ~50% (~27 km$^2$) of the terrestrial landmass of the archipelago and the remaining islands' median size is 0.14 km$^2$ (range 0.025–2.65 km$^2$).

Coin is the former plantation headquarters of Peros Banhos atoll and has been uninhabited since 1973 (Wenban-Smith & Carter 2017). At 1.26 km$^2$, it is the fourth largest island in the archipelago. Abandoned coconut plantations form ~92% of vegetation cover (Wilkinson 2017) that, when combined with invasive rat presence, means it supports an impoverished biome including only 51 breeding pairs of three seabird species (Carr et al. 2020). The extant vegetation communities on Coin are representative of all rat-infested former plantation islands >0.5 km$^2$ in the Chagos Archipelago ($n$ = 13 - Figs. 3A and S1).

### Breeding Seabird Habitat Mapping

We defined and mapped six seabird breeding habitat types (see Figs. 2A-F) for ~90% of the Chagos Archipelago based on Wilkinson (2017) and Bárrios and Wilkinson (2018). The unmapped 10% were categorized using expert local knowledge, satellite imagery, and aerial photographs (see Table S1).

### Breeding Seabird Habitat Selection

Breeding seabird populations were surveyed between 2008 and 2018 (for details see Carr et al. 2020). Across the archipelago, the maximum annual population was estimated at 281,149 breeding pairs of 18 species (Carr et al. 2020) and all nests were assigned to a breeding habitat (Figs. 2A-F). To test whether seabirds were preferentially selecting breeding habitats over others, we used resource selection functions (Manly et al. 2002). As a measure of available habitat, we modeled 10 pseudo-absences for each nest for 14 species across the 24 islands of the rat-free CTR. Four species, *Phaethon lepturus* (White-tailed Tropicbird), *P. rubricauda* (Red-tailed Tropicbird), *Sterna dougallii* (Roseate Tern), and *Sternula albifrons* (Little Tern), were omitted from the analysis because of small numbers (<5 pairs) and irregular (not annual) breeding, and two species, Red-tailed Tropicbird and Little Tern, only breed on rat-infested Diego Garcia (Carr et al. 2020). We randomly assigned each nest a vegetation type based on the percentage vegetation cover on the island that the corresponding "used" nest was located in. Habitat use (binary response variable; 1 = used, 0 = available) was modeled in response to a two-way interaction between vegetation type and species, to explore species specific nest-site habitat selection. Island and size were included as fixed effects to account for potential effects on breeding numbers. We were unable to fit island as a random effect because of issues with convergence and rank deficiency.

Models were run using the "glm" function in *lme4* (Bates et al. 2015), with a binomial error structure and logit link. Used and available points were given weightings of 10 and 1, respectively, thereby weights were proportionally equal between all used and available locations (Barbet-Massin et al. 2012). We selected the most suitable fixed effects structure based on corrected Akaike information criterion (AICc) values in backward stepwise selection (Table S2). We ensured model fit by calculating the area under the receiving operator characteristic curve (AUC—Zweig & Campbell 1993), predictive power, and sensitivity and specificity (Warwick-Evans et al. 2016) (Table S3). All analyses were conducted in the statistical software package R, version 4.0.3 (R Core Team 2017).

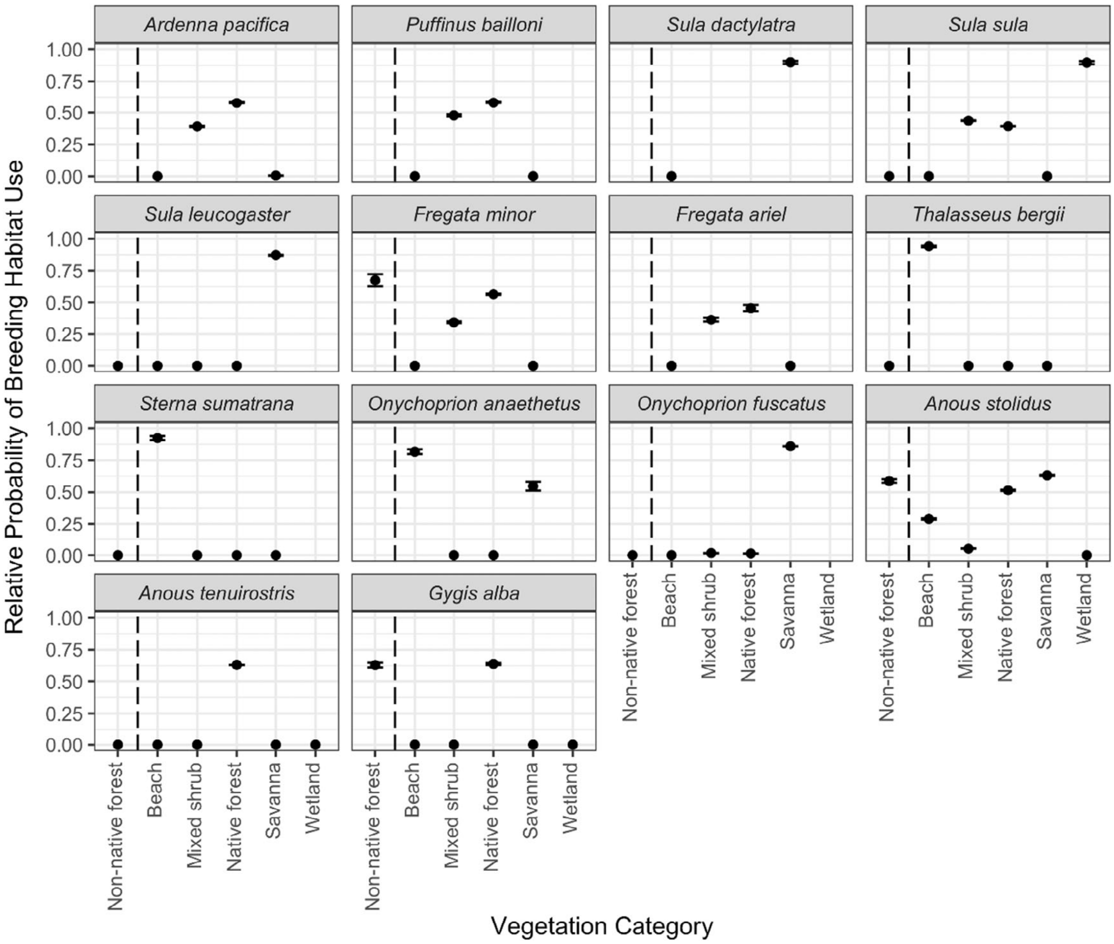


Figure 4. Breeding habitat selection for 14 species of tropical seabird from the (rat-free) contemporaneous reference site in the Chagos Archipelago. Error bars show ± SE.

**Table 2.** Ile du Coin, Chagos Archipelago, breeding seabird population (breeding pairs ± SD) from the present day and, after scenario A: following rat eradication with no vegetation management; scenario B: after theoretically converting abandoned coconut plantations on the island to a habitat ratio equivalent of the contemporaneous reference site; and scenario C: after 1 km$^2$ of abandoned coconut plantation is theoretically converted equally between savanna and native forest. BEAC, beach; MISH, mixed shrub; NATF, native forest; NONF, non-native forest; SAVA, savanna; WETL, wetlands.

| | *Breeding Pairs per Habitat* | | | |
|---|---|---|---|---|
| *Habitat Type* | *Present day* | *Scenario A* | *Scenario B* | *Scenario C* |
| Beach | 0 | 17 ± 0 | 391 ± 3 | 17 ± 0 |
| Mixed shrub | 0 | 214 ± 6 | 2,809 ± 72 | 214 ± 5 |
| Native forest | 13 | 3,397 ± 91 | 25,941 ± 633 | 29,133 ± 709 |
| Non-native forest | 38 | 678 ± 15 | 0 | 90 ± 1 |
| Savanna | 0 | 0 | 109,736 ± 591 | 290,307 ±1,564 |
| Wetland | 0 | 0 | 0 | 0 |
| Total | 51 (3 ssp.) | 4,306 ± 93 (14 ssp.) | 138,878 ± 1,299 (16 ssp.) | 319,762 ± 2,279 (16 ssp.) |

### Estimating Breeding Seabird Populations Post-Management

We employed a two-step process to estimate the number of breeding seabirds that could potentially be supported by Coin, following rat eradication, under three plantation conversion scenarios.

First, we calculated for each of the six habitats the breeding density (pairs per km$^2$) of all seabird species across the CTR (Tables 1 and S4). Second, we applied these habitat-specific population densities to Coin, following rat eradication, where (A) the vegetation composition remained the same as the current situation (Fig. 3A); (B) the plantation was converted to the habitat composition in the CTR (Fig. 3B), and (C) 1 km$^2$ of plantation was converted to 0.5 km$^2$ of native forest and 0.5 km$^2$ of savanna habitat, which were identified as the two habitats supporting the greatest abundance and number of species of breeding seabirds in the CTR (Fig. 3C; Table 1). Coin holds 1.154 $km^2$ of non-native forest (SI Worked Example), 1 $km^2$ was selected for conversion as this is the figure that would likely be used in a real-time conversion operation. A working example of calculating seabird breeding density following rat eradication on Coin is provided for scenario A in Supplement S1.

## Results

### Breeding Seabird Habitat Mapping

Archipelago-wide, there was ~12x more rat-infested than rat-free habitat (Table 1). Non-native forest on rat-infested islands covers the greatest area (15.87 $km^2$/~55%) of which 92% constitutes abandoned coconut plantations (Wilkinson 2017; Bárrios & Wilkinson 2018). Wetland on rat-free islands is the scarcest habitat (0.004 $km^2$/0.33%). Savanna on rat-free islands supported the greatest abundance of breeding pairs with a total of 197,409 (580,615/$km^2$), while no seabirds bred in savanna on rat-infested islands. Native forest supported the second highest abundance with 61,280 (51,471/$km^2$) breeding pairs and the highest number of species ($n$ = 10) on rat-free islands. Wetland only had a single species breeding in it regardless of rat status.

### Breeding Seabird Habitat Selection

Resource selection modeling (RSM) demonstrates scientifically the habitat selection made by breeding seabirds (use versus availability, not use because of availability). The model (Fig. 4) shows that beach is the only habitat selected by *Sterna sumatrana* (Black-naped Tern) and *Thalasseus bergii* (Great Crested Tern). Wetland is only selected for by *Sula sula* (Red-footed Booby). Savanna is the only habitat selected by two terrestrial nesting boobies, *S. leucogaster* (Brown Booby) and *S. dactylatra* (Masked Booby), and is the favored habitat of the super-abundant breeding *Onychoprion fuscatus* (Sooty Tern). Native forest is positively selected for by the highest diversity of species ($n$ = 7), one of which is the second most abundant breeding species, *Anous tenuirostris* (Lesser Noddy), which only breeds in this habitat. Non-native forest is selected by *Gygis alba* (Common White Tern), *Anous stolidus* (Brown Noddy), and *Fregata minor* (Great Frigatebird); these three species breed in trees in other habitats—the latter species appears to select for non-native forest above all others.

### Predicting Breeding Seabird Populations Post-Management

At present, Coin supports an impoverished biome that includes 51 breeding pairs of three species of seabird—Common and Lesser Noddy and Common White Tern. Following rat eradication without plantation conversion (scenario A), we estimate 4,306 (±93) breeding pairs of 14 species. If the abandoned plantations are converted to breeding habitat proportionately representative of the CTR (scenario B), this increases to 138,878 (±1,299) pairs. In scenario C, where 1 $km^2$ of abandoned plantation is converted to 0.5 $km^2$ each of native forest and savanna, 319,762 (±2,279) breeding pairs of 16 species are estimated. Savanna, which is not currently present on Coin, supports the greatest number of breeding pairs when created through habitat conversion in scenarios B and C (Table 2).

## Discussion

We believe our research is the first to combine quantitative analysis and resource selection modeling to demonstrate the potential benefits to breeding tropical seabirds of ecologically restoring abandoned coconut plantations on oceanic islands. Our results also reveal the limits of ecological restoration programs involving rat removal without including restoration of degraded habitat.

Our habitat modeling showed that seabirds selected natural habitats, with very weak selection for or, more commonly, selection against breeding in non-native forest (i.e. coconut plantations). These results highlight the importance of restoring abundant natural habitats for breeding seabirds in restoration programs.

In the worked example of Coin, this island could potentially support an ~84-fold increase in breeding pairs to 4,306 pairs of 14 species following rat eradication but without converting plantations. Intuitively, with 92% of the island remaining covered by the suboptimum, invasive habitat of abandoned plantations, this option does not constitute "restoration" of a seabird island and, because of the lack of seabird breeding habitat, is highly unlikely to lead to the full recovery of a seabird-driven ecosystem.

On the CTR, it is assumed that the mean breeding habitat ratio represents the habitat proportions necessary for supporting seabird-driven ecosystems. This assumption is supported by the cross-ecosystem benefits bestowed by nutrient transfer through abundant seabirds demonstrated by Graham et al. (2018) and Benkwitt et al. (2019) from some of these islands. Therefore, theoretically, if seabirds are breeding in these habitats on ecologically restored islands at similar breeding abundance and number of species, the island should be functional as a seabird island ecosystem. In the worked example of Coin, eradicating rats followed by converting abandoned plantations to habitat in proportion with what is present on the CTR produces a total of 138,878 breeding pairs of 16 species. Although reproducing habitat proportionately representative of a CTR appears the obvious target for ecological restoration, there are practical reasons why it cannot be applied.

Creating beach habitat in a remote environment where its extent and distribution naturally changes seasonally (Sheppard & Sheppard 2019) would be an expensive logistical challenge. The two Sternidae that only select beach habitat are IUCN Red-Listed Least Concern (BirdLife International 2018) and, at least in the Chagos Archipelago, are nomadic breeders displaying little natal philopatry (Carr et al. 2020), and therefore are not reliant on any single beach. The expense of creating beach would not justify the possible improved outcome. Creating wetland habitat on porous coralline islands that only has a single species selecting it as breeding habitat is also not justified.

Mixed shrub is a pioneering habitat that rapidly colonizes open areas and is an essential component of island formation (Hyland et al. 2010). In any restoration project, mixed shrub would occur naturally as successional growth (Mueller-Dombois & Fosberg 1998).

Non-native forest, which in the Chagos Archipelago is 92% abandoned coconut plantations (Wilkinson 2017; Bárrios & Wilkinson 2018), is invasive (Young et al. 2010a, 2010b) and a species-poor biome (Carr et al. 2013). In this study, it supports the least breeding pairs/km$^2$ and only two generalist breeding species of Least Concern, Common Noddy and Common White Tern (BirdLife International 2018), regularly breed in it. The five pairs of Great Frigatebird that bred in non-native forest are an anomaly and were only ever recorded once, in 2010 (Carr et al. 2020).

Therefore, in any ecological restoration project in the Chagos Archipelago, non-native forest in the form of abandoned coconut plantations would be the habitat to convert. Due to the impracticalities of creating beach and wetland, and the way that mixed shrub (particularly *Scaevola taccarda*) colonizes open areas naturally, native forest and savanna would become the replacement habitats. These two habitats also hold the greatest abundance of breeding pairs and number of species of all breeding habitats and RSM demonstrate they are the preferentially selected breeding habitats of nine of the 14 species modeled. This conclusion holds true for other island rehabilitation projects in the Western Indian Ocean. Abandoned coconut plantations on Denis Island, Republic of Seychelles, were successfully converted to savanna-type habitat for Sooty Tern recovery (Feare et al. 2015); on Cousine (Samways et al. 2010) and D'Arros islands (von Brandis 2012), native forest has been the goal. Further afield on Palmyra atoll, Northern Line Islands, Pacific Ocean, invasive abandoned coconut plantations are being converted to native *Pisonia* (*Coedes*) forest (Hathaway et al. 2011).

The breeding seabird habitat ratio of the CTR (that has functional seabird-driven ecosystems), combined with our estimations of breeding abundance and number of species in these habitats, allows us to recommend habitat cover requirements to restore seabird-driven ecosystems post-rat eradication. Based on our research, a minimum of 55% of an island must be composed of native forest (36.99% on CTR) and savanna (12.93% on CTR), and savanna must constitute at least 15% of the total land coverage for a seabird-driven ecosystem to fully recover. In the Chagos Archipelago, ecological restoration to this habitat ratio is essential to restore seabird-driven ecosystems. This is because all rat-infested islands are dominated by abandoned coconut plantations and seabird breeding abundance and numbers of species in native forest and savanna, coupled with the habitat selection results of RSM, demonstrate these are the two habitats required for seabirds to recolonize in sufficient numbers to drive ecosystem recovery.

The Chagos Archipelago provides a good example of the potential benefits of converting abandoned coconut plantations to native habitats post invasive predator eradication. However, this quantitative approach to predicting results of ecological restoration is relevant and widely applicable elsewhere. Tropical seabirds are declining and with them the quality of environmental services, e.g. nutrient transfer (Graham et al. 2018), they provide to associated ecosystems that are stressed from global threats such as climate warming. Our research has shown that the "panacea" of rat eradication alone is unlikely to restore seabird-driven ecosystems on islands previously used as coconut plantations. Restoration practitioners must consider the recovery of these islands as a two-phase operation: firstly, removing the invasive predators; secondly, managing and converting non-native habitat.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Ile du Coin extant vegetation cover in relation to all other rat-infested, ecologically degraded islands <0.5 km$^2$ in the Chagos Archipelago.
**Table S1.** Breeding habitat classification in the Chagos Archipelago.
**Table S2.** AICc values for model selection for models of rat-free islands.
**Table S3.** Model scores from receiving operator characteristic curves of most parsimonious models by model selection.
**Table S4.** Mean breeding population estimates for all 18 species of tropical seabird in the Chagos Archipelago for the six breeding habitats.
**Supplement S1.** Hypothetical future breeding seabird populations on a rat-cleared Ile du Coin, Chagos Archipelago, without conversion of plantations.

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