

1 **Influences on recovery of seabirds to islands eradicated of invasive**
2 **predators, with a focus on Procellariiformes**

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23

1 **Abstract**

2 Protecting the world's seabirds is a global conservation priority given that 29% of seabird
3 species are threatened with extinction. One of the most acute threats to seabirds is introduced
4 predators, which depredate seabirds at all life stages from eggs to adults. Consequently, invasive
5 predator eradication has been identified as an effective and commonly used seabird conservation
6 method. Seabird recovery post-eradication is influenced by complex and interacting environmental
7 and demographic factors, though gaps remain in our understanding of species-specific responses.
8 Here, we reflect on the recovery of seabirds to islands cleared of predators by drawing on the
9 equilibrium theory of island biogeography and synthesise key influences on recovery reported in the
10 literature. To illustrate this synthesis, we present a regionally specific case study on the recovery of
11 seabird colonies ($n=98$) in the Hauraki Gulf, New Zealand; a seabird diversity hotspot (27 species),
12 which has a long history of invasive predator eradication. We found that islands cleared of predators
13 show recovery of seabirds over time, and surprisingly had more diverse seabird assemblages than
14 islands that never had predators. This recovery appears to be influenced by a suite of site- and species-
15 specific factors. Managers may assume that given enough time following an eradication, seabirds will
16 recolonise. While time is a factor, island spatial distribution has a significant effect on the
17 recolonisation of seabirds, in addition to demographic traits, colonizing ability and habitat suitability.
18 Therefore, integrating expected site and species-specific recovery responses into planning seabird
19 island eradication could help guide post-eradication management actions.

20

21 **Key words:**

22 Biogeography, Restoration, Conservation, Threatened species, Animal Behaviour.

23

24 **Introduction**

25 Seabirds are often abundant on islands (Mulder et al., 2011). However, colonial nesting
26 habits, low reproductive output and extended periods of parental care at breeding grounds make

1 seabirds vulnerable to predators (here we use the term ‘predator’ to describe only non-native
2 mammalian predator species; Furness & Camphuysen, 1997; Baillie et al., 2004; Wolf et al., 2006;
3 Croxall et al., 2012). Introduced predators are the most acute and wide scale threat to seabirds, for
4 example rats (Kiore *Rattus exulans*; Norway rats *R. norvegicus* and ship rats *R. rattus*), which
5 depredate seabirds at every life-stage have invaded at least 80% of the world’s island groups (Towns
6 et al., 2006; Jones et al., 2008; Varnham, 2010; Croxall et al., 2012; Spatz et al., 2014). Consequently,
7 seabirds are now among the most globally threatened group of animals. Of approximately 365 species
8 worldwide, 29% have been listed as globally threatened, another 10% as near threatened and 5% are
9 listed as critically endangered (IUCN, 2015; Birdlife International, 2015). Accordingly, predator
10 removal is considered to be one of the most effective seabird conservation strategies (Jones, 2010;
11 Towns et al., 2013; Jones et al., 2016). In fact, the removal of predators can have positive feedbacks
12 for many biota and ecosystem processes affected by predator presence (Jones & Kress, 2012; Towns
13 et al., 2006; Towns, 2009; Lavers et al., 2010; Le Corre et al., 2015; Jones et al., 2016).

14 Despite considerable investment into the removal of introduced predators from islands, the
15 way seabirds respond subsequently remains poorly understood (but see: Lavers et al., 2010; Buxton et
16 al., 2014; 2015). Available research has described variable responses among species and islands
17 (Gaze, 2000; Lavers et al., 2010; Ismar et al., 2014). The same traits that make seabirds vulnerable to
18 predation, can also inhibit their natural recovery following predator removal (Jones et al., 2011;
19 Buxton et al., 2014). Species-specific differences in reproductive output, philopatry and behavioural
20 characteristics influence the response of seabirds to recovery and recolonisation of newly available
21 habitat (Danchin et al., 1998; Jones et al., 2011; Buxton et al., 2014). For example, there was no
22 observed increase of flesh-footed shearwater (*Ardenna carneipes*) or sooty shearwater (*Puffinus*
23 *griseus*) populations following the removal of Norway rats from Titi Island, Marlborough Sounds (-
24 40.95 S, 174.13 E) in the 1970s (Gaze, 2000). Similarly, on Raoul, Kermadec Islands (-29.26 S, -
25 177.92 E), there was no observed response of white-naped (white-necked) petrels (*Pterodroma*
26 *cervicalis*) following the removal of Norway rats, kiore, and cats (*Felis catus*) between 2002 and 2004
27 (Veitch et al., 2011). Conversely, on the same island there was a notable increase in nesting by black-

1 winged petrels (*Pterodroma nigripennis*), wedge-tailed shearwaters (*Ardenna pacifica*), and
2 recolonisation by Kermadec petrels (*P. neglecta*), Kermadec little shearwaters (*Puffinus assimilis*
3 *kermadecensis*), and Kermadec storm petrels (*Pelagodroma albicularis*; Gaskin, 2012; C. Gaskin,
4 unpublished data).

5 Twenty-five species of invasive predators of seabirds, have been successfully eradicated from
6 1016 islands around the world (Island Conservation, 2015; Jones et al., 2016). Responses of seabirds
7 and island ecosystems to these eradications are now being evaluated. The putative objective is to
8 identify how seabird colonies recover following predator removals, and if they can recover to a
9 ‘restored state’ at all (Jones, 2010). Understanding the recovery of seabirds following predator
10 eradication through space and time is crucial for informing continued conservation management of
11 seabirds, particularly for species experiencing population declines exacerbated by marine threats
12 (Rolland et al., 2009; Croxall et al., 2012), such as fisheries by-catch, plastic pollution, and climate
13 change.

14 The equilibrium theory of island biogeography states that species diversity maintains a
15 dynamic equilibrium over time, influenced by area and ecological diversity (Preston, 1962; McArthur
16 & Wilson, 1967; Simberloff, 1974). Therefore, we would expect that seabird diversity on islands to
17 also follow this pattern. By comparing islands cleared of introduced predators to islands that have not
18 been affected by the presence of predators or habitat modification, we may be able to discern the state
19 of recovery post-predator eradication. Here, with a basis of island biogeography theory, we
20 synthesize key influences on seabird recolonisation and recovery reported in the literature. We present
21 a case study to test biogeographical influences by examining whether there has been measurable
22 change to seabird assemblages on a large sample of islands cleared of invasive predators in New
23 Zealand. We discuss how these biogeographical influences and additional factors of behaviour,
24 demography, and within island habitat availability, may be driving seabird recovery. Ideally, pre-
25 eradication population census data should be used for comparative evaluations of species responses to
26 the removal of threats, but in practice such data are rarely available (Duffy, 1994). Therefore, we
27 evaluate changes in seabird richness on islands that have been cleared of invasive predators, and

1 compare them to a subset of islands, of comparable area, that remained free of predators and where
2 historical seabird species composition data were available. We focus on the Hauraki Gulf, northern
3 New Zealand, which has 27 species of breeding seabirds (Gaskin & Rayner, 2013). We used survey
4 data of seabird richness on islands, where species were confirmed to be breeding as of the Austral
5 winter of 2015.

6

7 **Study area**

8 The islands of the Hauraki Gulf are bounded in the north by the Poor Knights (-35.46 S,
9 174.73 E), the Great Barrier Island group to the east (-36.17 S, 175.52 E), and the Aldermen
10 (Ruamaahua) Islands (-36.96 S, 176.08 E) to the south (Fig. 1). The islands included in our study
11 represent a range of ecological states from extensively modified either through previous or current
12 influences from invasive mammals (e.g. Rakitu Island; -36.12 S, 175.49 E), to near pristine (e.g. most
13 islands in the Poor Knights group; Supporting information, Table S2). We excluded islands <1 ha
14 because of the small island effect (Burns et al., 2009), and because of the reliability of the survey data,
15 where predator presence, and seabird population data may be unreliable due to survey constraints
16 (Supporting Information; Appendix 1). We also excluded islands that have a permanent residential
17 population because of the potential effects of human activities on the establishment of seabird
18 colonies (e.g. land use, presence of domestic animals, light pollution; Le Corre et al., 2002). We
19 grouped islands (n=98) into three categories based on predator status. *Uninvaded* islands (n=30),
20 *invaded* islands (n=37) and *cleared* islands (n=31) (Fig. 1; Supporting information, Appendix 2). The
21 climate of the Hauraki Gulf is temperate-humid with a mean annual temperature 16°C, relative
22 humidity of 87% and mean average rainfall 1202 mm (CliFlo, 2016).

23

24 **Figure 1[Map of spatial data distribution] <<insert here>>**

25

1 **Methods**

2 **Data:** Long-term survey data of species confirmed to be breeding on the islands as of the Austral
3 winter of 2015 were from C. Gaskin (unpublished data), D.R. Towns (unpublished data) and
4 supplemented by peer reviewed literature (Fig. 1; Supporting information, Appendix 2). The data are
5 presence only. Absence data are rarely available due to more labour intensive sampling methods and
6 greater economic costs associated with identifying the absence of a species or community (Phillips et
7 al., 2006). In most cases the data are based on observations on islands that were made up to 30 years
8 ago, with recent presence (i.e. 2004 to present) confirmed through acoustic surveys, occasional island
9 visits and, in some cases, targeted species surveys (e.g. flesh-footed shearwater, Buller's shearwater
10 (*Ardenna bulleri*), grey-faced petrel (*Pterodroma macroptera gouldi*), black petrel (*Procellaria*
11 *parkinsoni*), Cook's petrel (*Pterodroma cookii*), New Zealand storm petrel (*Fregetta maoriana*); C.
12 Gaskin, unpublished data) where additional data on other species have been collected. These reports
13 are based on observations; impressions can vary in quality depending on the methodology, taxon and
14 skill of the observer (see Supporting information for further discussion). These sampling effort biases
15 may influence our results. However, the majority of data were collected by the same group of
16 researchers, and any potential biases are likely consistent across our study area.

17 We followed Birdlife International for taxonomy and nomenclature (Birdlife International,
18 2015). We included 16 seabird species in the study: Procellariiformes (n=14), Sphenisciformes (n=1),
19 and Pelecaniformes (n=1) (Supporting information, Appendix 1, Table S1). All of these species
20 exhibit natal site philopatry and they have a range of population level responses to introduced
21 predators. Terns (family: Sternidae), gulls (family: Laridae) and shags/cormorants (family:
22 Phalacrocoracidae) were discarded from the analysis because they exhibit ephemeral breeding site
23 selection behaviour (Monaghan, 1996; New Zealand Birds Online, 2015). We have generalised
24 assumptions about the behavioural traits, such as sex biases and habitat selection preferences.

25 We included rats (*Rattus rattus*, *R. novegicus*, *R. exulans*), mice (*Mus musculus*), cats (*Felis*
26 *catus*), and pigs (*Sus scrofa*; Harris, 1970; Medway, 2001) as known predators of seabirds. Predator
27 eradication data were obtained from the Department of Conservation, D.R. Towns (unpublished data),

1 Gaskin et al. (2011) and the Database of Island Invasive Species Eradication (2015). Eradications
2 were carried out over 77 years, from 1936 (pigs from Aorangi; -35.48 S, 174.74 E) to 2011 (*R.*
3 *exulans* from Taranga; -35.96 S, 174.71 E). We used the date of the last successful eradication, where
4 predators had not been identified in biosecurity follow-ups (Supporting information, Appendix 2).

5 Given the paucity of pre-eradication seabird species composition data for *cleared* islands,
6 temporal analysis of seabird recovery is challenging. Therefore, we used the available data for
7 *uninvaded* island census data as a basis for comparisons with seabird species richness of *cleared*
8 islands, i.e. this is essentially a natural experiment (Okasen, 2001). While, this approach simplifies
9 potential ecological complications, we assumed that species richness for a given island area would be
10 comparable given the similar geology, metapopulation proximity and habitat of the islands in the
11 region. In order to assess the stability of these assemblages, we used historical seabird survey data for
12 six *uninvaded* “reference” islands in our study (Table 1) with the earliest data collected in 1928.
13 While census surveys on our reference islands were not systematic, these data provide information on
14 the observed stability of seabird species composition over the survey period. Species were only
15 included on the list if they were recorded as breeding at that location. Disturbance history on these
16 islands varied from historical land clearance by burning and agricultural use by Māori to minimal
17 evidence of use (Table 1). These sites represent class I and II (pristine and outstanding quality;
18 Taylor, 1989; Supporting information, Appendix 1, Table S2.) because of which, we assumed that
19 there was no limitation of available breeding habitat for seabirds.

20

21 **Table 1 [Species composition of reference islands] <<insert about here>>**

22

23 **Quantitative analysis:** All statistical analyses were done in R statistical software v. 3.1 (R Core
24 Team, 2013). We used generalized linear models (GLMs) with Poisson-distributed errors to estimate
25 the species-area relationship by predator status for all islands (Supporting information, Appendix 1).
26 While the models of species richness and island area assume there is a linear increase in species as
27 island area increases, in reality this is limited to the number of seabird species in the region. Here, we

1 assume that maximum species richness is constrained by the number of species included in the
 2 analysis ($n=16$). GLM assumptions of a linear-mean variance relationship, and of spatially
 3 uncorrelated errors were checked using the dispersion test from the AER package (Kleiber & Zeileis,
 4 2008) and spatial correlation tests from the sp, ape and gstat packages (Supporting information,
 5 Appendix 1; Bivand et al., 2013; Paradis et al., 2004; Pebesma, 2004).

6 **Species-Area GLM model fitting and selection:** We considered three models for the species-area
 7 relationship by predator status, all being Poisson regressions of a semilog model (i.e. species count S
 8 as response, $\log_{10}(A)$ as predictor). The three models are all Poisson GLMs: $S \sim \text{Poisson}(\mu)$ with log
 9 link such that $\log \mu(S) = \boldsymbol{\beta}^T \mathbf{X} i$ where \mathbf{X} and $\boldsymbol{\beta}$ are the design matrix and the parameter vector,
 10 respectively.

11 1) effect of $\log(\text{area})$ only:

$$12 \quad \log \mu(S) = \beta_0 + \beta_1 \log_{10} A$$

13 2) additive effects of $\log(\text{area})$ and predator status, i.e. separate intercept per predator status but
 14 same slope:

$$15 \quad \log \mu(S) = \beta_0 + \beta_1 \log_{10} A + \beta_2 \text{Predator}$$

16

17 3) interaction of $\log(\text{area})$ and predator status, i.e. separate slope and intercept per predator
 18 status:

$$19 \quad \log \mu(S) = \beta_1 \text{Predator} + \beta_2 \log_{10} A \times \text{Predator}$$

20

21 Multi-model inference based on Poisson GLMs was used to explore possible predictors of
 22 species richness for the *cleared* islands (Burnham & Anderson, 2002). The predictors explored were
 23 size, time since eradication, distance to the mainland, i.e. the nearest point on the coastline of the
 24 North Island, and distance to Auckland city centre (36.85 S, 174.76 E) – the latter two being potential
 25 proxies for human disturbance and/or distance to offshore feeding grounds. Distances were calculated
 26 using the rgeos package (Bivand & Rundel, 2016). We used the MuMin package (Barton, 2015) to

1 generate a complete set of candidate models based on the above predictors and ranked the resulting
2 model fits by AICc.

3 We used Chi-squared tests (*alpha level* = 0.05) of frequency of occurrence to evaluate the
4 differences among species present on *cleared*, *uninvaded* and *invaded* islands respectively (R Core
5 Team, 2013). Because of poor representation or absence of some species within island categories,
6 analyses used a subset of six widely distributed species (Fig. 3).

7 **Exploratory AFR analysis:** We used a Kruskal-Wallis rank sum test to test for differences in the
8 mean age at first reproduction (AFR), a possible proxy for colonisation ability, for each island
9 assemblage. Species-specific AFR values (Tab. S1) were averaged over all breeding species on a
10 given island.

11

12 **Results**

13 The mean area of *uninvaded* islands was 13.88 ha (SD = 31.43), ranging from 1.04 to 155.92
14 ha and were biased towards <10 ha (n=23 of 30). *Invaded* islands mean area was 24.79 ha (SD =
15 62.34) and ranged from 1.14 ha to 312.33 ha. The mean area of *cleared* islands was 286.15 ha (SD =
16 675.7), and represented the most evenly spread area range of all three categories ranging from 1 ha to
17 2817 ha.

18 The final model for the species-area relationship included separate slopes and intercepts by
19 predator status. No significant overdispersion was detected (Overdispersion test: dispersion parameter
20 = 0.99; p = 0.53). Weak, but statistically significant spatial autocorrelation in the residuals was
21 indicated by Moran's I (I = 0.1, p = 0.011), and visual inspection of spatial residuals indicated that
22 this was due to the model overpredicting species richness for the islands of the inner Hauraki Gulf
23 (Supporting Information; Fig. S1). GLM parameter estimates are presented in Table 2, and model
24 predictions are illustrated in Fig. 2.

25 **Table 2 [GLM parameter estimates] <>insert about here>>**

26 For *uninvaded* islands the intercept (i.e. expected species count on a 1 ha island) is 2.43 (95%
27 CI: [1.77, 3.28]; β = 0.89, p < 0.001), and for a 10-fold increase in area the species count is expected

1 to increase 1.81-fold (95% CI: [1.36, 2.39]; $\beta = 0.26$, $p < 0.001$). For *cleared* islands the intercept is
2 4.31 (95% CI: [3.12, 5.84]; $\beta = 1.46$, $p < 0.001$), and no significant relationship was found between
3 species richness and area ($\beta = 0.04$, $p = 0.295$). For *invaded* islands the intercept is 0.62 (95% CI:
4 [0.34, 1.05]; $\beta = -0.48$, $p = 0.092$), and for a 10-fold increase in area the species count is expected to
5 increase 1.77-fold (95% CI: [1.14, 2.71]; $\beta = 0.25$, $p = 0.009$). Further, regardless of size, invaded
6 islands did not have more than four species (Fig. 2).

7 **Figure 2 [Observed species richness as a function of island area] <>insert about here>>**

8 The largest suite of species included in the analysis was on *cleared* islands, with the smallest
9 on *invaded* islands (Fig. 3). Standard residuals from the Chi-squared test showed a higher proportion
10 of *invaded* islands with grey-faced petrels than expected ($p = 0.001$, $df = 12$, standard residual = 4.66).
11 A higher proportion than expected of *cleared* islands had sooty shearwaters ($p = 0.023$, standard
12 residual = 2.39) and a higher proportion than expected of *uninvaded* islands had fluttering shearwaters
13 ($p = 0.033$, standard residual = 1.52). On *invaded* islands there were fewer than expected populations
14 of common diving petrels ($p = 0.027$, standard residual = -1.92). Seven species of seabirds present on
15 *cleared* and/or *uninvaded* islands were absent from *invaded* islands (Fig 3.).

16 Multi-model inference did not provide strong evidence for a link between the time since
17 eradication and species richness. Distance to Auckland was retained as predictor in all six models that
18 were within 3 AICc units of the optimal model, with higher species richness on islands further from
19 the city. Distance to mainland and island size were each retained in three of the top six models, but
20 effect sizes were close to zero when both predictors were retained in the same model. Island size had a
21 positive effect on species richness, whereas distance to mainland had a negative effect. (Table 3; Fig.
22 S4).

23 On the reference islands, species composition was stable for up to 85 years (Table 1). No
24 species identified in early reports disappeared from any island, but in one group (Ruamaahua) up to
25 four species not recorded previously were present in 2013 (Table 1).

26

27 **Figure 3 [Chi-squared results of expected species richness] <>insert about here>>**

1

2 **Discussion**

3 One of the benefits of invasive predator eradications is to allow affected resident seabird
4 populations to recover and to enable recolonisation by species that have been extirpated (Kappes &
5 Jones, 2014). The equilibrium theory of island biogeography states that area should be the best
6 predictor of species richness on islands (Preston, 1962; McArthur & Wilson, 1967). In our analysis,
7 we assumed that species richness of seabirds on *cleared* islands should resemble, or begin to resemble
8 *uninvaded* islands of a comparable area within a similar biogeographic region. While our data are
9 undoubtedly influenced by variable survey effort, plus temporal and spatial biases such as island size
10 and a lack of pre-invasion census data, we can show that seabirds are recolonizing *cleared* islands in
11 the Hauraki Gulf (Fig. 2). This recolonisation result is promising, especially since all of the species
12 absent from invaded islands are now breeding on *cleared* islands (Fig. 3). Furthermore, *uninvaded*
13 islands, Hongiora (-36.95 S, 176.05 E) and Ruamahuanui (-36.95 S, 176.09 E), appear to have
14 recruited species that had not been observed previously (Table 1.), perhaps as spillover from
15 populations increasing elsewhere as a part of natural assemblage equilibrium processes (C. Gaskin,
16 unpublished data; Simberloff, 1974; Buxton et al., 2015). While differing rates of re-colonisation and
17 local extinction may result in a species richness rebound effect following the removal of predators
18 (Cirtwill & Stouffer, 2015), ecological diversity is likely to exert a strong influence on the return of
19 seabird assemblages to equilibrium on *cleared* islands (Preston, 1962; McArthur & Wilson, 1967;
20 Simberloff, 1974). We posit that, within our case study system, the seabird assemblage structure on
21 cleared islands will likely reflect the effects of five components; 1) spatial distribution of islands
22 influencing proximity to source populations, foraging areas and/or human activities; 2) time since
23 eradication; 3) behavioural influences including interspecific interactions; 4) the availability of
24 suitable habitats; and, 5) the colonising ability of individual species (Fig. 4). We were able to
25 statistically support the influence of space (1) and to a lesser extent, time (2). However, our model
26 was not able to explain all of the variance. The literature provides some guidance for the behavioural

1 (3), within habitat (4), and demographic (5) influences on seabird recolonisation to islands cleared of
2 invasive predators in the Hauraki Gulf.

3

4 **Figure 4 [Schematic of influences on seabird recovery] <<insert about here>>**

5

6 **Space:** The rate and pattern of seabird recovery appears to be most affected by the proximity
7 of *cleared* islands to source populations, foraging areas and/or human activities. Distance to local
8 populations was the strongest influence on seabird recruitment in Buxton et al.'s (2014) study, where
9 the proportion of natural seabird recolonisation response fell below 50% when the source population
10 was equal to or more than 25 km from the recruitment site. Borrelle et al. (2015) found lower than
11 expected species richness on Hauraki Gulf islands beyond the 25 km radius, thus supporting distance
12 to source populations as a key driver of passive seabird recolonisation (Buxton et al., 2014). Further,
13 the recruitment of some species to cleared islands may be influenced by the proximity to foraging
14 grounds. The ideal situation for species is the juxtaposition of resources that reduces costs to the
15 individual (Estades, 2001). Seabirds represent the extreme end of these habitat resource spatial
16 patterns, reflected by foraging grounds often considerable distances from breeding sites and that are
17 discontinuously distributed across space and time (Estades, 2001). The disparity between breeding
18 sites and dynamic nature of foraging areas means that these relationships are not well understood
19 (Fernández-Chacón et al., 2013). While we found no compelling evidence of spatial correlation, we
20 note that islands located in the Inner Gulf all have negative residuals (Supporting information; Fig.
21 S1). This may be explained by the results from multi-model inference, which suggested that proximity
22 to Auckland negatively influenced the spatial distribution of seabird recovery (Table 3, Fig. S4). This
23 could be attributed to a combination of proximity to source populations, optimal foraging theory and
24 greater habitat modification and marine activities in these areas (Gaskin & Rayner, 2013; Borrelle,
25 2013). More detailed evaluation of effect modifiers in relation to proximity to human activities and
26 foraging patterns (e.g. using detailed telemetry data) may improve the predictability of the model.

1 **Time:** A positive, but statistically not significant increase in species richness was observed
2 with time since eradication. This result may be affected by a strong temporal artefact because our
3 analysis of seabird recovery on some islands reflects predator eradication effort concentrated
4 approximately 20 years ago (Supporting information, Fig. S4). Our comparisons of species richness
5 with island area strongly suggest that not all *cleared* islands resemble the seabird richness of
6 *uninvaded* islands of comparable size. This result may indicate that there has been insufficient time
7 for the recolonisation of seabirds to those islands, particularly on larger islands that were cleared more
8 recently following the resolution of logistical and operational challenges (Towns & Broome, 2003).
9 Further, variations in the speed and/or capacity of individual seabird species to recolonise may also be
10 a contributing factor. However, given the GLM predictions of species richness of *cleared* islands
11 compared to *invaded* islands, it appears that on many *cleared* islands species richness has increased
12 following predator eradications (Fig. 2). On some islands, these responses have been rapid and
13 unpredicted. For example, Burgess Island (-35.90 S, 175.11 E) has had remarkable recovery of seven
14 species of procellariiforms (Table 4; Ismar et al., 2014). Further, since the eradications of cats (1970s)
15 and kiore (2004) on Te-Hauturu-o-Toi (Little Barrier Island; -36.20 S, 175.08 E), the New Zealand
16 storm petrel has reached sufficient numbers for identification of a breeding population of this hitherto
17 presumed extinct species (Rayner et al., 2015). Cirtwill & Stouffer (2015) found that following
18 defaunation on disturbed mangrove islands, species richness increased temporarily once the
19 disturbance (predation) was removed. Species assemblages then stabilised with equilibrium between
20 immigration and extirpation (Cirtwill & Stouffer 2015). A similar process may be operating on some
21 of our study islands following predator eradication. However, little is known about the temporal
22 dynamics of seabird communities during recolonisation of islands. In the case of the volcanic island
23 of Surtsey (Iceland, 63.30 N, 20.60 W), nine seabird species successively established breeding sites
24 over the course of 55 years. Only one of these, the Arctic tern (*Sterna paradisaea*), failed to establish
25 a permanent presence and went locally extinct after three breeding attempts across four years
26 (Petersen, 2009).

27

1 **Table 4 [Example of pre- and post-predator eradication seabird species assemblage on Burgess**
2 **Island, Hauraki Gulf] <>insert about here>>**

3

4 **Behaviour:** Examples of intrinsic effects on seabird recovery can include situations where
5 intra- and inter-specific interactions exert strong influences on recovery rate and recruitment (Danchin
6 et al., 1998; Parejo et al., 2005; Buxton et al., 2014). Seabird recruitment to new breeding sites may be
7 limited by the number of immature individuals in local metapopulations; because of the life history
8 traits of seabirds, colony growth can be slow (Parejo et al., 2005). Further, the recruitment of
9 immature individuals is influenced by the availability of suitable habitat and social cues (Danchin et
10 al., 1998; Parejo et al., 2005). These interactions can influence breeding success or immigration rates
11 as a result of limited access to nest sites. Passive recolonisation of seabirds on 92 offshore islands in
12 New Zealand following the removal of introduced predators was greater where more than two seabird
13 species were present (Buxton et al., 2014); suggesting that this was likely due to conspecific attraction
14 to preferential habitat (Danchin et al., 1998; Parejo et al., 2005; Buxton et al., 2014). In contrast,
15 numbers of grey-faced petrels appeared to decline on the Poor Knights Islands as Buller's shearwaters
16 increased in abundance, even though grey-faced petrels are abundant on Taranga/Hen Island in the
17 neighbouring Hen and Chickens group (Harper, 1983). Inter-specific competition may play a greater
18 role than predator presence in the distribution of grey-faced petrels on the Poor Knight's group given
19 the higher than expected proportion of *invaded* islands with this species (Fig. 3).

20 **Size & Habitat:** We found that five of the 16 seabird species included in our analyses are
21 absent from *uninvaded* islands (Fig. 3). Instead, we found the full suite of seabird species across
22 *cleared* islands, which indicates rapid recolonisation by seabirds following a release from predation
23 pressure (Cirtwill & Stouffer, 2015), and/or area-related limitations on ecological diversity
24 influencing the availability of suitable habitat (Simberloff, 1974). Larger *invaded* islands may also be
25 serving as refugia for some species, despite predator presence, because of availability of preferred
26 habitat. For example, Cook's petrels and black petrels are not represented on *uninvaded* islands;
27 however, both species are present on *invaded* islands and *cleared* islands. Cook's petrel was widely

1 distributed on the mainland of New Zealand before the introduction of mammals (Imber et al.,
2 2003b), but is now restricted to only three breeding sites: Codfish Island (-46.77 S, 167.63 E), Aotea
3 (Great Barrier; -36.20 S, 175.40 E) and Te-Hauturu-o-Toi (Towns, 2009). Nest burrows are found in
4 tall forests, generally above 250 m elevation on both islands with the largest population being on Te-
5 Hauturu-o-Toi (estimated at 286,000 breeding pairs in 2007; Rayner et al., 2007). Similarly, black
6 petrels were once more widely distributed, breeding at five or more sites on the North Island before
7 1900 (Imber et al., 2003a). Black petrels are now restricted to Te-Hauturu-o-Toi and Aotea (estimated
8 at 2,000 breeding pairs; E. Bell, Wildlife Management International Ltd, personal communication
9 2015), also in colonies largely restricted to high altitude (> 400 m) tall forest (Francis & Bell, 2010;
10 Bell et al., 2012). For species such as Cook's and black petrels, habitat suitability and a lack of islands
11 of sufficient size or elevation may be a limiting factor in recruitment to newly predator free sites.
12 Conversely, more 'generalist' species, such as grey-faced petrels, common diving petrels and
13 fluttering shearwaters may be less constrained by habitat suitability (Buxton et al., 2015).

14 **Recruitment:** We found that the proportion of islands with fluttering shearwaters was greatest
15 on *uninvaded* islands (Fig. 3). Given that fluttering shearwaters are abundant in the region (estimated
16 population of 20,000 pairs; C. Gaskin, unpublished data), we might expect this species to be more
17 widely distributed on *cleared* islands, as was found for sooty shearwaters which have an estimated
18 population of less than 800 pairs (Fig. 3; C. Gaskin, unpublished data). Their contrary distribution
19 suggests that fluttering shearwaters may have a more limited capacity for recruitment to new breeding
20 sites than species such as sooty shearwaters. Behavioural or sex differences between species may also
21 influence recruitment rates (Dittman et al., 2007) but there is limited understanding about how these
22 influences might affect recruitment. Additional demographic traits, such as age at first breeding, may
23 influence the species-specific rate of recovery of the islands (Nur & Sydeman, 1999), where species
24 that have shorter pre-breeding states may recolonise more quickly. For example, on the Mokohinau
25 Islands, common diving petrel (*Pelecanoides urinatrix*) and white-faced storm petrel (*Pelagodroma*
26 *maoriana*) populations increased dramatically in the two decades following the removal of *R. exulans*
27 (Ismar et al., 2014). For white-faced storm petrels and common diving petrels age at first reproduction

1 (AFR) is 2 or 3 years, compared to black petrels and Pycroft's petrels with AFR of 5-10 years (New
2 Zealand Birds Online, 2015). Mean assemblage AFR was lowest on invaded islands and highest on
3 uninvaded islands, but these differences were not statistically significant (Kruskal-Wallis rank sum
4 test, chi-squared = 5.72, df = 2, p = 0.057; Fig. S3a). Furthermore, across cleared islands mean
5 assemblage AFR increased with time since eradication, although again this result was not statistically
6 significant (OLS regression, β = 0.013, p = 0.20; Fig. S3b). While we found no statistical evidence of
7 AFR influencing recolonisation potential in our study, the effect of AFR could be masked by the
8 small sample size, the relative recency of most eradication, and/or the lack of time-series
9 observations of the recovery process on individual islands. Further research may provide insight into
10 AFR and recovery rate relationships.

11

12 Predator eradication is an effective conservation tool for protecting and enhancing the world's
13 seabird colonies (Jones, 2010; Towns et al., 2013; Jones et al., 2016). Such actions can result in
14 fundamental changes to the structure and species richness of island seabird faunas. However, we also
15 found that once these assemblages form, they undergo little change over many decades despite
16 pervasive extrinsic influences such as fisheries bycatch and marine pollution. Constraints on natural
17 recolonisation are nonetheless numerous. For example, despite their mobility over water, seabirds
18 rarely establish new breeding sites due to K-selected traits (Schreiber & Burger, 2001; Hamer et al.,
19 2002), although some seabird colonies do show emigration and immigration so are not closed (Igual
20 et al., 2007, Lawrence et al., 2014). Demographic, intrinsic, extrinsic, habitat and spatial factors also
21 complicate seabird recovery following predator eradication, with additional variation caused by
22 strong species, and site-specific effects (e.g. Buxton et al., 2014). Given the complex influences on
23 recolonisation, seabird conservation that involves invasive species eradication should aim to improve
24 understanding of the species-specific and external effects on demographic traits and population
25 dynamics, since these may elicit responses peculiar to regional faunas. To achieve this, effective and
26 consistent seabird monitoring plans should be an integral component of any seabird island restoration
27 project.

1

2 **Acknowledgments**

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8

9 **Author contributions:**

10 SBB and DRT conceived and designed the study. DRT, CPG provided the data and SBB and PHBS
11 analysed data. SBB, DRT, PHBS, CPG wrote and edited the manuscript.
12

13

14 **Literature cited**

- 15 Baillie, J.E., Hilton-Taylor, C., & Stuart, S.N. (2004) 2004 IUCN Red List of Threatened SpeciesTM:
16 A Global Species Assessment. IUCN, Gland, Switzerland.
17
18 Bartoń, K. (2015) MuMIn: Multi-Model Inference. R package version 1.15.1. <http://CRAN.R-project.org/package=MuMIn>
19
20 Bell, E.A., Sim, J.L., Scofield, P., Francis, C., & NIWA. (2012) Population parameters of the black
21 petrels (*Procellaria parkinsoni*) on Great Barrier Island (Aotea Island), 2009/10. Unpublished report
22 prepared for the Department of Conservation, Wellington, New Zealand retrieved from <http://www.doc.govt.nz/publications/conservation/marine-and-coastal/conservation-servicesprogramme/csp-reports/population-parameters-of-black-petrels-on-great-barrier-aotea-island-2009-10>.
23
24 Birdlife International. (2015) Taxonomy. <http://www.birdlife.org/datazone/info/taxonomy> [accessed
25 14 April 2015].
26
27 Bivand R.S., Pebesma, E., & Gomez-Rubio, V. (2013) Applied spatial data analysis with R, Second
28 edition. Springer, NY
29
30 Bivand R.S. and Rundel, C. (2016) rgeos: Interface to Geometry Engine - Open Source (GEOS). R
31 package version 0.3-19. <http://CRAN.R-project.org/package=rgeos>
32
33 Borrelle, S. B. (2013) Recovery and re-colonisation of seabirds on islands in the Hauraki Gulf after
34 pest eradication. Auckland University of Technology, Auckland. Honours Dissertation.
35
36

- 1 Borrelle, S.B., Buxton, R.T., Jones, H.P., & Towns, D.R. (2015) A GIS-based decision making
2 approach for prioritizing seabird management following predator eradication. *Restoration ecology*.
3 DOI: 10.1111/rec.12229.
- 4 Burns, K.C., McHardy, P.R., & Pledger, S. (2009) The small-island effect: fact or artefact?
5 *Ecography*, 32, 269-276.
- 6 Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference: a practical
7 information-theoretic approach. 2nd ed. New York, Springer-Verlag.
- 8 Buxton, R.T., Jones, C.J., Moller, H., & Towns, D.R. (2014) Drivers of Seabird Population Recovery
9 on New Zealand Islands after Predator Eradication. *Conservation Biology*, 28, 333-344.
- 10 Buxton, R.T., Taylor, G., Jones, C.P., Lyver, P.O., Moller, H., Cree, A. & Towns, D.R. (2015)
11 Spatio-temporal changes in density and distribution of burrow-nesting seabird colonies after rat
12 eradication. *New Zealand Journal of Ecology*, 40(1).
- 13 Cade, B.S., & Noon, B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers*
14 in *Ecology and the Environment*, 1, 412-420.
- 15 Cirtwell, A.R., & Stouffer, D.B. (2015) Knowledge of predator-prey interactions improves predictions
16 of immigration and extinction in island biogeography. *Global Ecology and Biogeography*, 7, 900-911.
- 17 CliFlo. (2016) New Zealand National Climate Database, NIWA, Wellington, New Zealand.
18 [Http://cliflo.niwa.co.nz/](http://cliflo.niwa.co.nz/) [accessed 18 November 2015].
- 19 Croxall, J., Butchart, S.H., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., & Taylor, P.
20 (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird*
21 *Conservation International*, 22.
- 22 Danchin, E., Boulinier, T., & Massot, M. (1998) Conspecific reproductive success and breeding
23 habitat selection: implications for the study of coloniality. *Ecology*, 79, 2415-2428.
- 24 Dittmann, T., Ezard, T.H., & Becker, P.H. (2007) Prospectors' colony attendance is sex-specific and
25 increases future recruitment chances in a seabird. *Behavioural processes*, 76(3), 198-205.
- 26 Estades, C.F. (2001) The effect of breeding-habitat patch size on bird population density. *Landscape*
27 *Ecology*, 16(2), 161-173.
- 28 Fernández-Chacón, A., Genovart, M., Pradel, R., Tavecchia, G., Bertolero, A., Piccardo, J.....et al.
29 (2013) When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially
30 structured seabird population. *Ecography*, 36(10), 1117-1126
- 31 Francis, R.I.C.C. & Bell, E.A. (2010) Fisheries risks to the population viability of black petrel
32 (*Procellaria parkinsoni*). *New Zealand Aquatic Environment and Biodiversity Report No. 51*.
33 Ministry of Fisheries, Wellington, New Zealand.
- 34 Furness, R.W., & Camphuysen, K.C. (1997) Seabirds as monitors of the marine environment. ICES
35 Journal of Marine Science: *Journal du Conseil*, 54, 726-737.
- 36 Gaskin, C. (2012) Seabirds of the Kermadec region: their natural history and conservation. p. 71.
37 *Science for conservation*. Unpublished Report. Department of Conservation, Wellington, New
38 Zealand.

- 1 Gaskin, C., Fitzgerald, N., Cameron, E.K., & Heiss-Dunlop, S. (2011) Does the New Zealand storm
2 petrel (*Pealeornis maoriana*) breed in northern New Zealand? *Notornis*, 58, 104-112.
3
- 4 Gaskin, C., & Rayner, M.J. (2013) Seabirds of the Hauraki Gulf: Natural history, research and
5 conservation. Unpublished Report. Hauraki Gulf Forum, Auckland, New Zealand.
6
- 7 Gaze, P. (2000) The response of a colony of sooty shearwater (*Puffinus griseus*) and flesh-footed
8 shearwater (*P. carneipes*) to the cessation of harvesting and the eradication of Norway rats (*Rattus*
9 *norvegicus*). *New Zealand Journal of Zoology*, 27, 375-379.
10
- 11 Hamer, K.C., Schreiber, E., & Burger, J. (2002) Breeding biology, life histories, and life history-
12 environment interactions in seabirds. *Biology of Marine birds*, 217-262.
13
- 14 Harper, P. (1983) Biology and conservation of the Buller's shearwater (*Puffinus bulleri*) at the Poor
15 Knights Islands, New Zealand. p. 19. Unpublished Report. Northern offshore Islands Symposium,
16 Auckland, New Zealand.
17
- 18 Harris, M.P. (1970) The biology of an endangered species, the dark-rumped petrel (*Pterodroma*
19 *phaeopygia*), in the Galapagos Islands. *Condor*, 72, 76-84.
20
- 21 Hawkins, B.A., Diniz-Filho, J.A.F., Mauricio Bini, L., De Marco, P., & Blackburn, T.M. (2007) Red
22 herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology.
23 *Ecography*, 30, 375-384.
24
- 25 Igual, J.M., Forero, M.G., Gomez, T., & Oro, D. (2007) Can an introduced predator trigger an
26 evolutionary trap in a colonial seabird? *Biological Conservation*, 137, 189-196.
27
- 28 Imber, M.J. (1976) Breeding biology of the grey-faced petrel *Pterodroma macroptera*
29 *gouldi*. *Ibis*, 118(1), 51-64.
30
- 31 Imber, M.J., McFadden, I., Bell, E.A., & Scofield, R.P. (2003a) Post-fledging migration, age of first
32 return and recruitment, and results of inter-colony translocation of black petrels (*Procellaria*
33 *parkinsoni*). *Notornis*, 50, 183-190.
34
- 35 Imber, M.J., West, J.A., & Cooper, W.J. (2003b) Cook's petrel (*Pterodroma cookii*): historic
36 distribution, breeding biology and effects of predators. *Notornis*, 50, 221-230.
37
- 38 Island Conservation and Invasive Species Specialist Group. (2013) Database of Island Invasive
39 species Eradication. [Http://www.issg.org/database/welcome/](http://www.issg.org/database/welcome/) [accessed 3 July 2015].
40
- 41 Ismar, S.M., Baird, K.A., Gaskin, C.P., Taylor, G.A., Tennyson, A.J., Rayner, M.J., Bettesworth, D.,
42 Fitzgerald, N., Landers, T.J., & Imber, M.J. (2014) A case of natural recovery after the removal of
43 invasive predators—community assemblage changes in the avifauna of Burgess Island. *Notornis*, 61,
44 188-195
45
- 46 IUCN. (2014) *IUCN Red List of Threatened Species v. 2014.1*. [Http://www.iucnredlist.org](http://www.iucnredlist.org) [accessed 5
47 March 2016].
48
- 49 Jones, H.P., Towns, D.R., Bodey, T., Miskelly, C.M., Ellis, J., Rauzon, M.J., Kress, S.W., &
50 McKown, M. (2011) Recovery and restoration on seabird islands. In: *Seabird islands: ecology,*
51 *invasion, and restoration* (eds. C.P. Mulder, W. Anderson, D.R. Towns, & P. Bellingham), pp. 317-
52 357. Oxford University Press, Oxford, NY.
53
- 54

- 1 Jones, H.P., Holmes, N.D., Butchart, S.H., Tersh, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz,
2 A., Armstrong, D.P., Bonnaud, E., & Burbidge, A.A. (2016) Invasive mammal eradication on islands
3 results in substantial conservation gains. *Proceedings of the National Academy of Sciences*. 113(15),
4 4033-4038.
- 5
- 6 Jones, H.P. (2010) Prognosis for ecosystem recovery following rodent eradication and seabird
7 restoration in an island archipelago. *Ecological Applications*, 20, 1204-1216.
- 8
- 9 Jones, H.P., & Kress, S.W. (2012) A review of the world's active seabird restoration projects. *The
10 Journal of Wildlife Management*, 76, 2-9.
- 11
- 12 Jones, H.P., Tersh, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E., & Howald, G.R.
13 (2008) Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology*, 22,
14 16-26.
- 15
- 16 Kappes, P.J., & Jones, H.P. (2014) Integrating seabird restoration and mammal eradication programs
17 on islands to maximize conservation gains. *Biodiversity and conservation*, 23, 503-509.
- 18
- 19 Kleiber, C. & Zeileis, A. (2008) Applied Econometrics with R. New York: Springer-Verlag.
- 20
- 21 Lavers, J.L., Wilcox, C., & Donlan, C.J. (2010) Bird demographic responses to predator removal
22 programs. *Biolgical Invasions*, 12, 3839-3859.
- 23
- 24 Lawrence, H. A., Lyver, P. O. B., & Gleeson, D. M. (2014). Genetic panmixia in New Zealand's
25 Grey-faced Petrel: implications for conservation and restoration. *Emu*, 114(3), 249-258.
- 26
- 27 Le Corre, M., Ollivier, A., Ribes, S., & Jouventin, P. (2002) Light-induced mortality of petrels: a 4-
28 year study from Réunion Island (Indian Ocean). *Biological Conservation*, 105(1), 93-102.
- 29
- 30 Le Corre, M., Danckwerts, D.K., Ringler, D., Bastien, M., Orlowski, S., Rubio, C.M., ... & Micol, T.
31 (2015) Seabird recovery and vegetation dynamics after Norway rat eradication at Tromelin Island,
32 western Indian Ocean. *Biological Conservation*, 185, 85-94.
- 33
- 34 MacArthur, R.H. & Wilson, E.O. (1967) *Theory of Island Biogeography*. Princeton University Press
35 (pp. 200-205)
- 36
- 37 McCallum, J. (1980) The birds of the Northern Mokohinau Group. *Tane* 26: 69-78.
- 38
- 39 Medway, D.G. (2001) Pigs and petrels on the Poor Knights islands. *New Zealand Natural Sciences*,
40 26, 87-90.
- 41
- 42 Monaghan, P. (1996) Relevance of the behaviour of seabirds to the conservation of marine
43 environments. *Oikos*, 227-237.
- 44
- 45 Nur, N., & Sydeman, W.J. (1999) Demographic processes and population dynamic models of
46 seabirds. *Current Ornithology* (pp. 149-188). Springer US.
- 47
- 48 New Zealand Birds Online. (2015) New Zealand Birds Online: The digital encyclopaedia of New
49 Zealand birds. [Http://nzbirdsonline.org.nz/](http://nzbirdsonline.org.nz/) [accessed 1 July 2015].
- 50
- 51 Oksanen, L. (2001) Logic of experiments in ecology: is pseudoreplication a pseudo-
52 issue? *Oikos*, 94(1), 27-38.
- 53

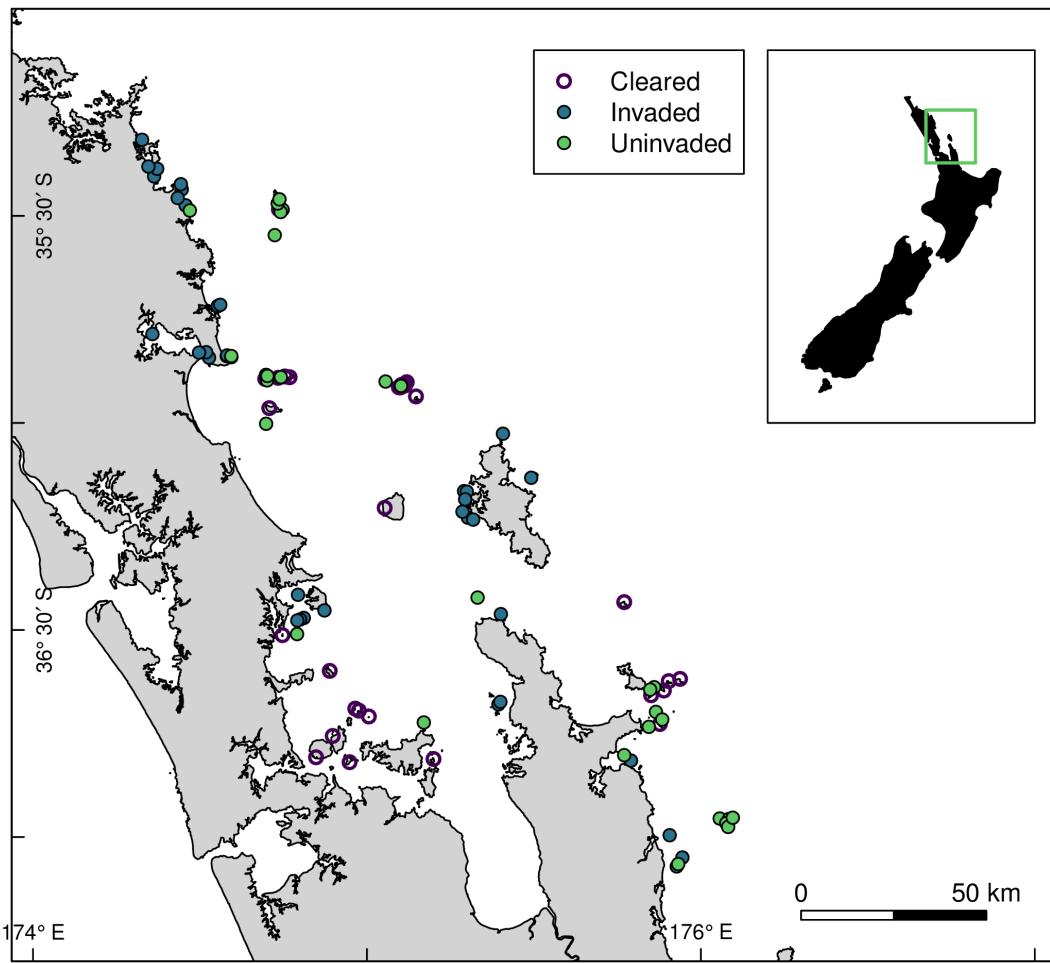
- 1 Paradis B., Claude, J., & Strimmer, J. (2004) APE: analyses of phylogenetics and evolution in R
2 language. *Bioinformatics* 20, 289-290.
3
- 4 Parejo, D., Danchin, E., & Avilés, J.M.. (2005) The heterospecific habitat copying hypothesis: can
5 competitors indicate habitat quality? *Behavioral Ecology*, 16, 96-105.
6
- 7 Pebesma, E.J. (2004) Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*.
8 30: 683-691.
9
- 10 Petersen, A. (2009) Formation of a bird community on a new island, Surtsey, Iceland.
11 *Surtsey Research*, 12, 133-148.
12
- 13 Phillips, S.J., Anderson, R.P., & Schapire R.E. (2006) Maximum entropy modeling of species
14 geographic distributions. *Ecological modelling*, 190, 231-259.
15
- 16 Pierce, R.J. (2002) Kiore (*Rattus exulans*) impact on breeding success of Pycroft's petrels and little
17 shearwaters. Unpublished Report. Department of Conservation, Wellington, New Zealand.
18
- 19 Preston, F.W. (1962) The canonical distribution of commonness and rarity: Part I. *Ecology*, 43(2),
20 185-215.
21
- 22 R Core Team. (2013) R: A language and environment for statistical computing, R Foundation for
23 Statistical Computing, Vienna, Austria.
24
- 25 Rayner, M.J., Clout, M.N., Stamp, R.K., Imber, M.J., Brunton, D.H., & Hauber, M.E. (2007)
26 Predictive habitat modelling for the population census of a burrowing seabird: a study of the
27 endangered Cook's petrel. *Biological Conservation*, 138, 235-247.
28
- 29 Rayner, M.J., Gaskin, C.P., Fitzgerald, N.B., Baird, K.A., Berg, M., Boyle, D., Joyce, L., Landers,
30 T.J., Loh, G., Maturin, S., Perrimen, L., Scofield, R.P., Simm, J., Southey, I., Tennyson, A.J.D.,
31 Robertson, B.C., Young, M., Walle, R., Ismar, S.M.H. (2015) Miniaturised radio telemetry to
32 discover endangered seabird breeding grounds: a case study of the New Zealand storm petrel *Fregetta*
33 *maoriana*. *IBIS* 157:754-766.
34
- 35 Robertson, H.A., Dowding, J.E., Elliott, G.P., Hitchmough, R.A., Miskelly, C.M., O'Donnell, C., &
36 Taylor, G.A. (2013) *Conservation status of New Zealand birds, 2012*. New Zealand threat
37 classification series. Department of Conservation, Wellington, New Zealand 4:22.
38
- 39 Rolland, V., Nevoux, M., Barbraud, C., & Weimerskirch, H. (2009) Respective impact of climate and
40 fisheries on the growth of an albatross population. *Ecological applications*, 19, 1336-1346.
41
- 42 Schreiber, E., & Burger, J. (2001) *Biology of marine birds*. CRC Press, Boca Raton, FL.
43
- 44 Simberloff, D.S. (1974) Equilibrium theory of island biogeography and ecology. *Annual Reviews of*
45 *Ecological Systems*, 5, 161-182.
46
- 47 Spatz, D.R., Newton, K.M., Heinz, R., Tershay, B., Holmes, N.D., Butchart, S.H., & Croll, D.A.
48 (2014) The biogeography of globally threatened seabirds and island conservation opportunities.
49 *Conservation Biology*, 28, 1282-1290.
50
- 51 Taylor, G.A. (1989) A register of northern offshore islands and a management strategy for island
52 resources. Department of Conservation, Wellington, New Zealand.
53

- 1 Towns, D. (2009) Eradications as reverse invasions: lessons from Pacific rat (*Rattus exulans*)
2 removals on New Zealand islands. *Biological Invasions*, 11, 1719-1733.
3
4 Towns, D., & Atkinson, I.A. (2004) Restoration plan for Korapuki Island (Mercury Islands), New
5 Zealand. Unpublished Report. Department of Conservation, Wellington, New Zealand.
6
7 Towns, D., Atkinson, I.A., & Daugherty, C.H. (2006) Have the harmful effects of introduced rats on
8 islands been exaggerated? *Biological Invasions*, 8, 863-891.
9
10 Towns, D., & Ballantine, W.J. (1993) Conservation and restoration of New Zealand Island
11 ecosystems. *Trends in Ecology & Evolution*, 8, 452-457.
12
13 Towns, D., & Broome, K.G. (2003) From small Maria to massive Campbell: forty years of rat
14 eradications from New Zealand islands. *New Zealand Journal of Zoology*, 30, 377-398.
15
16 Towns, D., West, C., & Broome, K. (2013) Purposes, outcomes and challenges of eradicating invasive
17 mammals from New Zealand islands: an historical perspective. *Wildlife Research*, 40, 94-107.
18
19 Townsend, A.J., de Lange, P.J., Duffy, C.A., Miskelly, C.M., Molloy, J., & Norton, D.A. (2008) *The
20 New Zealand Threat Classification System manual*. Department of Conservation, Wellington, New
21 Zealand.
22
23 Varnham, K. (2010) *Invasive rats on tropical islands: Their history, ecology, impacts and
eradication*. RSPB.
24
25 Veitch, C., Gaskin, C., Baird, K., & Ismar, S. (2011) Changes in bird numbers on Raoul Island,
26 Kermadec Islands, New Zealand, following the eradication of goats, rats and cats. In *Island Invasives:
eradication and management* (eds C.R. Veitch, M.N. Clout, and D.R. Towns). IUCN. Gland,
27 Switzerland.
28
29 Wolf, S., Keitt, B., Aguirre-Muñoz, A., Tershy, B., Palacios, E., & Croll, D. (2006) Transboundary
30 seabird conservation in an important North American marine ecoregion. *Environmental Conservation*,
31 33, 294-305.
32
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36 **Biographical sketches**

37 STEPHANIE BORRELLE's interests include island restoration, and how demography and at-
38 sea threats might be influencing seabird recovery following land-based conservation actions. PHILIPP
39 BOERSCH-SUPAN is a quantitative ecologist focused on marine ecosystems. He is particularly
40 interested in the ecology of oceanic predators and their prey. CHRIS GASKIN conducts surveys and
41 research on seabirds in northern New Zealand. He coordinated the Important Bird Area (IBA)
42 programme for New Zealand's seabirds. DAVID TOWNS's research has been based on understanding
43 the effects of invasive predators on island ecosystems, investigating methods for restoring modified
44 island ecosystems, and the development of biological and social metrics for measuring progress with

1 restoration projects. He is Principal Science Adviser for the New Zealand Department of
2 Conservation and Programme Leader for Applied Conservation at Auckland University of
3 Technology.

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2 *Figure 1: The Hauraki Gulf, New Zealand study area and seabirds presence data locations (n=98).*
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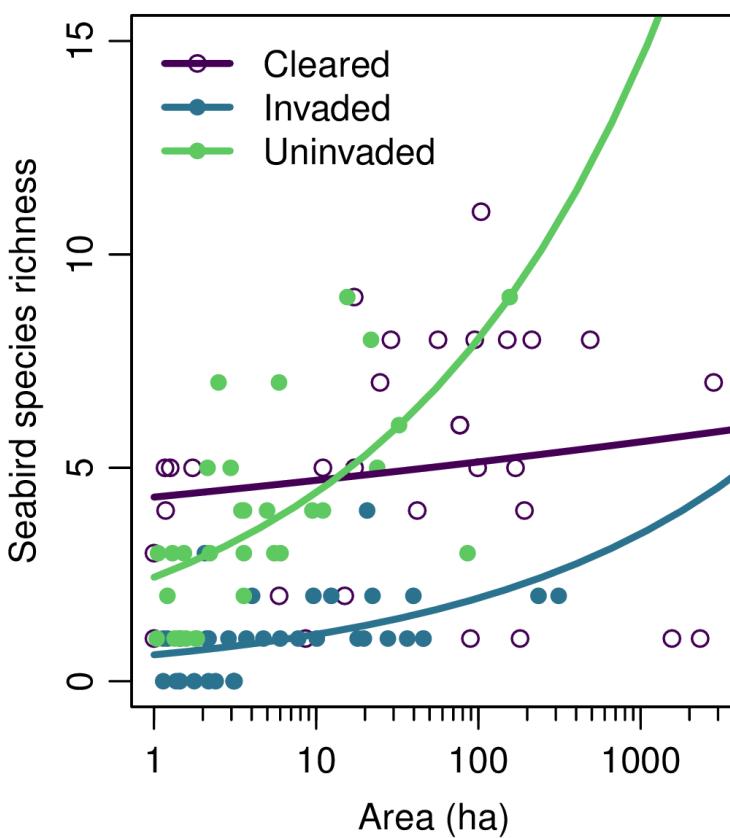
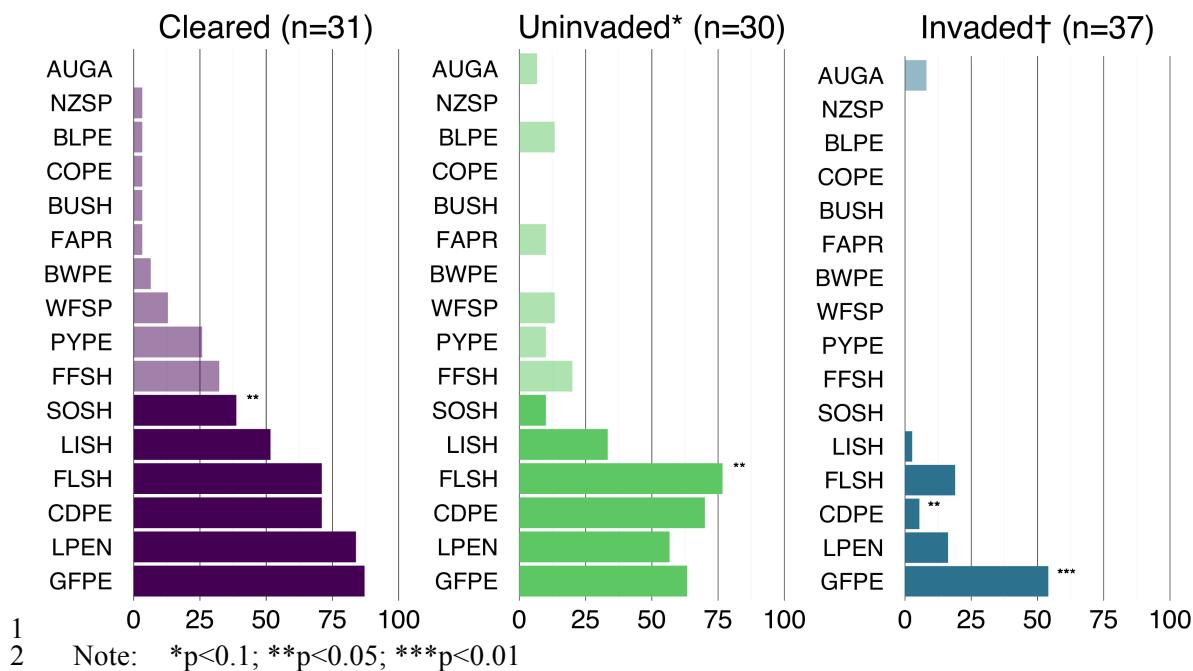


Figure 2: Observed species richness and GLM predictions as a function of island area comparing uninvaded islands (intercept = 2.43, slope = 0.26), cleared islands (intercept = 4.31, slope = n.s.), and invaded islands (intercept = 0.62, slope = 0.25). Model parameter estimates are detailed in Table 2.



1 Note: *p<0.1; **p<0.05; ***p<0.01

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4 *Figure 3: Proportion of islands with seabird species that are confirmed breeding on cleared, uninvaded*
5 *and invaded islands in the wider Hauraki Gulf region, New Zealand. The dark bars are those where*
6 *data met the assumptions of the Chi-squared test. AUGA: Australasian gannet, NZSP: New Zealand*
7 *storm petrel, BLPE: black petrel, COPE: Cook's petrel, BUSH: Buller's shearwater, FAPR: fairy prion,*
8 *BWPE: black-winged petrel, WFSP: white-faced storm petrel, PYPE: Pycroft's petrel, FFSH: flesh-footed*
9 *shearwater, SOSH: sooty shearwater, LISH: little shearwater, FLSH: fluttering shearwater, CDPE:*
10 *common diving petrel, LPEN: little penguin, GFPE: grey-faced petrel. * Bias of uninvaded islands was*
11 *towards areas < 10 ha, and † bias of invaded islands was towards areas > 155 ha.*

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2 *Figure 4. Schematic representation of the key influences on seabird recolonisation to islands cleared of*
3 *predators.*

1 Table 1: Species composition recorded over time on reference islands in the Hauraki Gulf, New Zealand that have never had predators.

Island	Disturbance History	Seabird assemblages	Dates observed (breeding)
Tawhiti Rahi (-35.45 S, 174.73 E) Poor Knights Islands 155.9 ha	Crop cultivation and seabird harvest (pre-European), burning of the flat areas of the island ⁹ .	Grey-faced petrel Pycroft's petrel Fairy prion Buller's shearwater Fluttering shearwater Little shearwater Common diving petrel White-faced storm petrel	1973 ¹⁵ , 1981 ^{9*} , 2013 ¹⁷ 1973 ¹⁵ , 1981 ^{9*} , 2013 ¹⁷ 1946 ⁶ , 1973 ¹⁵ , 1976 ⁸ , 1981 ^{9*} , 2013 ¹⁷ 1946 ⁵ , 1973 ¹⁵ , 1981 ^{9*} , 2013 ¹⁷ 1973 ¹⁵ , 1981 ^{9*} , 2013 ¹⁷
Hongiora (-36.95 S, 176.05 E) Aldermen Islands 15.55 ha	Extensive burning of vegetation prior to 1935. Muttonbird harvest by local Maori ^{7, 11} .	Grey-faced petrel Flesh-footed shearwater Sooty shearwater White-faced storm petrel Common diving petrel Fluttering Shearwater Little shearwater Little penguin Fairy prion	1973 ⁷ , 2013 ¹⁷ 1928 ¹² , 2013 ¹⁷ 1967 ¹ , 2013 ¹⁷ 1928 ¹² , 1973 ⁷ , 1986 ¹⁰ , 2013 ¹⁷ 1958 ⁴ , 1963 ¹ , 1973 ⁷ , 2013 ¹⁷ 2013 ¹⁷ 2013 ¹⁷ 2013 ¹⁷ 2013 ¹⁷
Ruamahuaiti (-36.97 S, 176.08 E) Aldermen Islands 23.79 ha	Pigs were briefly on the islands in 1842, but no records of how or when they were removed. The impact on seabirds was likely to be minimal according to observations from McFadden (1986) ¹⁰ .	Grey-faced petrel Fluttering shearwater Little shearwater Common diving petrel	1973 ⁷ , 2013 ¹⁷ 1928 ¹² , 1973 ⁷ , 2013 ¹⁷ 1967 ¹ , 2013 ¹⁷ 1973 ⁷ , 2013 ¹⁷
Ruamahuanui (-36.95 S, 176.09 E) Aldermen Islands 32.4 ha	Burned in the late 1800's ¹¹ .	Grey-faced petrel Fluttering shearwater Little shearwater Sooty shearwater Little penguin Common diving petrel	1972 ¹¹ , 1973 ⁷ , 2013 ¹⁷ 1972 ¹¹ , 2013 ¹⁷ 1972 ¹¹ , 2013 ¹⁷ 1928 ¹² , 1972 ¹¹ , 2013 ¹⁷ 2013 ¹⁷ 2013 ¹⁷

Middle

(-36.63 S, 175.86 E)
Mercury Islands
11 ha

Few signs of burning, undisturbed condition².

Grey-faced petrel:	1962 ^{3,16} , 1985 ¹³ , 2013 ¹⁷
Pycroft's petrel	1985 ¹³ (may not be breeding), 2013 ¹⁷
Flesh-footed shearwater	1962 ^{3,16} , 1985 ¹³ , 2013 ¹⁷
Fluttering shearwater	1962 ³ , 1985 ¹³ , 2013 ¹⁷
Little shearwater	1962 ³ , 1985 ¹³ , 2013 ¹⁷
White-faced storm petrel	1985 ¹³ , 2013 ¹⁷
Common diving petrel	1962 ^{2,16} , 1985 ¹³ , 2013 ¹⁷
Little penguin	1962 ^{3,16} , 1985 ¹ , 2013 ³

Green

(-36.64 S, 175.84 E)
Mercury Islands
2.5 ha

Few signs of burning, undisturbed condition².

Grey-faced petrel	1962 ^{3,16} , 1967 ¹⁴ , 2013 ¹⁷
Common diving petrel	1962 ^{2,16} , 1967 ¹⁴ , 2013 ¹⁷
Flesh-footed shearwater	1962 ³ , 1967 ¹⁴ , 2013 ¹⁷
Fluttering shearwater	1962 ¹⁶ , 1967 ¹⁴ , 2013 ¹⁷
Little shearwater	1962 ^{3,16} , 1967 ¹⁴ , 2013 ¹⁷
White-faced storm petrel	1967 ¹⁴ , 2013 ¹⁷
Little penguin	1962 ³ , 1967 ¹⁴ , 2013 ¹⁷

- 1 ¹Adams, G.P. 1967. Island survey form (unpublished; Wildlife Branch files). In: Fogarty & Douglas 1973. ² Atkinson, I.A.E. 1962. Report on the
 2 vegetation of the smaller Mercury Islands an Ohena Island. Unpublished Report. ³ Atkinson, I.A.E. 1964. The flora, vegetation, and soils of Middle and Green
 3 Islands, Mercury Islands group. *New Zealand Journal of Botany*, 2, 385-402. ⁴ Blackburn, A. 1958. Island survey form (unpublished; Wildlife Branch files). In:
 4 Fogarty & Douglas 1973. ⁵ Blackburn, A. 1958. Island survey form (unpublished; Wildlife Branch files). In: Fogarty & Douglas 1973. ⁶ Buddle, G.A. 1946. A
 5 second visit to the Poor Knights. *Emu*, 45, 315-318. ⁷ Fogarty, S.M. and Douglas, M.E. 1973. The birds of the Aldermen Islands. *Tane*, 19, 31-39. ⁸ Harper, P.C.
 6 1976. Breeding biology of the fairy prion (*Pachyptila turtur*) at the Poor Knights Islands, New Zealand. *New Zealand Journal of Zoology*, 3, 351-371. ⁹
 7 McCallum, J. 1981. Birds of Tawhiti Rahi Island, Poor Knights Group, Northland, New Zealand. *McCallum (1981)⁹ notes that seabirds that have been
 8 previously recorded on the island were not present on his visit in 1981, because it did not coincide with the breeding times of these birds. (1981 not
 9 confirmed breeding) *Tane*, 27, 59-66. ¹⁰ McFadden, I. 1986. Aldermen Islands, unpublished report. ¹¹ Merton, D., Crook, I., Whitaker, A. and Ramsay, G.
 10 1972. Island Survey form (Unpublished surveys). ¹² Sladden, B., Falla, R.A. 1958. Island survey form (unpublished; Wildlife Branch files). In: Fogarty & Douglas
 11 1973. ¹³ Southey, I. 1985. Birds of Middle Island, observations. Unpublished survey. ¹⁴ Thoresen, A.C. 1967. Ecological observations on Stanley and Green
 12 Islands, Mercury group. *Notornis*, 14, 182-199. ¹⁵ Veitch, C.R., Smuts-Kennedy, J.C., Moran, L.R., and Batchelor, C. 1973. Island survey form (unpublished;
 13 Wildlife Branch files). ¹⁶ Skegg, P.D.G. 1963. Birds of the Mercury Islands group. *Notornis*, 10, 153-168. ¹⁷ This study, and P. Lyver, September 2015, personal
 14 communication.
 15

1

2 *Table 2: GLM parameter estimates for the species-area relationship by predator status. Parameter values are given on the link scale.*

Parameter	Parameter estimate	Std. error	p
Predator_statusCleared	1.462	0.160	< 0.001
Predator_statusInvaded	-0.480	0.285	0.092
Predator_statusUninvaded	0.890	0.156	< 0.001
log(ha):Predator_statusCleared	0.038	0.036	0.295
log(ha):Predator_statusInvaded	0.249	0.096	0.009
log(ha):Predator_statusUninvaded	0.259	0.062	< 0.001

3

4

1 *Table 3: Parameter estimates and associated standard errors for the top ranked models for species richness on cleared islands. Models were ranked by AICc.*
 2 *Distance to Auckland was retained as a predictor in all six models, which were within 3 AICc units of the optimal model.*

Dependent variable: Species richness								
	(Model 1)	(Model 2)	(Model 3)	(Model 4)	(Model 5)	(Model 6)	(Model 7)	(Model 8)
Intercept	0.527	0.035	0.234	0.025	0.455	0.526	0.218	0.448
	(0.268)	(0.334)	(0.366)	(0.326)	(0.271)	(0.267)	(0.365)	(0.269)
Distance to Auckland (km)	0.015	0.014	0.015	0.013	0.013	0.015	0.014	0.012
	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)
Distance to mainland (km)	-0.012		-0.008			-0.012	-0.007	
	(0.005)		(0.006)			(0.005)	(0.006)	
Island size (log(ha))		0.089	0.059	0.091			0.062	
		(0.040)	(0.048)	(0.040)			(0.049)	
Time since eradication (years)				0.003		0.0005	0.002	0.001
				(0.005)		(0.005)	(0.005)	(0.005)
AICc	129.57	129.59	130.74	131.95	132.17	132.21	133.50	134.55
ΔAICc	0.00	0.02	1.17	2.38	2.60	2.64	3.92	4.98
Model weight	0.28	0.27	0.15	0.08	0.08	0.07	0.04	0.02

1 Table 4: Seabird species assemblage on Burgess Island prior to rat eradication in 1990 (McCallum, 1980) and post-eradication, from Ismar et al. (2014).

Species	McCallum (1980)	2010 October	2011 September	2013 February
Australasian gannet		•	•	
Grey-faced petrel	•	•	•	•
Common diving petrel		•	•	•
Little shearwater		•	•	•
Fluttering shearwater		•	•	•
Sooty shearwater		•		•
White-faced storm petrel		•		•
Black-winged petrel				•

2

1 Appendix 1: Supporting Information

2 Influences on seabird recolonization to offshore islands following
3 predator eradication

4 Stephanie B. Borrelle, Philipp Boersch-Supan, Chris P. Gaskin and David R. Towns

5

6

7 **Taxonomic considerations:**

8 We grouped the subspecies; New Zealand white-faced storm petrel (*Pelagodroma marina maoriana*)
 9 and the white-faced storm petrel (*Pelagodroma marina*) together and also the North Island little
 10 shearwater (*Puffinus assimilis haurakiensis*) and little shearwaters (*Puffinus assimilis*). Terns (family:
 11 Sternidae) and gulls (family: Laridae) were discarded from the analysis because they are confined to
 12 coastal areas, exhibit strong intraspecific aggression and individual nest sites are often up to 1 km
 13 apart. Shags/cormorants (family: Phalacrocoracidae) were also discarded because they exhibit
 14 ephemeral breeding site selection behaviour (New Zealand Birds Online 2015).

15

16 Table S1. Seabird species, IUCN trend status and age at first reproduction (AFR; mean)
 17 included in our review of seabird recovery on islands in the Hauraki Gulf, New Zealand
 18 following predator eradication.

Order	Scientific name	Common name	Description	AFR
Pelecaniformes	<i>Morus serrator</i>	Australasian gannet	Native IUCN: Least concern Population trend: Increasing	5.5
Procellariiformes	<i>Procellaria parkinsoni</i>	Black (Parkinson's) Petrel	Endemic IUCN: Vulnerable Population trend: Stable	6
Procellariiformes	<i>Pterodroma nigripennis</i>	Black-winged petrel	Native IUCN: Least concern Population trend: Declining	3
Procellariiformes	<i>Ardenna bulleri</i>	Buller's shearwater	Endemic IUCN: Vulnerable Population trend: Stable	~5
Procellariiformes	<i>Pelecanoides urinatrix</i>	Common diving petrel	Native IUCN: Least concern Population trend: Declining	2
Procellariiformes	<i>Pterodroma cookii</i>	Cook's petrel	Endemic IUCN: Vulnerable Population trend: Increasing	~3
Procellariiformes	<i>Pachyptila turtur</i>	Fairy prion	Native IUCN: Least concern Population trend: Stable	3

Procellariiformes	<i>Ardenna carneipes</i>	Flesh-footed shearwater	Native IUCN: Least concern Population trend: Declining Endemic	5
Procellariiformes	<i>Puffinus gavia</i>	Fluttering shearwater	IUCN: Least concern Population trend: Relict Endemic	~5
Procellariiformes	<i>Pterodroma gouldi</i>	Grey-faced petrel	IUCN: Least concern Population trend: Declining Native	5.5
Sphenisciformes	<i>Eudyptula minor</i>	Little penguin	IUCN: Least concern Population trend: Declining Native	2.5
Procellariiformes	<i>Puffinus assimilis</i>	Little shearwater	IUCN: Least concern Population trend: Declining Endemic	~4
Procellariiformes	<i>Fregetta maoriana</i>	New Zealand storm petrel	IUCN: Critically endangered Population trend: unknown Endemic	~2.5
Procellariiformes	<i>Pterodroma pycrofti</i>	Pycroft's petrel	IUCN: Vulnerable Population trend: Increasing Native	3
Procellariiformes	<i>Ardenna griseus</i>	Sooty shearwater	IUCN: Near threatened Population trend: Declining Native	6
Procellariiformes	<i>Pelagodroma marina</i>	White-faced storm-petrel	IUCN: Least concern Population trend: Declining	2.5

1

2

3 ***Data limitations:***

4 Some of the seabird data are from observations that are out of date, are biased towards heavily studied
 5 sites, or that may not be representative of colony densities at un-sampled locations (Rayner et al.
 6 2007). Furthermore, the number of records varied substantially in the dataset, with some species
 7 represented by a single data point. We did not account for occupancy during the breeding period;
 8 instead we assumed that all of the presence records were of breeding colonies (or individuals).
 9 Sampling effort bias was not accounted for. Population census data were excluded from the statistical
 10 analysis. Estimating population size can be technically and practically challenging because many
 11 Procellariiformes nest in rugged inaccessible locations and are nocturnal, and are therefore difficult to
 12 count directly (Rayner et al. 2007). While these biases mean that making clear inferences from the
 13 data are challenging, the dataset represents a relatively comprehensive picture of seabird presence and
 14 changes over time in response to predators and predator removals. Further, as the data were collected
 15 by a small group of individuals over the time period of the dataset, we believe the biases are likely to
 16 be consistent across the study area.

2

1

2 **Island status:** Island ecological status descriptions are adapted from Taylor (1989; Table. S2) the
 3 islands in the study ranged from class I to class VII. While the categories are broad, and lack specific
 4 criteria for a comprehensive description of the ecological status, they provide an overall guideline. We
 5 acknowledge that every island is influenced by a variety of biogeochemical and stochastic influences
 6 that affect the biological communities, and so classifying the islands into such broad categories may
 7 misrepresent the true ecological status of the island.

8

9 Table. S2: Class descriptions of the status of islands included in our study including
 10 introduced mammal and habitat modification status (adapted from: Taylor 1989).

Class Code	Class	Description
I	Near pristine natural environment	These islands have not had, or known to have had introduced mammals present. The vegetation may have been modified by historical human activity, but has recovered to or near pre-modified condition. The flora and fauna communities are likely to be representative of pristine island systems. Relict populations of rodent or mammal sensitive species are often present.
II	Outstanding quality natural environment	Introduced mammals are absent or have been removed. The vegetation has been modified through either land clearance (e.g. fires) or from the effects of introduced mammals. The islands flora and fauna are in mid-late stage recovery; forests are still in successional stages. Fauna are diverse, and include rodent sensitive species.
III	High Quality natural environment	Introduced mammals are present, or have recently been removed but are low impact species. These islands have been highly modified from cultural harvesting /land-use, intact forest remnants remain. The flora and fauna communities are recovering, although may be affected by the spread of invasive weeds and the continued disruption to seed dispersal, or seedling recruitment if mammals are still present.
IV	Moderate quality natural environment	Introduced mammals are present, and the islands have been extensively modified in the past. No intact forest remnants are present; however, the regeneration of successional stage forest is occurring (High potential for restoration)
V	Modified	Introduced mammals are either present or absent. The islands have been significantly modified by cultural or farming activities. The original vegetation is likely to have been completely cleared, and the islands used as farmland. The current vegetation is grassland, patches of shrubland and/or tree ferns (high potential for restoration).
VI	Recreational	Introduced mammals are present, and the island is at a high risk of continued reinvasion due to constant public use or is permanently inhabited. The islands are and continue to be extensively modified.
VII	Inshore	Introduced mammals are either present or not, but are within the swimming range of commensal rats, deer and stoats, and are at high risk for invasions. Rodent sensitive species may be present.

11

12

13 **Additional Poisson GLM results:**

1 Results from the model selection show that model 3 with separate intercepts and slopes by predator
 2 status has the lowest AICc (R Core Team, 2013; Table S3).

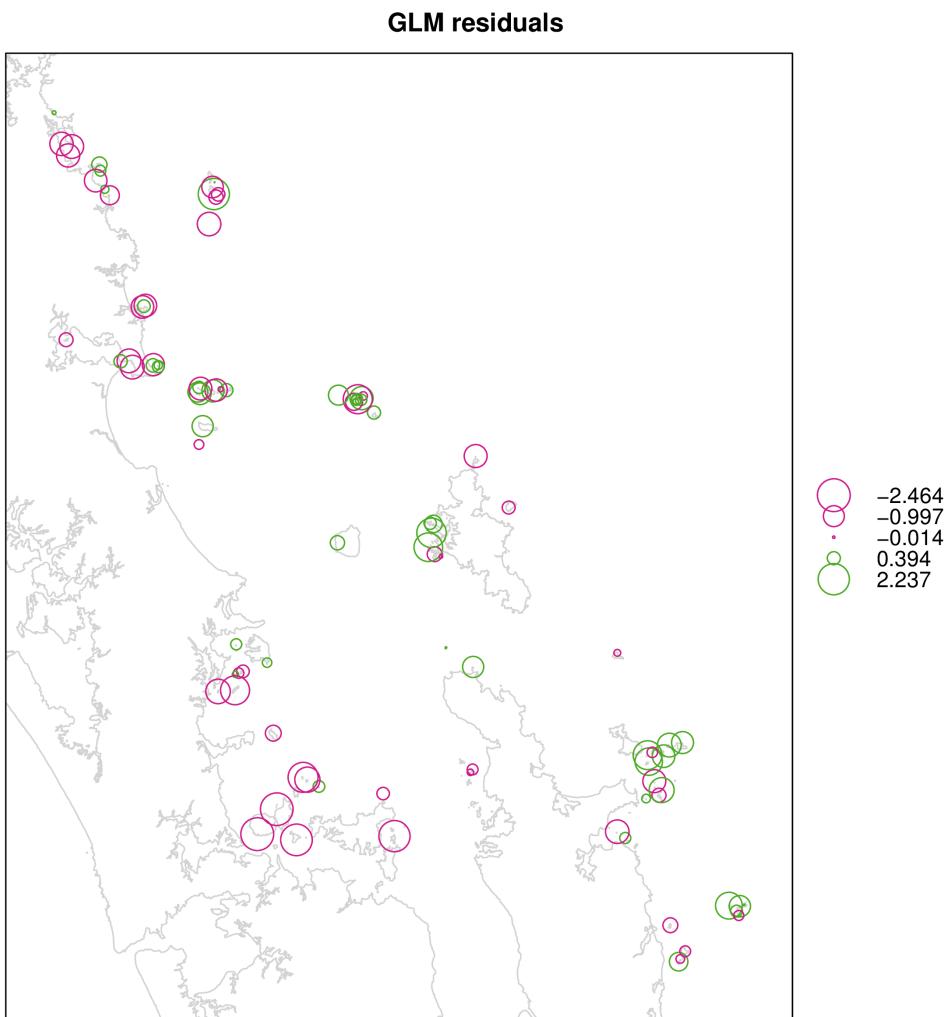
3 *Table S3: Model selection results for the Poisson GLM of the species-area relationship by predator*
 4 *status*

Predictors	df	AICc
log(area)	2	452.8
log(area) + Predator status	4	377.7
Predator status + log(area):Predator status	6	370.8

5

6 The Poisson GLM assumes a linear mean-variance relationship (dispersion parameter =1). We
 7 checked this assumption using a dispersion test (*AER* package, Kleiber & Zeilis 2015, R Core Team,
 8 2013). The dispersion parameter is estimated to be 0.99 and not significantly different from 1 ($z = -$
 9 0.09, $p = 0.53$). Hence, the assumption of a Poisson mean-variance relationship is met.

10 Weak, but statistically significant spatial autocorrelation in the residuals was indicated by Moran's I (I
 11 $= 0.1$, $p = 0.01$), and visual inspection of spatial residuals indicated that this was due to the model
 12 over-predicting species richness for the islands of the inner Hauraki Gulf (Fig. S1).



1

2 *Figure S1: Map of GLM residuals for the species-area relationship by predator status.*

3

4 **Cleared Islands GLMs:** Multi-model inference based on Poisson GLMs was used to explore
 5 possible predictors of species richness for the cleared islands (Burnham and Anderson, 2002). The
 6 predictors explored were size, time since eradication, distance to the mainland and distance to
 7 Auckland – the latter two being potential proxies for human disturbance and/or distance to offshore
 8 feeding grounds. Distances were calculated using the rgeos package (Bivand and Rundel, 2016). We
 9 used the MuMIn package (Barton, 2015) to generate a complete set of candidate models based on the
 10 above predictors and ranked the resulting model fits by AICc. Multi-model inference did not provide
 11 strong evidence for a link between the time since eradication and species richness. Distance to
 12 Auckland emerged as a significant predictor in all six models that were within 3 AICc units of the

5

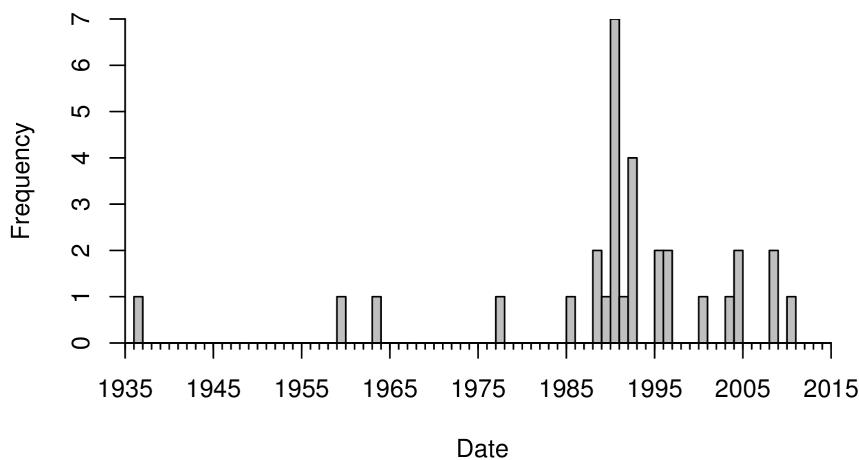
Please cite as: Borrelle et al. (in press) Influences on recovery of seabirds to islands eradicated of invasive predators, with a focus on Procellariiformes. Oryx.

1 optimal model, with higher species richness on islands further from the city. Distance to mainland and
2 island size were each retained in three of the top six models, and had a significant effect size only
3 when they were not retained in the same model. Size had a positive effect on species richness,
4 whereas distance to mainland had a negative effect. (Table 3; Fig. S4).

5

6

Distribution of eradication dates



7

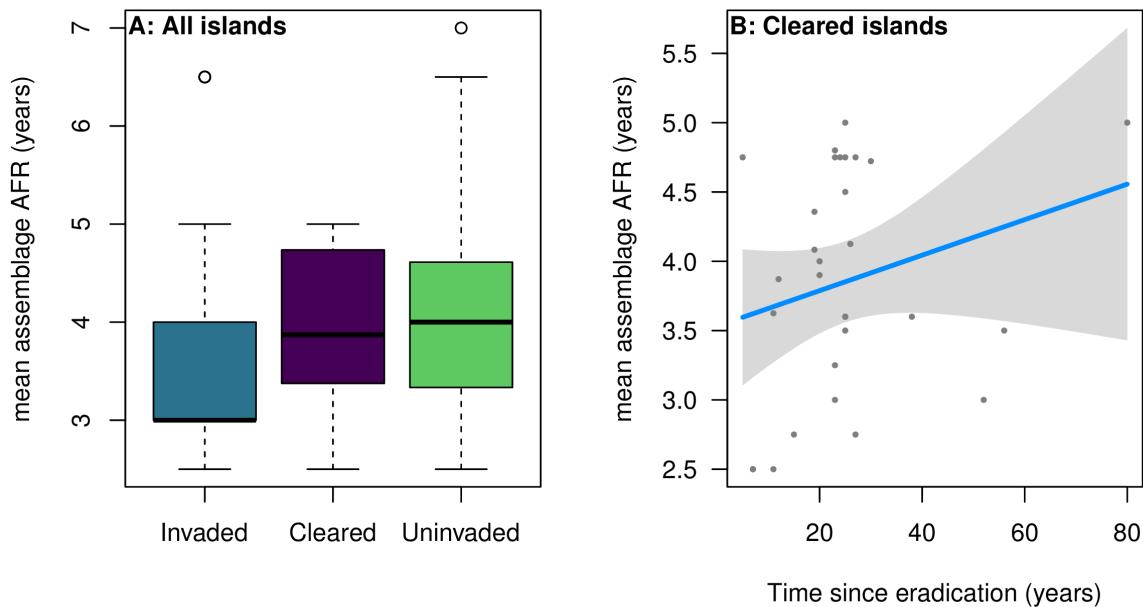
8 *Figure S2: Frequency distribution of eradication (n = 31) on islands in the Hauraki Gulf, New*
9 *Zealand included in our study.*

10

11 **Exploratory AFR analysis:** Mean age at first reproduction (averaged over all breeding species on a
12 given island) differed by predator status. Differences are not statistically significant (Kruskal-Wallis
13 rank sum test, chi-squared = 5.72, df = 2, p-value = 0.057).

14

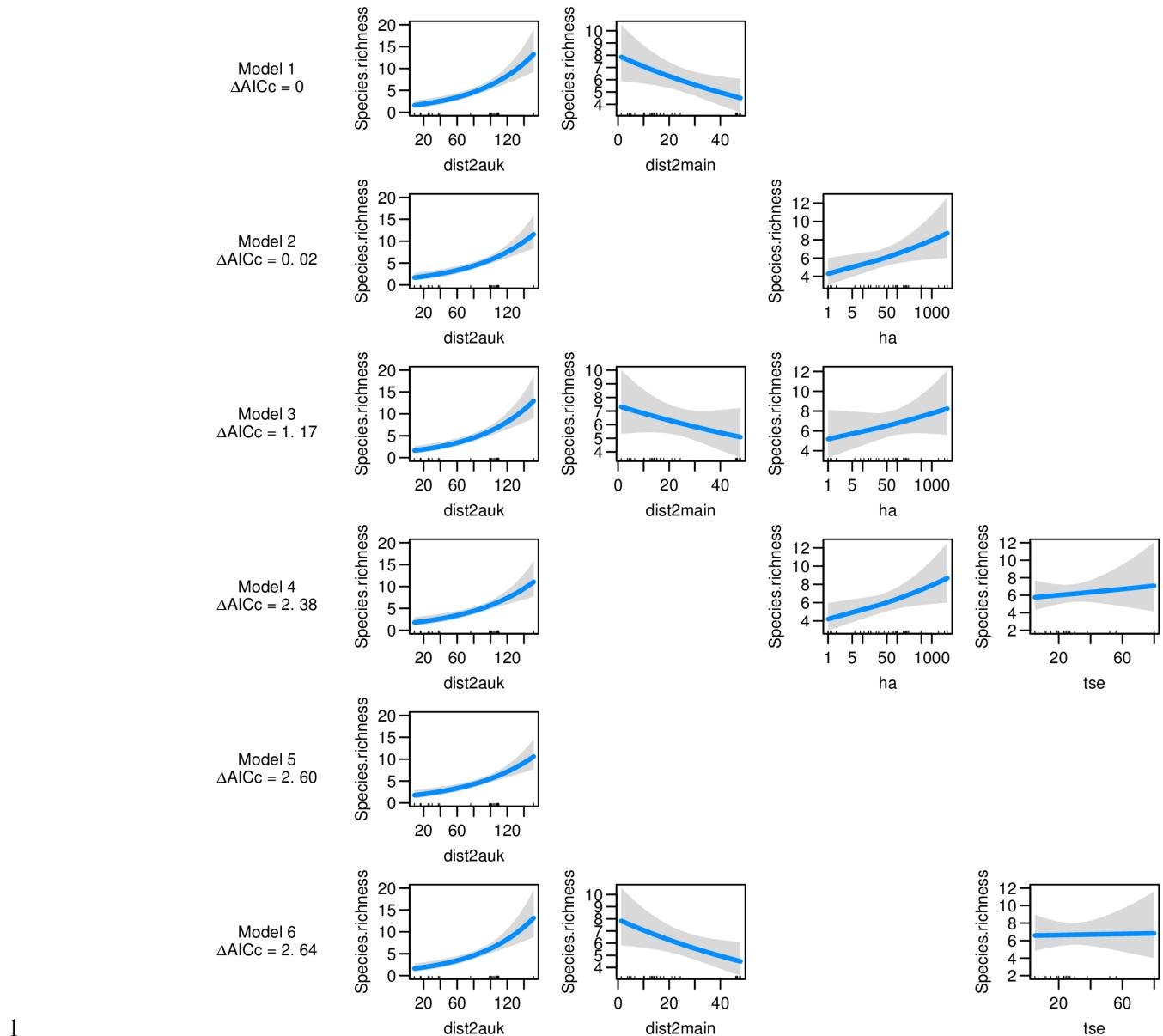
6



1

2 *Figure S3: A: Mean age at first reproduction (averaged over all breeding species on a given island)*
3 *by predator status. Differences are not statistically significant (Kruskal-Wallis rank sum test, chi-*
4 *squared = 5.72, df = 2, p-value = 0.057). B: Ordinary least squares regression of mean assemblage*
5 *AFR against time since eradication for the cleared islands. The positive trend is not statistically*
6 *significant ($\beta = 0.013$, $p = 0.20$).*

7



1

2 *Figure S4: Partial effect plots of the top six models of species richness on cleared islands from the*
3 *multi-model selection procedure. Model parameter estimates and associated standard errors are*
4 *given in the main manuscript in Table 3.*

5

6

7