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Seabird islands take mere decades to recover following rat eradication

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Abstract. Islands house a majority of the world's biodiversity and are thus critical for biodiversity conservation. Seabird nesting colonies provide nutrients that are integral to maintain island biodiversity and ecosystem function. Invasive rats destroy seabird colonies and thus the island ecosystems that depend on seabird-derived nutrients. After rat eradication, it is unclear how long ecosystem recovery may take, although some speculate on the order of centuries. I looked at ecosystem recovery along a chronosequence of islands that had 12–22 years to recover following rat eradication. I show that soil, plant, and spider marine-derived nitrogen levels and C:N ratios take mere decades to recover even after centuries-long rat invasion. Moreover, active seabird restoration could speed recovery even further, giving much hope to quickly conserve many endemic species on islands worldwide.

Key words: *biodiversity; chronosequence; ecosystem recovery; eradication; invasive species; New Zealand seabird islands; Rattus exulans; resilience.*

INTRODUCTION

Oceanic island ecosystems house a large proportion of global biodiversity despite representing a mere fraction of Earth's land mass (Groombridge 1992, Kier et al. 2009; see Plate 1). These exceptional levels of diversity are often supported by large nesting colonies of seabirds that provide critical nutrient subsidies in the form of marine-derived guano that drives primary production (Croll et al. 2005, Fukami et al. 2006). Invasive rats that have come to occupy 90% of the world's island archipelagos and devastate island seabird colonies now jeopardize ecosystem nutrient subsidies and associated biodiversity. In direct response to this threat, conservation programs have begun widespread and systematic rat-eradication programs. The putative goal is to facilitate the recovery of invaded islands to their original ecological states. Eradication programs are relatively recent, and so individual islands have not been monitored long enough to judge likelihood of success. Accordingly, there is the looming possibility that recovery will take centuries (Miskelly 1999, Towns and Atkinson 2004), or it may be precluded entirely given the specter that these ecosystems may become entrained into alternative states (Mulder et al. 2009). Such highly

uncertain outcomes raise questions about whether the expenditure of recovery effort and funds is even warranted.

I reduce this uncertainty by examining the ecosystem-wide effects of seabird-derived guano nitrogen ($\delta^{15}\text{N}$) and C:N ratio on islands in various stages of recovery following rat eradication. The 15 New Zealand study islands have different histories of rat (*Rattus exulans*) invasion, impact, and eradication and as such provide a unique chronosequence with which to quantify ecosystem recovery rates.

METHODS

I measured soil, plant, and spider $\delta^{15}\text{N}$ and C:N ratios on 15 islands that are dispersed along the northeastern part of New Zealand's North Island of (Fig. 1). Nine of the islands had rats removed between 12 and 22 years ago, another two continue to have rats (positive controls), and four islands have never had rats (controls [sensu Mulder et al. 2009]; Table 1). The collection of islands thus represents sufficient variation in recovery times (with appropriate benchmarks) to analyze the potential temporal sequence of recovery (i.e., a chronosequence). Chronosequences are powerful techniques to detect hysteretic responses to disturbances and are one way to indicate the presence of alternate states (Scheffer et al. 2001).

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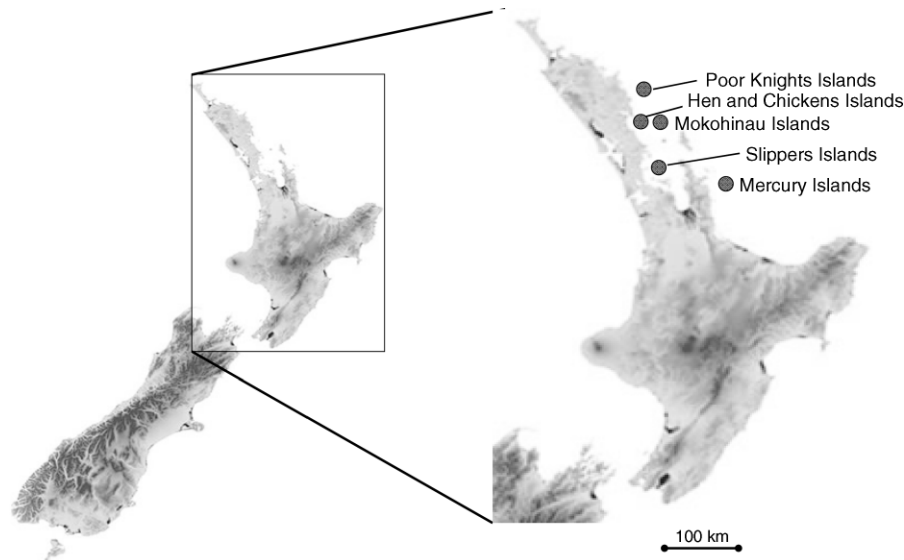


FIG. 1. Location of the 15 study islands along the northeastern part of North Island, New Zealand.

Seabird effects to island nutrient dynamics are likely to diminish as island size increases but the chosen study islands are well within the range of seabird-influenced island size (Mulder et al. 2011). Eradicated islands range in size from 16 ha to 225 ha while both control islands range from 2 ha to 13 ha (Table 1). I did not include control islands that span the size range of eradicated islands because there were none available in the geologically and geographically confined study area. However, there are islands elsewhere in New Zealand that are within the size range of eradicated islands and exhibit similar nutrient dynamics to this study's control islands (see Fukami et al. 2006, Mulder et al. 2009, Jones 2010).

I chose islands in a geographically confined area (the northern tip of New Zealand's North Island; Fig. 1) to be of similar sizes, geologic ranges, and climate regimes to reduce any variation in measurements caused by parent materials or differing climate (Leathwick et al. 2003). I took samples a minimum of 100 m from the shoreline (except on the smallest islands, where I took samples at the furthest point from the shoreline) to reduce the possibility of shore carrion or beach wrack contaminating samples with a source of marine-derived nutrients other than that contributed by nesting seabirds. Seabird densities varied among islands, but I could not measure them directly. Qualitatively, densities were very high for never-invaded islands, nonexistent for currently invaded islands, and increased along the continuum of time since eradication for eradicated islands. It is unclear whether or not remnant populations of seabirds survived rat predation on eradicated islands or were completely extirpated by rats as seabird surveys were not undertaken prior to eradication. While some seabirds have been shown to coexist with invasive rats, the eradicated study islands had low to nonexistent seabird densities during the time of study, suggesting

coexistence of rats and seabirds was rare if it occurred at all. Previous evidence on recovering islands suggests that seabird influence is localized in colonies until seabirds reach high enough densities to produce an island-wide effect (Jones 2010). Therefore, if seabirds were present on an island, I selectively took samples outside colonies to ensure the variables measured were not due to

TABLE 1. Island sizes, treatments, and the years since rat eradication (as of 2009), by treatment.

Treatment, by island-group	Time since eradication (years)	Island size (ha)
Rats eradicated		
Mercury Islands		
Korapuki	22	18
Double	20	32
Stanley	17	100
Red	17	225
Mokohinau Islands		
Atihau	18	16
Fanal	12	75
Hen and Chickens Islands		
Coppermine	12	80
Whatupuke	16	102
Lady Alice	15	155
Controls (never invaded)		
Poor Knights Islands		
Archway		7
Aorangaia		6
Mercury Islands		
Middle		13
Green		2
Positive controls (rats present)		
Slipper Islands		
Penguin		10
Rabbit		11

Note: For location of island groups, see Fig. 1.

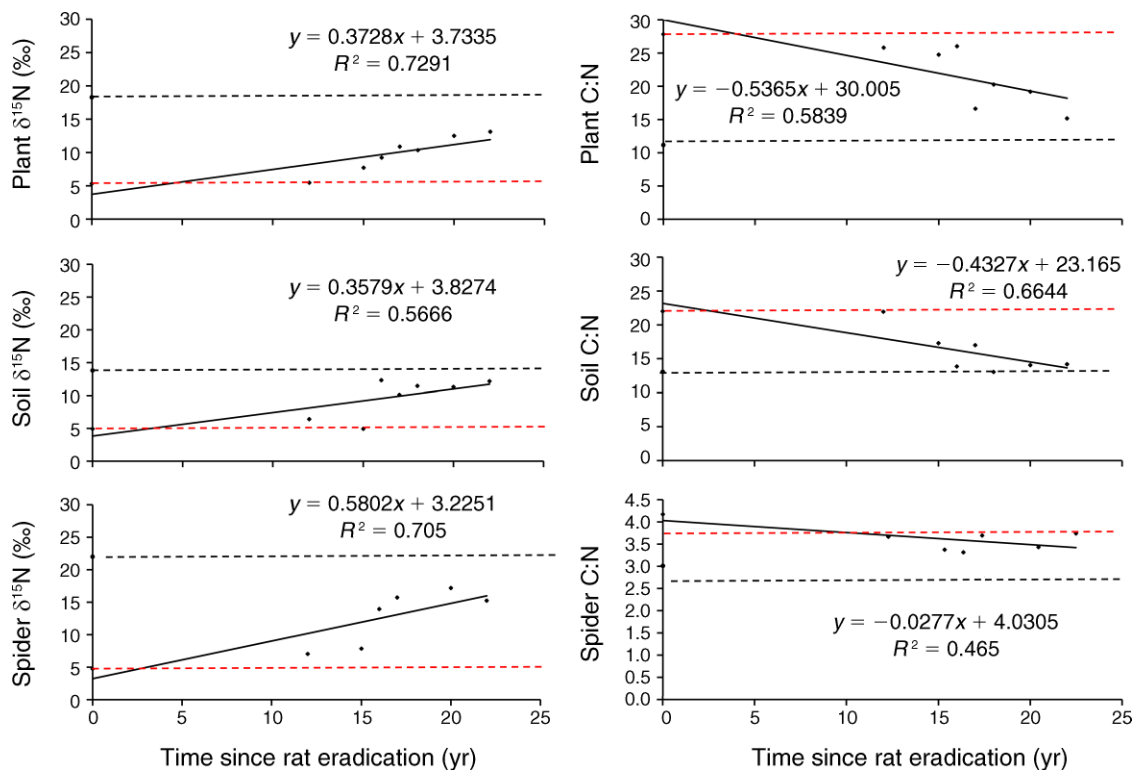


FIG. 2. Values for $\delta^{15}\text{N}$ (left panels) and C:N ratios (right panels) in plants, soil, and ground-dwelling spiders on northeastern New Zealand islands. The black dashed lines are average values for control islands that were never invaded, and the red dashed lines are average values for control islands that are currently invaded.

localized seabird effects but rather reflected island-wide dynamics. This was not possible for control islands that were never invaded as they are completely dominated by seabird burrows. All islands have different human-use histories (e.g., farming), so I took samples in primary (undisturbed) forest to avoid sample variation from human use. Although all three invasive rat species have invaded New Zealand's islands, I only sampled islands involving one species, *Rattus exulans*, in order to avoid variation due to rat species identity. No study islands include introduced predators other than *R. exulans*.

I treated islands that were the sole representative for time since eradication as single temporal samples. I averaged samples to achieve a single value for multiple islands with the same time since eradication and for control islands. Because seabirds play an integral role in uninhabited island ecosystems (Fukami et al. 2006, Mulder et al. 2009, Jones 2010), the level of seabird-derived nutrient input can be used as an indicator of the degree of island ecosystem recovery following rat eradication. I used stable-isotope analysis to measure the amount of seabird-derived nitrogen ($\delta^{15}\text{N}$) entering the different trophic levels. Both marine- and seabird-derived nitrogen are enriched in the heavier isotopic forms compared to terrestrial nitrogen (Kline et al. 1990, Furness 1991).

Collection methods follow Jones (2010) and Fukami et al. (2006). I collected 50 g of soil from 0–10 cm beneath

the litter layer O-horizon, three newly grown leaves from different individuals of the common forest plant species *Coprosma repens*, and three ground-dwelling spiders on each island. I took one soil sample per island and pooled the leaves and spiders to yield one sample per island. Previous work based on extensive sampling on offshore islands indicated one sample per island would be sufficient; there were no significant differences between soil, plant, and spider samples taken across multiple spatial locations on a single island (Jones 2010).

I washed all isotope samples with distilled water, dried for 48 h in a 60°C drying oven, ground to a fine powder, and weighed them. Spider samples consisted of leg material supplemented with head capsules. I selectively used leg and head capsules to ensure maximum protein content and to reduce the amount of muscle or cuticle in samples. I used a Delta^{Plus} (Thermo-Finnigan, Bremen, Germany) continuous-flow, isotope-ratio mass spectrometer at both the National Institute of Water and Atmospheric Research (NIWA; Wellington, New Zealand) stable isotope laboratory and Yale Earth System Center for Stable Isotopic Studies (ESCSIS; New Haven, Connecticut, USA) for all stable-isotope analyses. To ensure machine compatibility, I ran the same samples on both machines with results within $\pm 0.03\%$.

I plotted ecosystem variables against time since rat eradication (using 0 for invaded positive controls) and

used the best-fit equations of the linear regressions to calculate the amount of time it would take variables to recover to uninvaded control levels.

RESULTS

Ecosystem function responded in a linear fashion to the time since rat eradication ($P < 0.05$ for all except spider C:N where $P = 0.09$; Fig. 2). Although linear models produced the best fit, recovery trends suggest a threshold effect where no recovery occurs for at least 15 years post-eradication, followed by periods of rapid recovery in the subsequent years. Indeed, it took at least 15 years in all cases for eradicated-island variables to show significant differences from invaded islands. Best-fit line equations for the linear regression suggest that soil, plant, and spider $\delta^{15}\text{N}$ levels and C:N ratios should take 39 and 35, 28 and 23, and 32 and 37 years, respectively, to passively recover following rat eradication.

DISCUSSION

Islands are critical areas for biodiversity conservation and are increasingly threatened by invasive species. Invasive rats prey on native insular species, disrupt island species interactions, and reduce seabird populations and the nutrient pulses they provide to island ecosystems. Rat eradication is an important first step for islands to begin recovering from this disturbance, but few studies have investigated island-recovery trajectories after rats are removed. This first look at island recovery following rat eradication shows that ecosystem variables could recover more quickly than previously thought; seabird recolonization will play a major role in full ecosystem recovery.

Rattus exulans were introduced to many offshore New Zealand islands nearly 1000 years prior to their eradication (Howald et al. 2007). It is thus likely that the seabird-derived nutrients on these islands have been disrupted for centuries, although there are no data to support this suggestion, as is often the case with such ancient invasions. Even so, islands are recovering their ecosystem properties much faster than previously expected (see Miskelly 1999, Towns and Atkinson 2004). This result indicates that the alternative states hypothesis—that these islands are irreversibly locked and thus will fail to recover following rat eradication (Mulder et al. 2009, Jones 2010)—is probably not tenable. That said, other ecosystem components, such as vegetation and faunal composition, may take much longer to recover than the ecosystem variables measured here (Bellingham et al. 2010).

Island biodiversity and flora and faunal composition are often critically dependent on the nutrients that seabirds provide (Polis and Hurd 1994, Croll et al. 2005, Bellingham et al. 2010). Therefore, it may be necessary for ecosystem nutrient dynamics such as those measured here to recover their preinvasion levels before slower-responding variables are able to recover. My results indicate that this critical first step to full recovery may only take a few decades. Detailed studies of slower-

recovering variables over a chronosequence of eradicated islands could help clarify the timeline for full ecosystem recovery.

In addition to their roles in maintaining nutrient cycling, seabirds are integral to maintaining specific species interactions on some islands. For example, seabirds dig burrows that tuatara (*Sphenodon* spp.) share; seabird burrowing behavior also creates a lack of low-lying vegetation, thereby improving the hunting abilities of tuatara (Walls 1978, Newman 1987). Seabird soil disturbances and nutrient deposition also makes it easier for tuatara to dig burrows and increase their prey availability (Walls 1978, Newman 1987). These latter indirect interactions may take many more years to be restored than the initial nutrient impulses studied here.

The recovery trajectories suggest that it takes at least 15 years for islands to show statistically detectable differences in ecosystem variables following rat eradication from invaded islands (Fig. 2). Therefore, programs seeking to evaluate the ecosystem outcomes of eradication may need to wait until 15 years post-eradication to detect preliminary nutrient recovery and would need to continue through 50 years post-eradication to detect full nutrient recovery. This finding could help explain the lack of recovery seen in studies undertaken on islands that had rats eradicated less than 15 years ago (e.g., Mulder et al. 2009, Jones 2010). Full nutrient recovery on islands could be documented by measuring a combination of response variables that, when taken together and found to be indistinguishable from controls that were never invaded, would suggest full nutrient recovery. These variables may include N and P soil pool size through mass-balance calculations, seabird-derived nitrogen levels and C:N ratios in different trophic levels, and calculations of the amount of seabird- vs. algae-derived nitrogen used in different trophic levels.

A global review of rat predation on seabirds showed that the three invasive rat species (*R. exulans*, *R. rattus*, and *R. norvegicus*) have similar effects on seabird populations through direct predation (Jones et al. 2008). Although my present study focused only on islands previously invaded by *R. exulans*, evidence suggests the other invasive rat species have similar effects on island nutrient dynamics through their predation on seabirds (see Fukami et al. 2006, Mulder et al. 2009, Jones 2010). Thus, the island nutrient-recovery patterns investigated here are not unique to *R. exulans* and likely apply to all seabird islands that have been impacted by invasive rats.

Seabird nutrient input is heterogeneous at low seabird densities (Jones 2010). Thus relatively dense seabird colonies will be needed to produce island-wide ecosystem recovery. Indeed, qualitative analysis on the study islands showed that seabird densities were much higher on never-invaded islands than on islands recovering from rat invasion. Moreover, islands exhibited a continuum of increasing seabird density with increasing time since recovery. Even so, none of the recovering islands had anywhere near the seabird densities observed

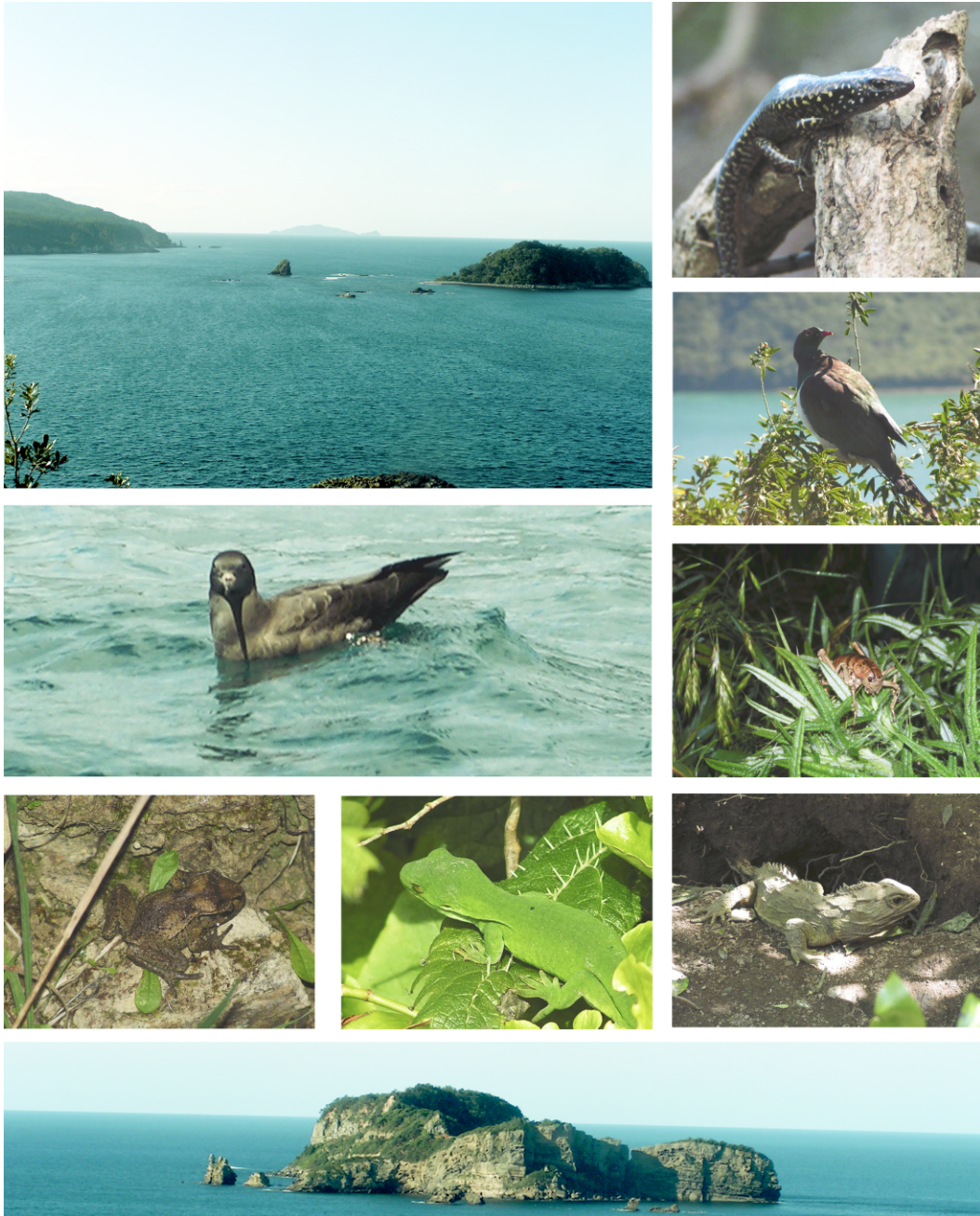


PLATE 1. New Zealand island ecosystems (top left and bottom) house a vast number of endemic species (clockwise from top right: Whitaker's skink, *Cyclodina whitakeri*; New Zealand Pigeon, *Hemiphaga novaeseelandiae*; Giant weta, *Deinacrida rugosa*; Tuatara, *Sphenodon punctatus*; Green gecko, *Naultinus elegans*; and Maud Island frog, *Leiopelma pakeka*) that often critically depend on seabird nutrient inputs from (middle left) Sooty Shearwater, *Puffinus griseus*, and/or the absence of invasive rats for survival. Most of these species are unable to survive on islands with invasive rats but can recover or be actively reintroduced following rat eradication. Photo credits: H. P. Jones.

on islands that were never invaded by rats. Given that many seabird species have low reproductive rates, and are subject to Allee effects, vagaries of food availability, and climate change, their slow recolonization may delay complete recovery, making my prognosis somewhat optimistic. Indeed, if the N pools on never-invaded

islands are larger than the N pools on recovering islands, which previous research suggests is likely (Paetzold et al. 2008), the ratios measured here are likely to recover more quickly than slower-responding N pool sizes.

While passive seabird colonization will contribute to ecosystem recovery over time, it is dependent upon various

factors such as proximity to source populations, whether source populations are increasing or declining, and the biology of the particular seabird species. Augmenting seabird populations through chick translocation and or social attraction (e.g., using various combinations of acoustic playback, decoys, mirrors, scent, or artificial burrows to replicate signals of existing colonies) may be useful restoration measures (e.g., Kress 1998, Miskelly et al. 2009). This management tool can establish colonies of reluctant natural recolonizers and thus speed the slower-responding ecosystem recovery variables. Seabird restoration will be especially useful for establishing colonies of species that are philopatric, have low reproductive rates, and strong Allee effects such as hole-nesting Procellariidae seabirds (Jones et al. 2011). Hole-nesting procellariids are widely represented among seabird species and are more vulnerable to invasive rat predation than many other species (Jones et al. 2008), so actively restoring them can help speed the ecosystem recovery process following rat eradication. Once recolonization begins, recovery is likely to happen more rapidly as the new colonists attract new immigrants and species to the colony (Kress 1998). Indeed, islands with seabird restoration projects in their earliest stages have higher soil ammonium and nitrate levels and marine-derived nitrogen levels in restoration colony trophic levels relative to islands with rats eradicated and no seabird restoration (Jones 2010).

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