

The ghost of invasives past: rat eradication and the community composition and energy flow of island bird communities

MICHAEL A. TABAK,^{1,2,†} SALLY PONCET,³ KEN PASSFIELD,³ JACOB R. GOHEEN,^{1,2}
AND CARLOS MARTINEZ DEL RIO^{1,2,4}

¹Department of Zoology and Physiology, University of Wyoming, 1000 E. University Avenue, Laramie, Wyoming 82071 USA

²Program in Ecology, University of Wyoming, 1000 E. University Avenue, Laramie, Wyoming 82071 USA

³Beaver Island LandCare, P.O. Box 756, Stanley, FIQQ IZZ Falkland Islands

⁴Wyoming Biodiversity Institute, University of Wyoming, 1000 E. University Avenue, Laramie, Wyoming 82071 USA

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Abstract. In the Falkland Islands, islands with invasive rats have fewer passerine species compared to islands without rats. On islands on which rats have been eradicated, passerine species richness is indistinguishable from that found on islands historically free of rats, but community composition differs between these two island types. In particular, the most dominant species on historically rat-free islands, *Cinclodes antarcticus*, is less abundant and prevalent on eradicated islands. We compared passerine energy flow on islands with rats, islands from which rats have been eradicated, and islands on which rats were historically absent. Passerine communities on islands historically without rats used nine times more energy than on islands with rats present. Despite equivalent passerine species richness, passerine energy flow was approximately half on islands from which rats had been eradicated compared to historically rat-free islands. Because passerine energy flow was determined by community composition and not by species richness, passerine species within this community appear to be functionally complementary and not functionally redundant. At least one species, *C. antarcticus*, plays an irreplaceable role. Our results also document the dramatic and lingering effects of invasive species following their eradication, and the importance of species complementarity for the resilience of community properties.

Key words: *Cinclodes antarcticus*; community structure; competition; ecosystem; energy flow; eradication; global change; invasive species; island; metacommunity; *Rattus norvegicus*; species complementarity.

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† **E-mail:** tabakma@gmail.com

INTRODUCTION

Invasive species change native island biotas by altering the abundance and distribution of native species (Atkinson 1985, Vitousek et al. 1997, Mack et al. 2000, Sax et al. 2002, Blackburn et al. 2004, Athens 2009, Simberloff 2013). To restore native communities, conservation managers have eradicated introduced species from islands in archipelagoes worldwide (Genovesi 2011, Keitt et al. 2011). These eradication efforts often lead to the recovery of vulnerable species and to the recuperation

of species richness, vegetation cover, and soil-nutrient content (Towns 2009, Jones 2010a, Tabak et al. 2015a). However, the effects of invasive species eradications on ecosystem processes have been scarcely documented. We compared an ecosystem process—energy flow—through the community of native passerines on islands with invasive rats, islands from which invasive rats had been eradicated, and islands to which rats had never been introduced in the Falkland Islands.

The Falkland Islands (or “Falklands”) is a South Atlantic archipelago of approximately 500 islands.

Norway rats (*Rattus norvegicus*, henceforth “rats”) were introduced to the archipelago in the late 18th century (Woods and Woods 1997) and are now present on about half of the islands (Tabak et al. 2015b). Passerine species richness is statistically indistinguishable on rat-free islands and on eradicated islands, but is lower on rat-invaded islands in the Falklands (Tabak et al. 2015a). Tabak et al. (2015a) assessed the similarity in community composition (i.e., the identity and abundance of each species in the assemblage) among island types using non-metric multidimensional scaling. They found that bird communities on islands with rats and eradicated islands were more similar to each other, in multidimensional space, than they were to historically rat-free islands. We sought to understand whether rat invasion impacted passerine energy flow and, if so, how energy flow responded following rat eradication. Similar levels of passerine energy flow between historically rat-free islands and islands where rats have been eradicated would support the hypothesis of functional redundancy (Walker 1992, Lawton and Brown 1994, Naeem and Li 1997, Wohl et al. 2004, Hubbell 2006), in which species are equivalent in their ability to procure available energy. Consequently, we hypothesized that if passerines in the Falklands are functionally redundant, energy flow on historically rat-free islands and eradicated islands would be similar (see White et al. 2004) and higher than on rat-invaded islands.

We focused some of our analyses on the effect of a single species, *Cinclodes antarcticus* (henceforth “*Cinclodes*”). Our observations suggest that this species plays a disproportionate role in passerine island communities in the Falklands. This species is not only present on almost all islands where rats are absent, it is also very abundant on these islands (Tabak et al. 2014b). However, *Cinclodes* is absent from islands with rats, and its prevalence and abundance on eradicated islands are lower than those on historically rat-free islands (Tabak et al. 2015a). Stable isotope measurements indicate that this species is a generalist that can feed in both terrestrial and intertidal environments, which likely explains its high abundance (Tabak et al. 2016), while other passerines are unlikely to feed in the intertidal (Sabat et al. 2006).

We hypothesized that if *Cinclodes* is not substitutable by other passerines in the community, its reduced abundance on rat-eradicated islands

would be accompanied by reduced passerine energy flow on these islands compared to historically rat-free islands. We argue that differences in passerine energy flow between eradicated islands and historically rat-free islands would support the hypothesis of functional complementarity: Individual species’ abilities to use resources would lead to differences in passerine energy flow in spite of similar levels of species richness (Loreau 2004, Thibault et al. 2004, Resetarits and Chalcraft 2007). Because energy use in individual organisms depends allometrically on body mass (West et al. 1997, Enquist et al. 2003, Brown et al. 2004), energy flow through an ecological community depends both on the biomass of each of the species that make up this community and on the distribution of abundances and body masses of these species (Maurer and Brown 1988, Srivastava and Lawton 1998, White et al. 2004). We used estimates of species’ abundances (i.e., individuals per unit transect length; Tabak et al. 2014a) and body masses (Dunning 2008), and the allometric relationship that relates daily field metabolic rate with biomass (Nagy 1987) to estimate energy flow through the passerine community. We focused on passerines rather than other taxa as a result of the availability of data for this group (Tabak et al. 2014a).

METHODS

Our study is based on a large data set on the abundance and distribution of passerines in the Falkland Islands analyzed in detail by Tabak et al. (2014b, 2015a). We describe the islands, the passerine fauna that inhabits them, and the effects of Norway rats on this fauna in detail in Tabak et al. (2014b, 2015a). We estimated the mean biomass (on a per-km transect basis) of each passerine species on each island for which abundance data were available in the Falkland Islands (159 islands: 67 islands historically without rats, 57 islands with rats, and 35 islands from which rats had been eradicated; Tabak et al. 2014a) as the abundance (per-km) times the mean body mass of an individual of that species. Mean biomass was therefore estimated as the product of the mean mass of an individual of the species (M_i , in g; from Dunning 2008) times the estimated average abundance of this species i on the island (n_i , in number of individuals detected per kilometer of transect; Tabak et al. 2014a). We compared the

biomass of each species in each island type with Kruskal–Wallis one-way ANOVA tests (Kruskal and Wallis 1952) and a series of Mann–Whitney U tests (Sokal and Rohlf 1981). To compare passerine energy flow among each of the island types, we estimated passerine community energy flow (E_{Tot}) on each island. E_{Tot} was standardized by transect length, as we used the number of individuals detected per kilometer instead of total number of individuals on each island (data for total number of individuals were not available; Tabak et al. 2014a). E_{Tot} is the sum of energy flow across all species (Brown et al. 2004, White et al. 2004),

$$E_{\text{Tot}} = \sum_{i=1}^S n_i (b_0 \overline{M}_i)^{3/4}$$

where $b_0 \overline{M}_i^{3/4}$ is the allometric relationship relating daily field metabolic rate (in kJ/day; Nagy 1987) to the average body mass of species i (in grams; Dunning 2008), b_0 is a standardization constant with units (kJ/day \times gram $^{3/4}$), n_i is the estimated average abundance of species i on the island (in number of individuals counted per kilometer of transect; Tabak et al. 2014a), and S is the island's detected species richness. We used a Kruskal–Wallis test (Kruskal and Wallis 1952) and a series of Mann–Whitney U tests (Sokal and Rohlf 1981) to compare E_{Tot} among each of the island types (Quinn and Keough 2002).

We distinguished the energy flow for the most abundant species on rat-free islands (*Cinclodes*; Tabak et al. 2014b; $E_{\text{Cinclodes}}$) and for all non-*Cinclodes* passerines ($E_{\text{Non-Cinclodes}}$), where

$$E_{\text{Cinclodes}} = N_{\text{Cinclodes}} (b_0 \overline{M}_{\text{Cinclodes}})^{3/4}$$

and $E_{\text{Non-Cinclodes}}$ is the difference between E_{Tot} and $E_{\text{Cinclodes}}$. We compared contribution of *Cinclodes* to E_{Tot} ($E_{\text{Cinclodes}}/E_{\text{Tot}}$) among island types with a Kruskal–Wallis test (Kruskal and Wallis 1952) and Mann–Whitney U tests (Mann and Whitney 1947, Sokal and Rohlf 1981). We calculated the biomass of each species as the abundance of each species times the average mass of individuals from that species (White et al. 2004):

$$B_{\text{Tot}} = \sum_{i=1}^S n_i \overline{M}_i$$

To assess the potential effect of time since eradication on E_{Tot} and $E_{\text{Cinclodes}}$, we calculated the Pearson rank correlation (r) between these estimates and the amount of time since eradication.

There were no statistically significant differences between the island characteristics that we measured (island area, vegetation, and number of seabird species) among island groups (i.e., rats absent, rats present, and rats eradicated; Appendix S1). While similarity across this set of variables does not guarantee that all islands were similar with regard to vegetation and resources, these are the only quantifiable variables that were available to compare among island groups (Falkland Islands Government 2013), and we did not find any statistically significant relationship among groups. Additionally, while there are differences in vegetation and resources among individual islands, the islands surveyed within each group were a random subset and there was no observable trend between vegetation/resources and island group (field observations). Therefore, we think it is reasonable to assume that passerines had equal access to resources among island groups.

RESULTS

Most species of passerines differed significantly in biomass per unit transect among island types (Fig. 1). Three species (*Troglodytes*, *Cinclodes*, and *Turdus*) had significantly lower biomasses on islands with rats than on historically rat-free islands (Fig. 1). Three species (*Cistothorus*, *Muscisaxicola*, and *Sturnella*) exhibited higher biomasses on eradicated islands than on both historically rat-free and rat-invaded islands. The biomass of *Cinclodes* differed among the three island types. On eradicated islands, the biomass of *Cinclodes* was intermediate between that found on historically rat-free islands and the low biomass found on rat-invaded islands (Fig. 1).

For islands on which rats were historically absent, passerine energy flow [E_{Tot} in kJ/(day \times km)] was nearly an order of magnitude higher than that of rat-invaded islands ($\chi^2 = 83.69$, $P < 0.0001$; Fig. 2) and was nearly double that of islands from which rats had been eradicated ($P = 0.006$). Islands with rats eradicated had a median passerine energy flow that was 4.5 times higher than that of rat-invaded islands ($P < 0.0001$; Fig. 2). The average total contribution of *Cinclodes* to E_{Tot}

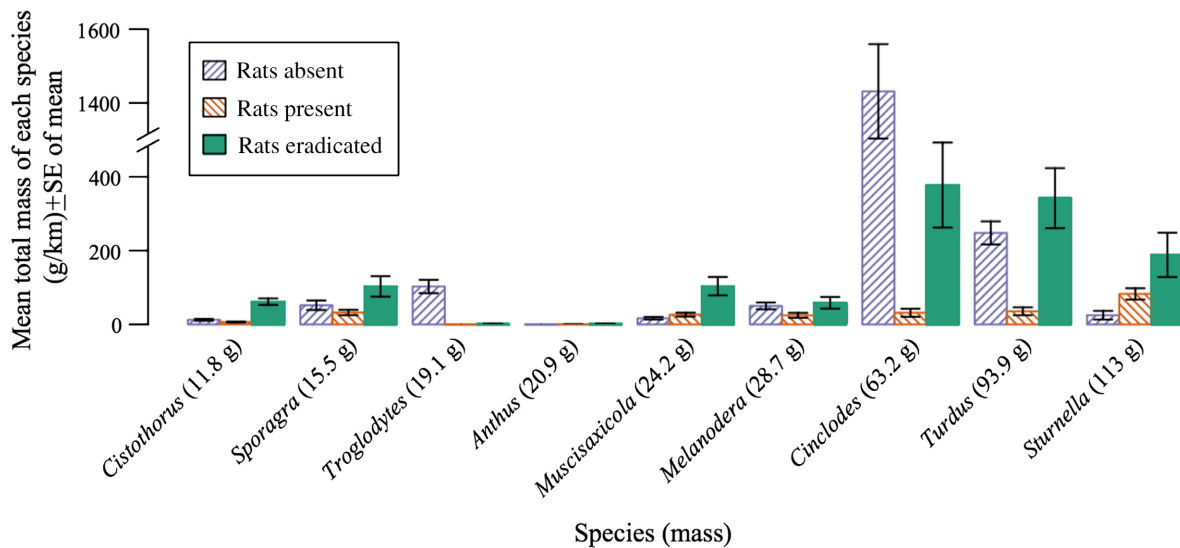


Fig. 1. The distribution of total biomass (which is a function of a species' mean mass times its abundance) used by each species differed among the three rat statuses. Total biomass was higher on eradicated islands compared to rat-invaded islands for six species. Each species is listed by its genus name and the mean mass for this species.

also differed significantly among island types ($\chi^2 = 61.76$, $P < 0.0001$; Fig. 3). On historically rat-free islands where *Cinclodes* was the most abundant passerine (Tabak et al. 2014b), it contributed $63.5\% \pm 3.3\%$ (SE) to passerine energy flow. Because this species was either absent or occurred at very low abundances on rat-invaded islands, its contribution to E_{Tot} was very small $7.6\% (\pm 2.7\%)$. On eradicated islands, *Cinclodes* contributed $20.0\% (\pm 4.3\%)$ of E_{Tot} and the energy flow of *Cinclodes* ($E_{\text{Cinclodes}}$) increased linearly with time since eradication ($r = 0.53$, $P < 0.001$). Because of the increase in $E_{\text{Cinclodes}}$ with time since eradication, E_{Tot} also increased with the amount of time since eradication ($r = 0.35$, $P = 0.04$; Fig. 4). The energy flow of all species excepting *Cinclodes* ($E_{\text{Non-Cinclodes}}$) did not increase significantly with time since eradication ($r = 0.06$, $P = 0.71$).

DISCUSSION

Islands where rats have been eradicated had much higher values of passerine energy flow than islands with rats; however, this value was lower than that found on islands historically free of rats. The energy flow through passerine communities on eradicated islands retained a legacy of rat invasion over the 11 years since rat eradication (Fig. 2), which was due to the delayed recolonization of

Cinclodes on eradicated islands (Fig. 3). We predict that E_{Tot} will continue to increase with time on eradicated islands (Fig. 4) to the value of historically rat-free islands as the prevalence and abundance of *Cinclodes* increases.

The large difference in passerine energy flow among island types is the consequence, not only of differences in the abundance of species among island types (Fig. 1), but also of differences in community composition. Specifically, the difference in energy flow between eradicated islands and historically rat-free islands is the consequence of the rarity of *Cinclodes* on eradicated islands (Tabak et al. 2015a). Although several other species have significantly higher abundances (Tabak et al. 2015a) and total biomasses (Fig. 1) on eradicated islands than on historically rat-free islands, these increased abundances were not sufficient to compensate for the lower abundance of *Cinclodes* (Tabak et al. 2015a). Lower energy flow on eradicated islands relative to historically rat-free islands—in spite of similar species richness—lends support to the hypothesis of functional complementarity among species (Frost et al. 1995, Thibault et al. 2010), rather than functional redundancy (Lawton and Brown 1994, Wohl et al. 2004). Species appear to be complementary in the Falklands, as field observations and stable isotope data suggest that a large fraction of *Cinclodes*' diet

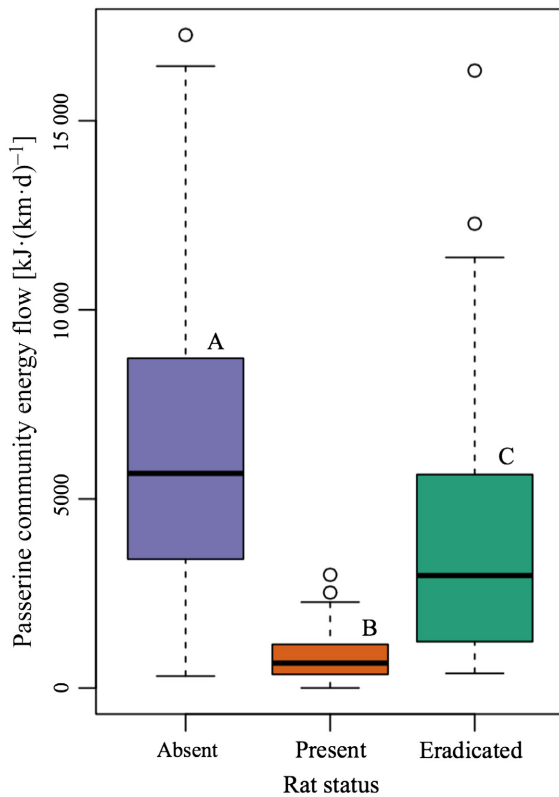


Fig. 2. Passerine energy flow was about an order of magnitude lower on islands with rats present ($n = 67$) than on historically rat-free islands ($n = 57$). Energy flow was intermediate on islands following rat eradication ($n = 35$), suggesting that rats leave a legacy of reduced energy flow through the community following their removal.

(over 50%) has a marine origin (Tabak et al. 2016); this is a dietary source that is unlikely to be utilized by other passerines due to physiological constraints (Sabat et al. 2006). Consequently, it is likely that this species contributes disproportionately to passerine energy flow because it is able to capitalize on unique resources that are unavailable to other passerines. In contrast, the hypothesis of functional redundancy relies on the premise that species can have similar ecological roles and thus similar community- and ecosystem-level impacts (Walker 1992, Pringle et al. 2014). The unique dietary breadth of *Cinclodes* makes this species non-replaceable (i.e., non-redundant) by other species in the community.

Two non-mutually exclusive mechanisms can potentially explain the reduction of energy flow of

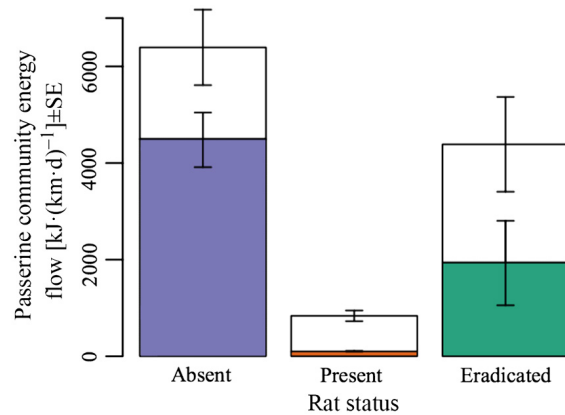


Fig. 3. The contribution of *Cinclodes antarcticus* to passerine energy flow (colored portions of bars) was different among all rat statuses. *Cinclodes* is the most dominant (and the largest contributor to energy flow) on historically rat-free islands, but rats significantly reduce its role in island communities. Following eradication, *Cinclodes* contributes a larger proportion of energy flow compared to rat-invaded islands, but its contribution is significantly lower than that on historically rat-free islands.

passerine communities in the presence of rats: predation and exploitative competition (i.e., reducing the resources available to passerines; Hunt 2007, Sprott 2011). The strongest evidence for predation comes from two ground nesting species, *Cinclodes* and *Troglodytes cobbi* (the only endemic passerine to the Falklands), which were extirpated from islands where rats are present (Tabak et al. 2014b), likely due to predation on nestlings and adults (Drake et al. 2011). Evidence for competition comes from the use of similar resources by rats and passerines. Evidence for use of similar resources is inferred from the effects of rats on the abundance of invertebrates, upon which several passerines feed (Athens 2009, Meyer and Butaud 2009, St Clair et al. 2010). In the Falklands, the abundance of endemic Falkland camel crickets (*Parudenus* spp.), a common food for passerines (Woods and Woods 2006), is an order of magnitude lower on rat-invaded islands than on rat-free islands (St Clair et al. 2010). Additionally, based on similar use of marine vs. terrestrial resources, Tabak et al. (2016) found that the isotopic niche of rats overlapped between 85% and 95% with those of *Cinclodes* and *Troglodytes*. The population densities and rates of energy use of mammals are

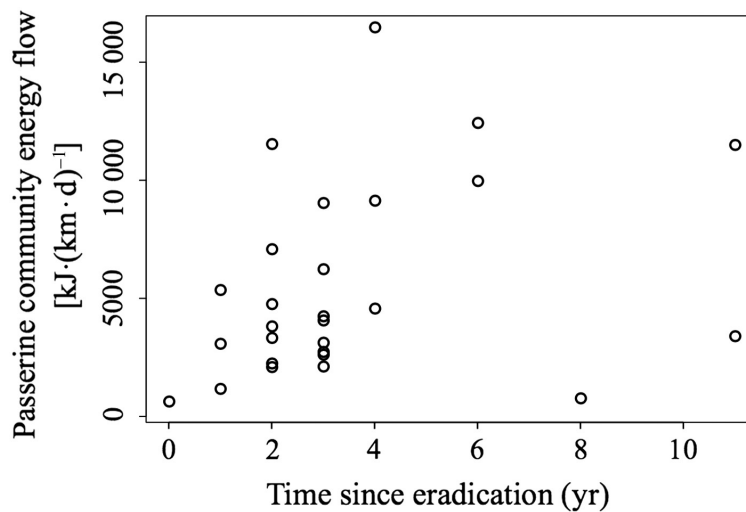


Fig. 4. Passerine community energy flow on eradicated islands increased with the amount of time since rats had been eradicated.

at least an order of magnitude higher than those of birds of the same body mass (Blackburn et al. 1997, Silva et al. 1997, Benkman et al. 2008), so rats can have comparatively large effects on ecosystem properties. Therefore, the suppression of energy flow of passerines by rats is likely the result of the high abundance, high metabolic rates, and generalized feeding habits of rats (Wiles 1981, Currie and Fritz 1993).

In the aftermath of perturbations, the rate and trajectory of community reassembly should be driven by both the colonization and competitive ability of species in the metacommunity (Leibold et al. 2004). Species differences in colonization and competitive abilities should thus shape the recovery of ecosystem-level processes, which was evident in our study from the shift in energy flow following rat eradication. *Cinclodes* is probably both a poor colonizer and a good competitor, as evidenced by a negative correlation between its abundance and that of other species (Tabak et al. 2014b). Most (75%) of the species that have higher abundances on eradicated islands than on historically rat-free islands also have higher occupancies than *Cinclodes* on eradicated islands of a given size (Tabak et al. 2015a), suggesting that their superior colonization ability comes at the cost of poor competitive ability (Levins and Culver 1971, Yu and Wilson 2001).

Justifiably, the eradication of rats has been pronounced as one of the major successes in

conservation of native island biotas (Stolzenburg 2011). For example, Jones (2010a, b) found that seabird recovery following rat eradication was accompanied by ecosystem-level effects including increased marine subsidy in soil, plants, and invertebrates. Eradications are not only successful conservation practices, but also experimental manipulations that can reveal the factors that shape the properties of ecological communities and ecosystems. Eradication of rats in the Falklands revealed that (1) passerine species are not functionally redundant in this system (at least one species, *Cinclodes*, seems to play an inordinately large role and to be non-replaceable), (2) community composition of passerines is linked to passerine community energy flow, and (3) therefore, the pattern of colonization determines the pace at which an ecosystem-level process (energy flow) recovers. Because rats have strong effects that extend from populations to communities and ecosystems (Jones 2010a, Tabak et al. 2014b), their eradication has had equally strong and remarkably rapid consequences (Jones 2010b, Tabak et al. 2015a).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1442/supinfo>