

Rat eradication and the resistance and resilience of passerine bird assemblages in the Falkland Islands

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Summary

1. Norway rats (*Rattus norvegicus*) were introduced to the Falkland Islands and are detrimental to native passerines. Rat eradication programmes are being used to help protect the avifauna.

2. This study assesses the effectiveness of eradication programmes while using this conservation practice as a natural experiment to explore the ecological resistance, resilience and homeostasis of bird communities.

3. We conducted bird surveys on 230 islands: 85 in the presence of rats, 108 that were historically free of rats and 37 from which rats had been eradicated. Bird detection data were used to build occupancy models for each species and estimate species–area relationships. Count data were used to estimate relative abundance and community structure.

4. Islands with invasive rats had reduced species richness of passerines and a different community structure than islands on which rats were historically absent. Although the species richness of native passerines was remarkably similar on eradicated and historically rat-free islands, community structure on eradicated islands was more similar to that of rat-infested islands than to historically rat-free islands.

5. The results suggest that in the Falkland Islands, species richness of passerines is not resistant to invasive rats, but seems to be resilient following their removal. In contrast, community structure seems to be neither resistant nor resilient. From a conservation perspective, rat eradication programmes in the Falkland Islands appear to be effective at restoring native species richness, but they are not necessarily beneficial for species of conservation concern. For species that do not recolonize, translocations following eradications may be necessary.

Key-words: community structure, detection probability, ecological homeostasis, eradication, invasive species, occupancy modelling, resilience, species–area relationship

Introduction

Introduced species can alter the characteristics of island biotas by changing the abundance and composition of native species through extirpation and extinction (Atkinson 1985; Vitousek *et al.* 1997; Mack *et al.* 2000; Sax, Gaines & Brown 2002; Courchamp, Chapuis & Pascal 2003; Blackburn *et al.* 2004; Simberloff 2005). The pervasive negative effects of introduced species have been used to justify many (ca. 950) attempts to eradicate introduced organisms from islands throughout the world (Keitt *et al.* 2011). While it is possible that the negative effects of

invasive species on natives will remain after the invasive has been removed (Crooks 2005; Strayer *et al.* 2006; Bodey *et al.* 2011), the goal of these eradication operations is to protect native species and to restore characteristics of island biotas (e.g. diversity and abundance) to pre-invasion states (Jones 2010; Genovesi 2011). The eradication of invasive species thus represents both a conservation strategy and an ecological experiment (or a quasi-experiment *sensu* DiNardo 2008) that provides an opportunity to investigate both the resistance and resilience of island communities.

Following Lake (2013), we define resistance as the capacity of ecological properties to remain relatively stable in the face of a perturbation. For example, species

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composition of a native assemblage would be deemed resistant to an introduced species if the diversity (i.e. species richness), abundance and identity of native species were not significantly different than undisturbed sites (Knapp *et al.* 2005), that is those lacking the introduced species. Resilience is the capacity of a community to recover from a disturbance (Scheffer *et al.* 2001; Allison & Martiny 2008). Consequently, community structure (defined as the composition and relative abundance of species on an island) of a native assemblage would qualify as resilient to an introduced species if, following eradication of the introduced species, its characteristics returned rapidly (Holling 1973; D'Antonio & Chambers 2006) to those before the introduction, or to those of islands on which introductions had not occurred. The terms resilience and resistance are implicitly related to the idea of ecological homeostasis, which Ernest & Brown (2001a) conceptualized as the tendency of an ecological system to maintain approximate stability in its characteristics in the face of environmental and biotic changes (Brown *et al.* 2001). Ernest & Brown (2001a) concluded that species richness is a 'homeostatic' property of ecological communities, as it has been shown to remain relatively constant despite changes in environmental conditions (McNaughton 1977; Kelt 1996; Brown *et al.* 2001; Lekve *et al.* 2002), and independent of shifts in species composition (Ernest & Brown 2001b; Goheen *et al.* 2005). Ernest & Brown (2001a) hypothesized that one of the mechanisms that confers homeostasis in species richness is compensation: if one species is absent, it is replaced by another, leading to a negative correlation among species abundances (Klug *et al.* 2000; Supp & Ernest 2014).

Islands in which invasive species have been eradicated, therefore, offer a unique opportunity to study resistance and resilience of ecological communities. Conservation managers eradicate invasive species because those invasives reduce the abundance and diversity, or alter the composition, of native species (Genovesi 2011; Towns 2011). Hence, eradications are performed following observations, or under the assumption, that native species are not resistant to invasives (Simberloff *et al.* 2013). After invasive species have altered native communities, eradications are implemented in an attempt to restore native communities to their pre-invasion state (Myers *et al.* 2000; Carrion *et al.* 2011). Consequently, eradication attempts are conducted under the implicit assumption that ecological communities are resilient (Jäger & Kowarik 2010).

We aimed to test these assumptions using data collected from 230 islands, some of which exhibited reduced richness and abundance of passerine birds following the introduction of Norway rats (*Rattus norvegicus*; hereafter 'rats'; Tabak *et al.* 2014a). Understanding the resistance, resilience and homeostasis of island assemblages to an introduced species requires either (i) data prior to the introduction of an invasive, in the presence of the invasive and following its eradication; or (ii) data from collections

of islands from which the invasive is present, eradicated and historically absent. In the Falkland Islands, we collected data on the latter.

Here we use a quasi-experimental approach to explore homeostasis in ecological communities in an attempt to answer several complementary questions. First, are species richness and community structure of native passerine communities in the Falkland Islands resistant to the presence of an invasive species? Secondly, if richness is not resistant, is it resilient (i.e. does richness recover following eradication)? Finally, if community structure is not resistant, is it resilient (i.e. is community structure the same on eradicated islands as on historically rat-free islands), or do some species compensate for the absence of others (i.e. are some species more abundant on eradicated islands than on historically rat-free islands)?

Materials and methods

STUDY SYSTEM

The Falkland Islands (or 'Falklands') is a remote archipelago of approximately 500 islands located 500 km off the coast of South America. Rats were introduced to the Falklands in the late 18th century (Woods & Woods 1997) and are currently present on many, albeit not all, of the islands in the archipelago (M. A. Tabak, S. Poncet, K. Passfield, C. Martinez del Rio, in review). The passerine avifauna of the Falklands includes an endemic wren that is vulnerable to extinction (*Troglodytes cobbi*; IUCN, 2012), an ovenbird whose distribution is likely limited to the Falkland Islands and the few islands that remain free of rats around Tierra del Fuego (*Cinclodes antarcticus*; Strange 1992; Pina & Cifuentes 2004) and several passerines that are also found in continental South America (*Melanodera melanodera*, *Sporagra barbata*, *Sturnella loyca*, *Cistothorus platensis*, *Muscisaxicola maclovianus* and *Anthus correndera*; Woods & Woods 2006). Henceforth, and for simplicity, these species will be referred to by their generic names. Since 2001, rat eradication operations have been implemented on 66 islands in the Falklands (Falkland Islands Government 2014), following the observation that rats reduce the occupancy and abundance of several bird species (Hall *et al.* 2002; Woods & Otley 2008; St Clair *et al.* 2010). The aim of these operations is to restore the characteristics of island biotas (Poncet *et al.* 2011).

Tabak *et al.* (2014a) investigated differences in the species richness and community structure of passerine bird assemblages on rat-free and rat-infested islands in the Falklands. They documented reduced species richness on islands with rats and differences in community structure between islands with and without rats. They found that the lower species richness on rat-infested islands and the difference in composition between rat-infested and rat-free islands are partially explained by the effect of rats on the two dominant passerines: *Troglodytes* and *Cinclodes*. Passerine assemblages appear not to be resistant to invasive rats, as richness and community structure differ between rat-free and rat-infested islands. Here we elaborate on the results of Tabak *et al.* (2014a) with a comparison of passerine species richness and community structure on a larger sample of islands. This sample includes 37 islands in which rats have been eradicated, 85 islands with rats and 108 islands that have been historically free of rats.

ISLAND SURVEYS

Surveys for passerines were systematically conducted on 230 islands in the Falklands by SP and KP from 2007 to 2013. Surveys were conducted for bird detection/non-detection on all 230 islands, while a subset of these islands ($n = 159$) was simultaneously surveyed for bird abundance. Passerines were detected using visual sightings and calls. Surveys involved walking at least 1 km of coastline, or the entire island perimeter for smaller islands (<10 ha). Coastline perimeters ranged from 0.09 to 670 km. Surveyors also walked one transect across the interior of the island. Transects varied in length based on island area [range 0.5–6.4 km; mean length = 1.54 ± 0.09 (SE) km] and were measured using a global positioning system receiver (Garmin). The 230 islands ranged in area from 0.1 to 5595 ha; island areas were obtained from the Falkland Islands Biodiversity Database (Falkland Islands Government 2014). The area of islands with rats, historically free of rats and from which rats had been eradicated did not differ significantly (Kruskal–Wallis one-way analysis of variance by ranks $P > 0.10$).

On a subset of 159 islands, SP and KP counted the number of individuals seen while walking transects. Surveyors maintained a slow and consistent pace and noted birds that moved ahead or accompanied the surveyor to avoid counting the same bird multiple times. The same two individuals conducted all surveys in exactly the same manner on each island (both SP and KP surveyed each island). Counts were standardized by total transect length for analysis. Although this method does not allow for density estimation, it provides an estimate of the detected relative abundance of each species that can be used to compare among islands with different rat statuses.

The most prominent vegetation on most of the islands surveyed was tussac grass (*Poa flabellata*), and the density of this plant could potentially affect bird occupancy (Pye & Bonner 1980; Woods & Woods 2006). The abundance of tussac grass on islands was ranked using a 5-point scale (where 0 = no tussac, 1 = remnant tussac at some spatial points, 2 = erosion of former tussac, 3 = partial tussac cover, 4 = complete tussac cover; Hall *et al.* 2002). The history of grazing by sheep and cattle on each island was quantified using a 6-point scale (where 0 = never grazed, 1 = grazed more than 20 years ago, 2 = grazed 10–20 years ago, 3 = grazed 1–10 years ago, 4 = currently grazed intermittently, 5 = currently grazed year round). Grazing history was determined by interviews with farmers and island owners and by referring to relevant unpublished reports to the Falkland Islands Government.

Because weather and seasonality might affect species detections, weather was evaluated using three metrics. Cloud cover (C) was estimated to the nearest okta, which ranges from $C = 0$ (clear sky) to $C = 8$ (completely cloudy sky; World Meteorological Organization 1974). Wind speed and direction were measured using an anemometer (Skywatch Xplorer, Skyview, Sudbury, England). Seasonality was incorporated into the surveys by determining the applicable austral season of the date of survey.

OCCUPANCY MODELLING

Because it is possible that some species were present on islands but not detected in surveys (MacKenzie *et al.* 2002), detection probability of each species was incorporated into estimates of occupancy with a double-sampling approach (MacKenzie &

Royle 2005). SP and KP conducted repeated surveys on a random sample of 10 islands. Each island in the random sample was surveyed five times over a 5-day period, during which time populations were considered to be closed (MacKenzie *et al.* 2006). Occupancy of each passerine was modelled with the R program ‘unmarked’ v. 0.10-4 (Fiske & Chandler 2011) using a double-sampling approach (MacKenzie & Royle 2005). Detection data from the collection of islands that were resurveyed were used to estimate detection probability (P) for each species using maximum likelihood (Pollock *et al.* 2002; MacKenzie & Royle 2005). Using these species-specific detection probabilities, the probability of species occupancy (ψ) was estimated following MacKenzie *et al.* (2002). Generalized linear models (GLMs) with a logit-link function and a binomial distribution were used to model the effects of habitat covariates on ψ . The full model included effects of island area (log-transformed, $\text{Log}_{10}\text{Area}$), presence of rats at the time of survey (*RatPres*, a binomial variable), whether or not rats had been successfully eradicated (*RatErad*, a binomial variable), each of the habitat covariates (tussac grass cover, *Tussac*, and grazing history, *Graze*), weather covariates (cloud cover, *Cloud*, wind speed, *Wind*, and season, *Season*), the amount of time since rat eradication (in years, *Time*), and the interaction between island area and each of the other covariates on ψ . The full model was compared with all possible reduced models. For each species, the top candidate models were selected based on AIC_C scores and goodness-of-fit tests. Models were first considered for that species ($\Delta\text{AIC}_C < 7$). Then, for each candidate model, goodness-of-fit was estimated following MacKenzie & Bailey (2004). This test assesses whether there is a significant difference between χ^2_{obs} (test statistic from observed data) and χ^2_{b} (test statistic for bootstrapped data) using 1000 bootstrapped samples that were generated following the method of MacKenzie & Bailey (2004). To confirm that all of the models in the top candidate set fit the data, $\alpha = 0.05$ was used as a criteria from this test. For each species, model averaging was performed on all models in the candidate set (Burnham & Anderson 2002).

RECONSTRUCTING SPECIES–AREA RELATIONSHIPS FROM OCCUPANCY MODELS

Although the data set provides an observed species richness for each island surveyed, these species richness values do not account for detectability and can therefore underestimate species richness. To construct species area curves that account for detectability, occupancy functions were used to simulate species-richness values associated with each island. For each island, a 9×1000 matrix was constructed in which the value of each entry (α_{ij} , where i denotes a species and j one of 1000 simulated islands) was determined in a Bernoulli trial with the probability of occupancy of species i estimated by our averaged occupancy models and the covariates associated with each island (the logarithm of island area and rat status). The sum across all nine species represents an estimated species richness for each simulation. Means of these 1000 simulations represent the estimated richness of an island with a given suite of covariates. To compare the species area relationships [i.e. estimated species richness vs. $\text{Log}_{10}(\text{Area})$] among islands with rats, islands on which rats have been eradicated and islands historically free of rats, GLMs with an identity link function and a normal distribution were used. The same set of GLMs was used to compare differences in detected species richness.

RELATIVE ABUNDANCE

The relative abundance of each passerine was estimated on the 159 islands for which count data were available. This data set consisted of 67 islands on which rats were historically absent, 57 islands on which rats occurred at the time of survey and 35 islands on which rats had been eradicated. For each island where a passerine was present, relative abundance was estimated as the number of individuals counted divided by the total length of transects (in km) walked on that island. For each species, the mean relative abundance in each rat status was compared by first determining whether there was a significant difference between any of the three groups (i.e. rats historically absent, rats present and rats eradicated) using a Kruskal–Wallis one-way analysis of variance (Kruskal & Wallis 1952; Sokal & Rohlf 1981). If there were significant differences between the rat statuses, a *post-hoc* Mann–Whitney *U*-test was used to determine whether there were significant differences between each pair of rat statuses (Mann & Whitney 1947; Sokal & Rohlf 1981). A Bonferroni correction was used to correct α values (Quinn & Keough 2002) where comparisons between rat statuses for each species were treated as a family (i.e. three comparisons in each family). To determine whether there was an effect of time since rat eradication on relative abundance, Spearman rank correlation (r_s) was estimated between each species' abundance and time since eradication. To test the effect of *Troglodytes* and *Cinclodes* on the abundance of other species, Spearman rank correlation coefficients were estimated between the abundance of these two species and those of all other species (Kutner, Nachtsheim & Neter 2004).

STRUCTURE OF THE PASSERINE BIRD ASSEMBLAGE

The community structure of passerine assemblages was compared among islands with rats, islands historically without rats and islands in which rats have been eradicated using non-metric multidimensional scaling (NMDS; Kruskal 1964) with the Jaccard index of dissimilarity. These analyses were carried out with the R package 'vegan' v.2.0-8 (Oksanen *et al.* 2013). A vector of species abundances characterized the community structure of each island. The NMDS algorithm was allowed to use as many as 1000 random starts to select a solution with the smallest stress (McCune & Grace 2002). NMDS scores for each island were plotted in ordination space, and 95% confidence ellipses associated with the scores for each rat status were calculated. Permutational analysis of variance (PERMANOVA) was used to compare centroid values in multidimensional space (Anderson 2001; Anderson & Walsh 2013) while correcting α for multiple comparisons using a Bonferroni correction.

Results

OCCUPANCY MODELLING

For all passerines, the models in the top candidate set included effects of \log_{10} Area, RatPres and RatErad on probability of island occupancy (ψ). Habitat correlates (i.e. *Tussac* and *Graze*), weather correlates (i.e. *Cloud*, *Wind* and *Season*), and time since eradication (*Time*) did not appear in the candidate set for any species ($\Delta\text{AIC}_C > 7$). All of the models in the top candidate sets

were well supported by data as confirmed by goodness-of-fit tests ($P < 0.05$). *Cinclodes* was less likely to occur on islands in the presence of rats, and the occurrence of *Cinclodes* on eradicated islands was intermediate between its occurrence on historically rat-free and rat-infested islands (Fig. 1). Like *Cinclodes*, the occurrence of *Troglodytes* increased with area on historically rat-free islands, and most islands larger than 10 ha were occupied (Fig. 1). The contemporary and historic presence of rats was associated with the extirpation of *Troglodytes*; only a single individual of this species was detected on two islands with rats, and only a single individual was detected on a small (1 ha) eradicated island. Patterns of occupancy in *Melanoderes* and *Turdus* were similar to each other (Fig. 1). In *Sturnella* and *Muscisaxicola*, there was a strong effect of island area on occupancy, but a negligible effect size of rat status (Fig. 1). In *Sporagra*, occupancies were similar on islands with and historically without rats, and those islands had higher occupancies than eradicated islands (Fig. 1). Both *Cistothorus* and *Anthus* had higher occupancy on islands in which rats had been eradicated than on historically rat-free and rat-present islands.

RATS, ERADICATION AND SPECIES–AREA RELATIONSHIPS

Inferences on species–area relationships did not differ between analyses conducted on detected versus estimated richness (Fig. 2, Table 1). For models based on raw detections, all models in the top candidate set ($\Delta\text{AIC}_C < 7$) included the logarithm of island area ($\log_{10}\text{Area}$) and whether or not rats were present at the time of survey (RatPres). Although RatErad (i.e. whether or not rats had been successfully eradicated at the time of survey) appeared as a main effect and an element of interactions in our top model set (Table 1), the 95% CIs for estimated species richness overlapped broadly between islands historically without rats and eradicated islands over the 750 ha spanned by our sample of eradicated islands (Fig. 2). In contrast, estimated species richness was lower on islands with rats, and the CI did not overlap with the CIs for islands historically without rats and eradicated islands. Using detected species richness for the analysis produced a similar result (Table 1).

RELATIVE ABUNDANCE

The statistical effects of rat status on relative abundance differed among passerines (Fig. 3). The relative abundances of *Cinclodes*, *Troglodytes* and *Turdus* were lower on islands with rats than on historically rat-free islands. On eradicated islands, the relative abundance of *Cinclodes* fell between that of historically rat-free and that of rat-occupied islands, whereas in *Turdus*, relative abundance did not differ significantly between islands historically without rats and eradicated islands, and *Troglodytes* was largely absent from islands with rats eradicated.

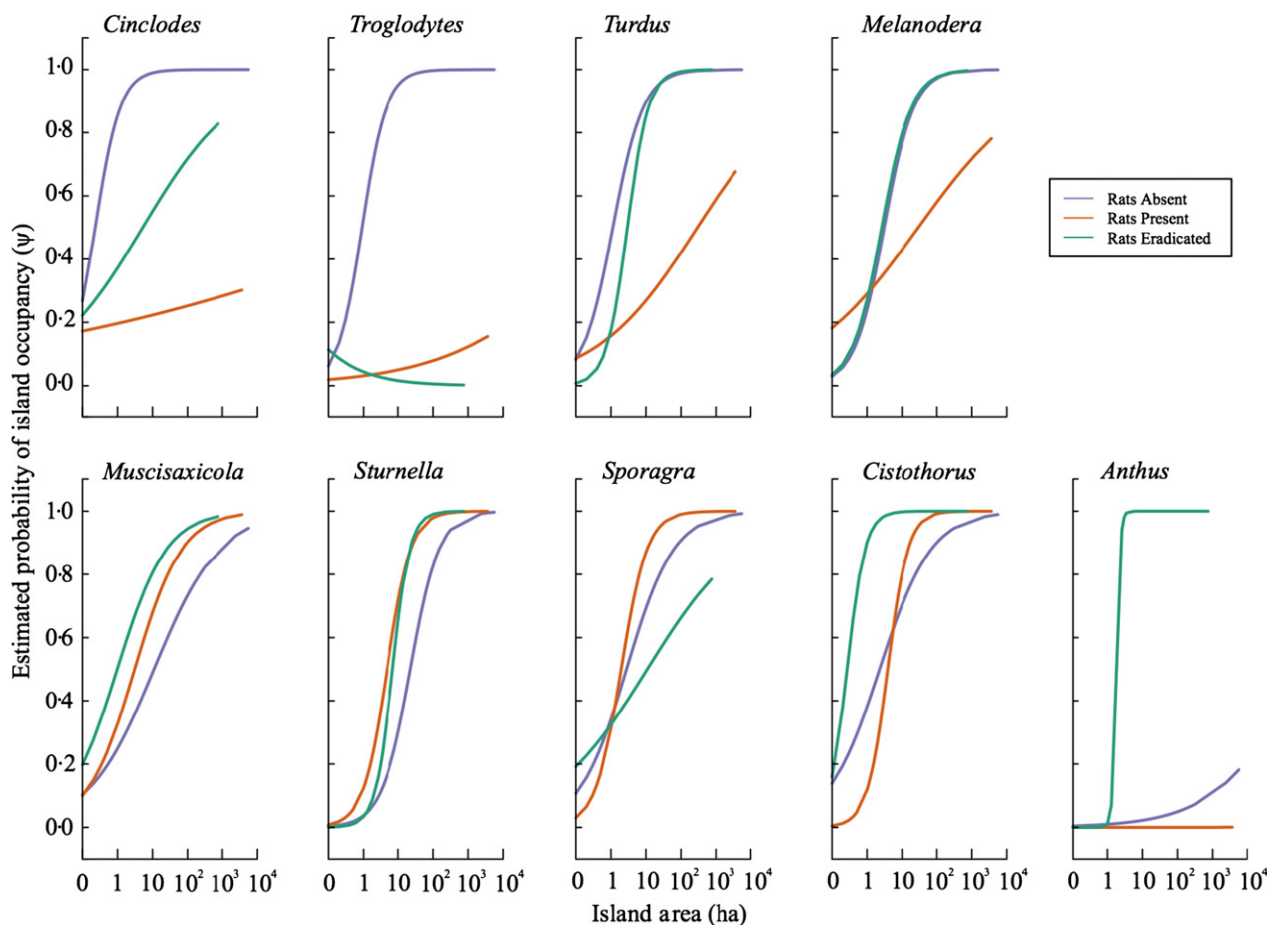


Fig. 1. Model-averaged estimates of occupancy for each species. Occupancy was estimated using a double-sampling approach and modelled based on several covariates. The significant parameters in the model for each species included the logarithm of island area and rat status.

In contrast, *Sporagra*, *Cistothorus*, *Muscisaxicola* and *Sturnella* had higher relative abundances on eradicated islands than on islands with and historically without rats. *Anthus* was detected on too few islands to allow comparison among island types.

Relative abundance did not increase with time since eradication for any species ($r_s < 0.04$, one-tailed $P > 0.1$), except for *Cinclodes*, which increased with the number of years since eradication ($r_s = 0.40$, one-tailed $P = 0.0014$). The relative abundances of *Cistothorus*, *Muscisaxicola* and *Sturnella* were negatively correlated ($r_s \leq -0.3$, one-tailed $P < 0.05$, Table S1) with that of *Cinclodes*. Similarly, the relative abundances of *Cistothorus* and *Muscisaxicola* were negatively correlated with that of *Troglodytes* ($r_s \leq -0.3$, one-tailed $P < 0.05$, Table S1).

COMMUNITY STRUCTURE

The NMDS ordination in two dimensions adequately represented data on community structure, as evidenced by low stress values (stress = 0.06, Fig. 4, Kruskal 1964). The algorithm required 21 random starts to reach a solution that minimized stress. The centroids in ordination space differed significantly (PERMANOVA $F_{2,156} = 23.91$,

$P < 0.001$). The 95% confidence ellipse for the centroid of islands historically without rats did not overlap with that of eradicated islands or that of islands with rats on NMDS axis 1 (PERMANOVA $F_{2,156} = 52.77$, $P < 0.001$), but there was broad overlap on axis 2 (PERMANOVA $F_{2,156} = 1.96$, $P > 0.1$). In contrast, the 95% confidence ellipses for the centroids of eradicated islands and islands with rats overlapped, and these centroids did not differ significantly on either of the two NMDS axes (PERMANOVA $F_{1,90} = 2.25$, $P > 0.1$). These results suggest that eradicated islands and islands with rats are more similar to each other in community structure than they are to historically rat-free islands.

Discussion

In the Falkland Islands, the species richness of passerine birds on islands with rats was lower than on islands historically without rats and on islands from which rats had been eradicated. Islands historically without rats and eradicated islands had similar numbers of passerine species, suggesting that species richness is resilient following the eradication of invasive rats. In spite of this result, eradicated islands and islands with rats exhibited more

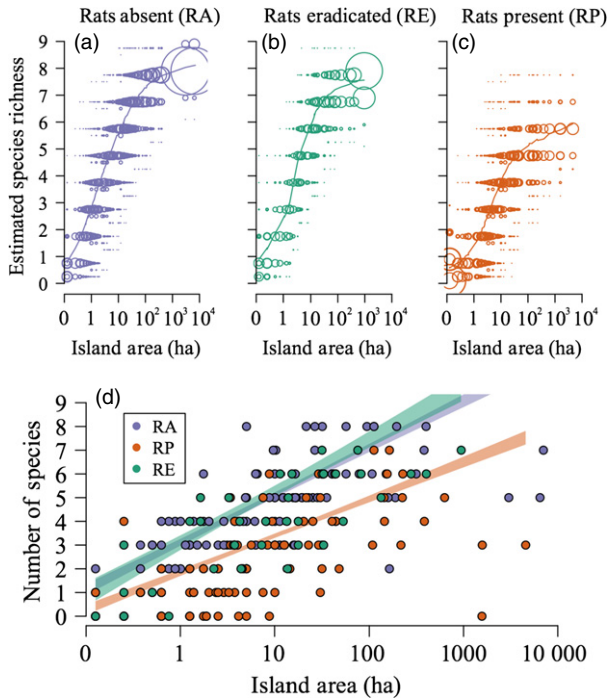


Fig. 2. Species–area relationship. Panels a, b and c show output from 1000 simulations of species richness for each island. Bubble size in a, b and c is proportional to the number of simulations with that number of species, and curves connect mean estimated species-richness values for each island. Shaded polygons in d represent 95% confidence intervals for generalized linear models relating estimated species richness and area for islands with and without rats, and islands in which rats were eradicated. Points in d represent the number of species detected on islands of a given size.

Table 1. Top candidate models for both estimated species richness (S) and detected S. Models were ranked based on AIC_C scores

	AIC _C	ΔAIC _C	w _i
Parameters in model (for estimated S)			
RatPres, RatErad, Log ₁₀ Area, Log ₁₀ Area * RatPres, Log ₁₀ Area * RatErad	380.71	0	0.65
RatPres, Log ₁₀ Area, Log ₁₀ Area * RatPres	381.91	1.2	0.35
Parameters in model (for detected S)			
RatPres, Log ₁₀ Area, Log ₁₀ Area * RatPres	847.43	0	0.49
RatPres, RatErad, Log ₁₀ Area, Log ₁₀ Area * RatPres, Log ₁₀ Area * RatErad	848.26	0.83	0.32
RatPres, Log ₁₀ Area	849.4	1.97	0.18

For both estimated and detected S, predictors in the best models included whether or not rats were present (RatPres), whether or not rats had been successfully eradicated at the time of survey (RatErad) and the logarithm of island area (Log₁₀Area).

similar community structures in comparison with islands in which rats have been historically absent. In the relatively short span of time since rats have been eradicated

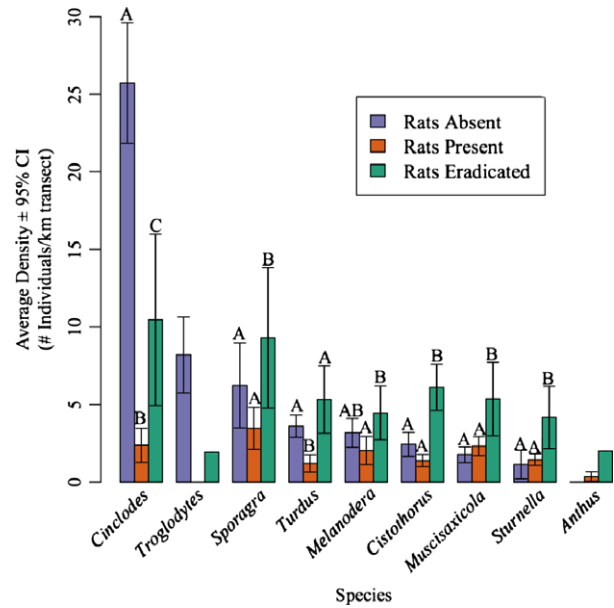


Fig. 3. Relative abundance distribution for different rat statuses. Bars are means, error bars represent 95% CIs, and different letters above bars represent means that differed significantly. *Troglodytes* and *Anthus* were detected on too few islands in one of the rat statuses to allow statistical analyses.

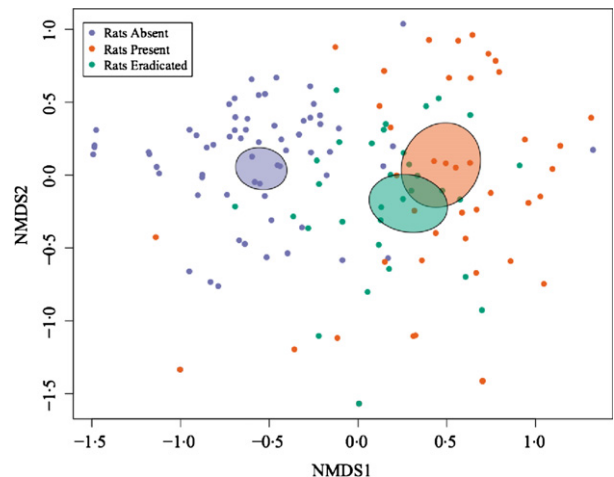


Fig. 4. Community structure using non-metric multidimensional scaling (NMDS). Ellipses represent 95% confidence estimates for mean NMDS scores.

in the Falklands, eradications do not seem to have been accompanied by a return to the passerine community structure of historically rat-free islands. The difference in structure between eradicated and historically rat-free islands can partially be explained by the two most prevalent and abundant species (*Troglodytes* and *Cinclodes*) on historically rat-free islands. Our results suggested that *Troglodytes* does not recolonize eradicated islands rapidly and that the abundance and occurrence of *Cinclodes* on eradicated islands was lower than on historically rat-free islands. Here we discuss hypotheses that can potentially explain the recovery in species richness following rat

eradication despite differences in community structure compared to historically rat-free islands. We conclude by inferring that eradications in the Falkland Islands appear to be an effective means of restoring native species richness, although their benefit to species of conservation concern is less clear. For some species of conservation concern, eradication is a necessary condition for conservation success, but not a sufficient one. Additional interventions may be necessary for such species.

RAT ERADICATION AND SPECIES RICHNESS

As expected from classic island biogeography theory (MacArthur & Wilson 1967), species richness of passerines increased with island area in the Falklands (Fig. 2). For a given island size, there were fewer species on islands with rats than on islands without them (i.e. historically rat-free islands and eradicated islands). The species richness of passerines on eradicated islands was similar to that of islands that have been free of rats historically. This result is surprising because the two most abundant and prevalent species on historically rat-free islands, *Troglodytes* and *Cinclodes*, occurred much less frequently and at greatly reduced abundances on eradicated islands (Figs 1 and 3). Therefore, the resilience of species richness to rat eradication is not due to the recovery of the two species that rats affect most severely. Instead, it appears to be the result of higher frequency of occupancy of other species on eradicated islands relative to islands without rats (Fig. 1).

We hypothesized that when *Troglodytes* and *Cinclodes* are present, they reduce the ability of other species to colonize and establish and hence the abundance and occupancy of other passerines. Therefore, we predicted that passerines other than *Troglodytes* and *Cinclodes* would have higher occupancy and abundance on eradicated islands than on islands historically without rats. In support of this hypothesis, we found that four species (*Cistothorus*, *Anthus*, *Sturnella* and *Muscisaxicola*) occupied more eradicated than historically rat-free islands (Fig. 1). Three of these species (*Cistothorus*, *Sturnella* and *Muscisaxicola*) also had higher relative abundance on eradicated islands than on both rat-free and rat-occupied islands (Fig. 3). We hypothesized that the occurrence and abundance of these species was higher on eradicated islands as a consequence of the absence and/or relatively low abundance of *Cinclodes* and *Troglodytes*. In tentative support of this hypothesis, we found that the relative abundance of *Cistothorus* and *Muscisaxicola* was negatively correlated with the abundance of *Cinclodes* and *Troglodytes* and the relative abundance of *Sturnella* was negatively correlated with that of *Cinclodes* (Table S1). Our results suggest that *Cinclodes* and *Troglodytes* are strong competitors that reduce both the probability of colonization and the abundance of several other species.

Our inferences must be qualified by the observation that our data are only quasi-experimental (*sensu* DiNardo

2008), rather than truly experimental (Connor & Simberloff 1986), because islands were not assigned at random to treatments. A similar quasi-experimental approach was used by Hejda, Pyšek & Jarošík (2009) to assess the impact of invasive plants on the species richness of invaded communities, and by Hulme & Bremner (2006) to evaluate the consequences of removal of invasive species on native richness. Several additional quasi-experimental approaches have been employed using removal of exotic species (Donlan, Tershy & Croll 2002; Mulder *et al.* 2009, 2011). Although the associations identified by quasi-experiments meet some requirements of causality, and outcomes can be shown to vary statistically with an intervention, statistical associations do not imply causal association (Shadish & Heinsman 1997). Therefore, we emphasize the provisional nature of our inference and offer three predictions that, if confirmed, would support our *post-hoc* hypothesis that *Cinclodes* and *Troglodytes* competitively suppress the occurrence and abundance of other native passerines.

First, *Cinclodes* was not detected on 17 out of 37 eradicated islands, its abundance was lower on eradicated islands than on historically rat-free islands and it was positively correlated with time since eradication. If our hypothesis is correct, the abundance and occupancy of *Cinclodes* should continue to increase with time since eradication, and the occupancy and abundance of *Cistothorus*, *Sturnella* and *Muscisaxicola* will decrease on eradicated islands. Secondly, *Troglodytes* was only detected on a very small fraction of eradicated islands (1 out of 37) suggesting poor dispersal and hence limited ability to colonize eradicated islands. *Troglodytes* appears to be mostly extirpated from islands where rats are present. If *Troglodytes* are re-established (either by reintroduction or by natural dispersal) on eradicated islands, we predict a decrease in the occurrence and abundance of *Cistothorus* and *Muscisaxicola*. Thirdly, we predict differences in habitat and resource use in *Cistothorus*, *Sturnella* and *Muscisaxicola* on islands with and without *Cinclodes* and *Troglodytes*. (While we did not find island habitat covariates to be important in predicting the distribution of these species, it is possible that they shift to different habitats on the same island in the presence of competitors.) For example, Woods & Otley (2008) report that *Cistothorus* can be observed foraging on boulder beaches, *Troglodytes*' preferred habitat, on eradicated islands. On historically rat-free islands where both species are present, *Cistothorus* do not frequent *Troglodytes*-occupied boulder beaches (field observations).

RESISTANCE, RESILIENCE, HOMEOSTASIS AND COMPENSATION IN ISLAND PASSERINE BIRD ASSEMBLAGES

Passerine bird assemblages in the Falkland Islands seem to be sensitive (or non-resistant) to the introduction of rats (Hall *et al.* 2002), exhibiting depressed richness and a

distinct community structure from historically rat-free islands. Tabak *et al.* (2014a) found that the two most dominant species in the absence of rats (*Cinclodes* and *Troglodytes*) experienced reduced abundance and distribution in the presence of rats. They argued that the large effects of rats on these two species drove differences in community structure (Tabak *et al.* 2014a). Analyses on islands in which rats were eradicated both complement and enrich this interpretation. These analyses suggest that species richness is a resilient characteristic of these island passerine bird assemblages, whereas community structure is not. Our analyses also hint at the importance of *Troglodytes* and *Cinclodes* for evaluating the resilience in species richness and community structure. Although our results are broadly consistent with the notions of ecological homeostasis (Brown *et al.* 2001) and with the hypothesis of compensation as the process that 'regulates' species richness (Goheen *et al.* 2005), the details of our approach differ from those of previous studies.

According to the compensation hypothesis, the maintenance of relatively constant species richness requires that colonization events counterbalance extinction (Lekve *et al.* 2002). If species richness falls below the equilibrium number of species, the probability of colonization increases. Conversely, if local richness is above this equilibrium, then extinction should increase (Goheen *et al.* 2005, 2006). Consequently, most of the evidence in favour of (or against) the compensation hypothesis has been obtained from the analysis of temporal dynamics of species richness that document relatively constant species richness due to counterbalancing colonization and extinction (Brown *et al.* 2001). In contrast, our analyses relied on a spatially replicated quasi-experiment (DiNardo 2008) on islands with well-defined boundaries and in which we estimated the effect of an external factor (the presence of rats) on a response variable (species richness) and then measured the magnitude of this response variable after this factor was removed (rat eradication).

Brown *et al.* (2001) emphasized that their hypotheses on the homeostasis of species richness were more likely to apply to open systems than to systems that are dispersal-limited and isolated by an inhospitable matrix. They contended that islands should have weak diversity-regulating forces and should often be far from species-richness equilibrium (Brown *et al.* 2001; Sax, Gaines & Brown 2002). In the light of this observation, the resilience of species richness to rat eradication may seem surprising. The passerine avifauna that inhabits the islands in the Falkland archipelago may represent an intermediate situation between a completely unbounded system and one in which colonization is limited by a dispersal barrier. Because islands in the Falklands are relatively close to each other, there seems to be relatively free exchange of species, so that species richness is not limited by colonization. There are three notable exceptions to the seemingly free exchange of animals between islands. Two of the exceptions are passerines: *Troglodytes*, which seems to

have very limited dispersal ability (Woods & Otley 2008); and *Cinclodes*, which seems to colonize and thus occupy eradicated islands at lower rates than other species (Fig. 1). The third exception appears to be rats, which are unable to colonize islands that are farther than about 1000 m away from a rat source (Tabak *et al.* in press).

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

The apparent outcomes of rat eradication in the Falkland Islands have potential implications for passerine conservation practice. These implications are best highlighted by the alternative metrics chosen to evaluate the eradications' consequences and hence their success. In spite of the relatively short time elapsed since eradication (1–11 years), species richness on eradicated islands was very similar to that of historically rat-free islands. The rapid recovery of species richness of passerines is likely the consequence of compensatory colonization from a regional species pool in which many, albeit not all, species can disperse readily among islands. From this perspective, rat eradications in the Falklands have been successful, even after a remarkably short time (Crooks 2005; Strayer *et al.* 2006; Bodey *et al.* 2011). Species richness, however, is only one of many metrics with which we can evaluate the effectiveness of eradications as a conservation strategy. Another metric is the effectiveness of eradications in protecting species of conservation concern, such as *Troglodytes* and *Cinclodes* (Courchamp *et al.* 2011). Indeed, one motivation for the eradication of rats in the Falkland Islands is to secure and increase the current population of these two species, especially of *Troglodytes* (Woods & Otley 2008).

From this perspective, the success of rat eradications in the Falklands is modest, but translocations might be an effective tool to meet the original conservation objectives. In the relatively short time since eradication, *Troglodytes* has not yet established breeding populations on any of the eradicated islands. Woods & Otley (2008) characterize *Troglodytes* as weak and reluctant fliers (i.e. poor dispersers). *Cinclodes* appear to be better at dispersing onto and establishing breeding populations on eradicated islands, although the occupancy and relative abundance of this species on these islands remain lower than those on historically rat-free islands (Figs 1 and 3). Additionally, *Cinclodes*' relative abundance increases with time since eradication, suggesting that this species will become more widely established on eradicated islands in the future. When a vulnerable species has failed to recolonize following invasive species eradication in other archipelagoes, conservation managers have conducted translocations to eradicated islands with the purpose of either increasing population numbers and/or re-establishing a population extirpated by exotics (Carlile, Priddel & Madeiros 2012). In New Zealand, translocation of threatened bird species to offshore islands has become a common practice

(Atkinson 2001). For example, the Little Spotted Kiwi (*Apteryx owenii*), while previously widespread, had only a small, remnant population on one island before translocations lead to viable populations of this species on five offshore islands (Colbourne & Robertson 1997). The combination of endemism, seemingly limited dispersal, and vulnerability to extinction makes *Troglodytes* a good candidate for experimental translocation with the intent of re-establishing populations on eradicated islands (Woods & Otley 2008; Seddon *et al.* 2014). It is possible that given enough time, this species can recolonize eradicated islands on its own. However, reintroduction can hasten the goals of securing current *Troglodytes* populations and increasing its distribution in the Falklands (Woods & Otley 2008).

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.dj524> (Tabak *et al.* 2014b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Spearman rank correlation coefficient (r_s) among species abundances for each species and *Cinclodes* and *Troglodytes* ($n = 230$ islands).