Recovery of both a mesopredator and prey in an insular ecosystem after the eradication of rodents: a preliminary study

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Abstract   There is growing evidence that rodent eradication often enables the substantial recovery of native species. However, most previous studies have focused on the recovery of conspicuous and charismatic species directly affected by rodents. We examined the responses of the terrestrial ecosystem of Surprise Island, New Caledonia to the eradication of invasive ship rats (*Rattus rattus*) and mice (*Mus musculus*) in 2005. Communities of invertebrates and skinks were compared before and after rodent eradication. Because skinks are prey for rodents and are predators of invertebrates (i.e., mesopredators), we were concerned that rodent eradication would induce mesopredator release (i.e., invertebrates would decrease because of increased skink abundance). Our results showed that skink abundance increased, but counter to our expectations, the abundances of most invertebrates also increased or were not affected. The negative indirect effects of skink abundance on the invertebrate community were likely overcome by both the decreased direct effect of rodent predation and the positive indirect effects of recoveries of other organisms. These included seabirds, which provide resource inputs from the sea and vegetation. These results highlight that increased mesopredator abundance does not always exert negative effects on native ecosystems, and while these changes are important to consider, they should not be the sole reason for renouncing the benefits of eradicating alien predators.

Keywords: Rat, mouse, mesopredator release, indirect effects, top-down effects, bottom-up effects, surprise effect, seabirds, vegetation

INTRODUCTION

Over the past decade, successful eradications of introduced rats (*Rattus* spp.) and mice (*Mus musculus*) have increasingly been reported from islands worldwide (Howald *et al.* 2007). Rodent eradication generally results in the substantial recovery of native species (Towns *et al.* 2006; Howald *et al.* 2007) and is now recognised as a useful restoration tool for island ecosystems (Howald *et al.* 2007). Most previous eradication studies have focused on the recovery of conspicuous and charismatic species such as seabirds and vegetation (Caut *et al.* 2009; Mulder *et al.* 2009). Most of these have examined the direct effects of rodent predation, even though rodents can also affect native species in other ways (e.g., Towns 2009). Therefore, it is important to assess other native groups, such as the invertebrate community, which can have important functions in recipient ecosystems. Moreover, these organisms should be assessed within a community-wide context, as the invertebrate community may not only be affected by direct predation but also by less obvious indirect effects (Fukami *et al.* 2006; Watari *et al.* 2008; Norbury *et al.* 2009; Towns *et al.* 2009). For example, on Amami-Ōshima Island, Japan, the introduced mongoose *Herpestes auropunctatus* has nearly extirpated frogs and skinks by direct predation, resulting in an increase in several insect species that were preyed upon more heavily by frogs and skinks than by the mongoose (Watari *et al.* 2008).

One indirect effect of invasive species eradications can be unexpected population explosions of suppressed species, leading to adverse effects on native ecosystems (Courchamp *et al.* 2003; Zavaleta *et al.* 2001). Examples include introduced mesopredator or herbivore release after invasive predator eradication (Bergstrom *et al.* 2009; Courchamp *et al.* 1999; Rayner *et al.* 2007; Ritchie and Johnson, 2009), and invasive plant explosions after invasive herbivore eradication (Kessler 2001; Kessler 2011; West and Havell 2011). In recent years, such "surprise effects" have raised awareness of the importance of long-term monitoring and an ecosystem-wide perspective during eradication efforts (Simberloff 2001). However, studies that consider these factors are rare.

In the present study, we examined the preliminary results of a long-term project on Surprise Island, New Caledonia. We eradicated the ship rat (*Rattus rattus*) and mouse population on this island by poisoning in 2005 and monitored the entire ecosystem, specifically targeting seabirds, sea turtles, lizards , invertebrates, and vegetation before and after the eradication (Caut *et al.* 2009; Courchamp *et al.* 2011). Rodents can affect lizard populations as well as the invertebrate community (Towns *et al.* 2006). Our preliminary analysis of stomach contents of skinks on Surprise Island indicated that skinks prey on terrestrial invertebrates such as insects, spiders, isopods, and land snails (Watari *et al.* unpublished data). We thus expected that the eradication of rodents would be followed by an increase in the abundance of skinks (a mesopredator) with a concomitant decline in the mesopredator's prey of terrestrial invertebrates, whereas there would be no effect on flying insects that are less vulnerable to skink predation. We analysed the results of skink and invertebrate abundances, with special attention to this potential "surprise effect".

MATERIALS AND METHODS

Study site

Surprise Island (Fig. 1), on the D'Entrecasteaux Reefs 230 km north of the main island of New Caledonia, is 24 ha in area and reaches 9 m elevation. Habitats on the island include a central open patch (the "plain") with bare ground and patches of various herbaceous plant species (e.g., Graminae, Compositae, and Portulaceae) surrounded by woody vegetation dominated by *Argusia argentea* Heine, *Suriana maritima* Arnott, *Scaevola sericea* Gaertn and *Pisonia grandis* Brown (Caut *et al.* 2008, 2009; Fig. 1).

Surprise Island provides refuge for 14 species of seabird, 10 of which breed on the island. Ship rats and house mice were probably introduced to Surprise Island during guano mining in the late 19th to the early 20th century, and/or in the late 20th century, when an automatic meteorological station was established. Two species of terrestrial reptiles were also likely introduced to the island: a New Caledonian
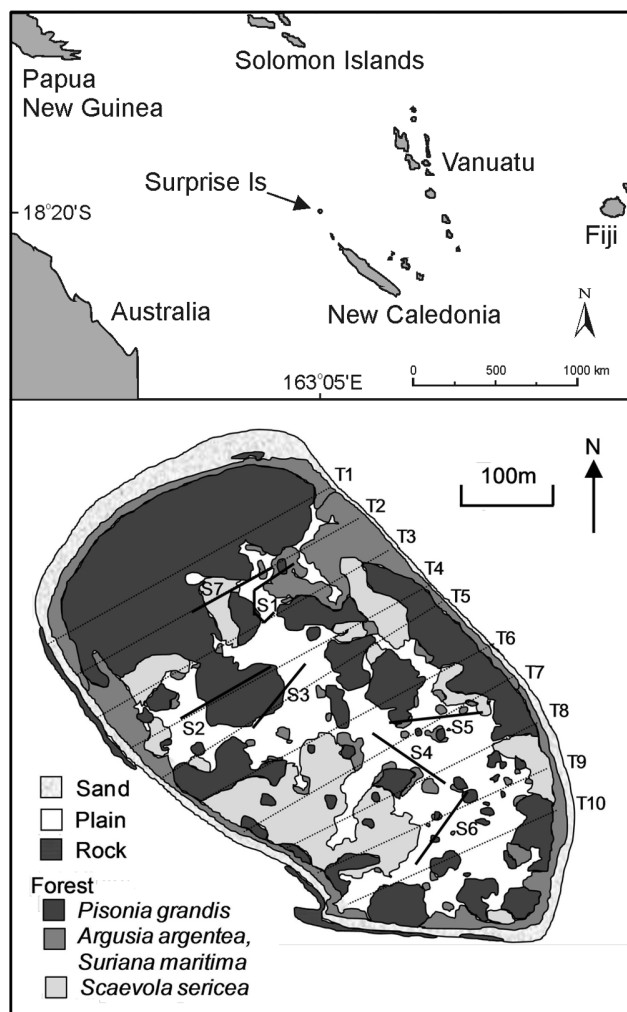
Fig. 1 Surprise Island and its four major distinct habitats of open sand flat and three vegetation types (modified from Caut *et al.* 2009). T1–T10 indicate invertebrate transects. S1–S7 indicate skink transects.

skink (*Caledoniscincus haplorhinus*), and a non-native gecko (*Lepidodactylus lugubris*) (Caut *et al.* 2009).

Rats and mice are assumed to have been eradicated, as none have been detected since 2006 following the application of rodenticide in 2005, despite trapping and hair trap surveys for four years (Caut *et al.* 2009, Courchamp *et al.* unpublished data).

Assessing animal communities

We compared the community composition four years before rodent eradication (2002–2005 for the skink and 2003 for invertebrates) and four years after the eradication (2006–2009 for both the skink and invertebrates). Surveys were conducted in November and December of each year (Caut *et al.* 2009).

For the estimates of skink abundance, we established seven 100 m transects in the main habitat unit (Fig. 1), along which we counted the number of skinks within a 2 m width during 15 minute walks. The transects were located in the plain and *Pisonia grandis* patches, as the dense vegetation in the other forest patches, such as *Augusia argentea*, *Suriana maritima*, and *Scaevola sericea*, made it difficult to conduct lizard surveys (Caut *et al.* 2009; Fig. 1). Surveys were conducted between 12:00–15:00 hours on

three separate days per visit. As some transects traversed plain and forest vegetation types, each transect was also divided into four 25 m-long sub-transects, for which the number of skinks and major vegetation types were recorded. We also recorded the weather conditions (sunny or not sunny), which were likely to affect skink activity.

To collect invertebrate samples, we used yellow surface traps ($20 \times 20 \times 10$ cm) primarily for flying insects as well as pitfall traps (10 cm diameter $\times$ 15 cm height) mainly for ground-dwelling invertebrates. All traps were partially filled with soapy water and set along the 10 transects across the island, spaced 50 m apart to maintain independence between traps (Fig. 1). Together, the transects covered a total of about 3000 m, covering all habitats on the island. Arthropod traps were deployed one time per visit over 48 h in 2003 and 2006 and over 24 h in 2007–2009 (surface traps every 75 m and pitfall traps every 50 m; Fig. 1). Trapped invertebrates were stored in 70% alcohol until identification in the laboratory. We analysed data from 20 surface traps and 29 pitfall traps from 2003 (before eradication) and 38 surface traps and 60 pitfall traps from 2006–2009 (after eradication). Invertebrates with lengths >3 mm were assume to be in the size range of skink prey and were included in analyses, but ant samples were excluded, as a separate analysis was conducted for ant populations (Cerda pers. comm.).

Statistical analyses

To examine the effect of rodent eradication on the skink population, we used a generalised linear mixed-effect model (GLMM) with Poisson distribution (Faraway, 2006) using R (R Development Core Team, 2007) with the lme4 package (Douglas 2007). We used the number of skinks observed along each 25-m sub-transect (*Skink*). Because there may be a time lag for numerical responses of skinks to dynamics of the rodent populations (Schmidt and Ostfeld 2003), we assumed either no delay, a 1-year delay, or a 2-year delay to the effect of rodent eradication. Presence and absence of rodents was assigned values of 0, 1 in either the year of (*Eradication*$_{year+0}$), 1 year before (*Eradication*$_{year-1}$), or 2 years before (*Eradication*$_{year-2}$) the actual skink field surveys as explanatory variables. The effect of vegetation type (*Vegetation*; forest and plain: 0, 1), and their interaction (*Eradication* $\times$ *Vegetation*) were also included in the model as fixed factors, because the strength of top-down effects may vary in different environments (Towns *et al.* 2003; Rayner *et al.* 2007; Ritchie and Johnson 2009). We also included *survey-day*, *survey-year*, *transect*, *sub-transect*, and *weather* (sunny or non-sunny) as random factors, all of which may affect the number of observed skinks. Based on Akaike's Information Criterion (AIC) values, we conducted model selection among the models with all possible combinations of factors.

To examine the effects of rodent eradication on the community composition of invertebrates, we conducted two separate redundancy analyses (RDAs) for the samples caught in surface and pitfall traps. In these analyses, the capture rate of each species per trap-night was used as the response variable, and both *Eradication* (before and after rodent eradication: 0, 1) and *Vegetation* (forest and plain: 0, 1) were included as explanatory variables. Among the three types of forest patches (Caut *et al.* 2009; Fig. 1), we analysed data from the patches of *Pisonia grandis* in the preliminary study. Unfortunately, because we lack replication in the year before eradication (i.e., we only have before-eradication data from 2003), we did not consider the effect of the survey year. In the RDAs, the significance of each explanatory variable was tested using comparisons to Monte Carlo permutations with 999 iterations. All RDAs

and permutation tests were performed using CANOCO for Windows, version 4.5.

To illustrate the patterns of the response of each species to rodent eradication (when *Eradication* was detected as a significant factor), another RDA was conducted using *Eradication* and *Vegetation* as fixed and random factors, respectively, from which species scores on the first axis could be considered characteristics of species response to rodent eradication (Leps and Smilauer 2003).

RESULTS

Skink population

The abundances of skinks observed in the transect surveys from 2002 to 2009 increased substantially after rodent eradication (Fig. 2). The model 1 with *Eradication*$_{year-1}$, *Vegetation*, and *Eradication*$_{year-1}$ × *Vegetation* as the explanatory variables was clearly superior to the other models (ΔAIC of all the other models > 2) (Table 1).

Invertebrate community

We collected at least 40 taxa of invertebrates in surface traps and 35 species in pitfall traps, covering a total of 13 orders (Table 2). The surface traps more frequently captured a greater diversity of invertebrates (e.g., Diptera, Hemiptera, and Hymenoptera) than did the pitfall traps (Table 2). Based on the Monte Carlo permutation tests of RDA ordinations (Fig. 3), an effect of rat and mouse eradication was not detected in the invertebrate community caught in surface traps but was significant among invertebrates collected in pitfall traps (surface trap: $\lambda = 0.019$, $F = 1.093$, $P = 0.316$, Fig. 3a; pitfall traps: $\lambda = 0.094$,

$F = 9.126$, $P = 0.001$, Fig. 3b). The effect of vegetation on invertebrate community composition was significant in surface traps and was marginal in pitfall traps (surface trap: $\lambda = 0.047$, $F = 2.791$, $P = 0.018$, Fig. 3a; pitfall traps: $\lambda = 0.026$, $F = 2.555$, $P = 0.062$, Fig. 3b). The RDA ordination diagram with vegetation type as a random (v fixed) factor is presented in Figure 3c. RDA scores of the 12 species with sufficient sample sizes (frequency of occurrence > 0.1; Table 2) obtained from Fig. 3c and summarised in Fig. 4 identified nine species with negative coefficients (i.e., directing toward the *Eradication* axis in Fig. 3c), indicating that they were positively affected by rodent eradication.
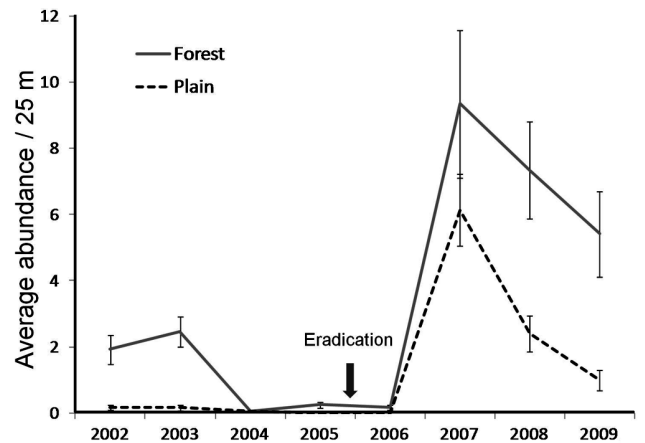

Fig. 2 Average abundance of skinks (± SE) observed in 25 m sub-transects.

Table 1 The GLMM models explaining skink abundance and their AIC values. All models include *survey-day*, *survey-year*, *transect*, *sub-transect*, and *weather* as random factors.

Model	Combination of explanatory Variables	Estimate	SE	AIC	ΔAIC	deviance
1	*Eradication*$_{year-1}$	1.9536	0.7994	1011	-	992.8
	Vegetation	-2.0106	0.3130			
	Eradication$_{year-1}$ × *Vegetation*	1.6228	0.2411			
2	*Eradication*$_{year-0}$	0.8036	1.0695	1020	9	1002
	Vegetation	-1.9732	0.3135			
	Eradication$_{year-0}$ × *Vegetation*	1.5800	0.2416			
3	*Eradication*$_{year-2}$	2.3085	1.1077	1043	32	1025
	Vegetation	-0.2475	0.2210			
	Eradication$_{year-2}$ × *Vegetation*	-0.6608	0.1207			
4	*Eradication*$_{year-1}$	2.4517	0.7982	1068	57	1052
	Vegetation	-0.5170	0.2151			
5	*Eradication*$_{year-1}$	2.4479	0.7991	1071	60	1057
6	*Vegetation*	-0.5159	0.2152	1072	61	1058
7	*Eradication*$_{year-2}$	2.0187	1.1074	1072	61	1056
	Vegetation	-0.5163	0.2152			
8	*Eradication*$_{year-0}$	1.2927	1.0682	1073	62	1057
	Vegetation	-0.5161	0.2152			
9	*Null Model*	-	-	1075	64	1063
10	*Eradication*$_{year-2}$	2.016	1.108	1075	64	1061
11	*Eradication*$_{year-0}$	1.290	1.069	1076	65	1058

Table 2 Frequency of occurrence of invertebrate species per trap (FO).

Species	ID*	FO in surface traps[1]	FO in pitfall traps[2]	Species	ID*	FO in surface traps[1]	FO in pitfall traps[2]
BLATTODEA				HYMENOPTERA			
Blaberidae sp.	1	0.052	0.017	Ichneumonidae sp.	28	0.026	-
Blattidae sp.	2	0.181	0.067	Halictidae sp.	29	0.026	-
COLEOPTERA				Platygasteridae sp.	30	0.155	-
Coleoptera sp.1	3	-	0.044	Pteromalidae sp.	31	-	0.011
Chrysomelidae sp.	4	0.034	-	LEPIDOPTERA			
Coccinellidae sp.	5	0.009	-	Geometridae sp.	32	0.052	0.006
Curculionidae spp.	6	0.241	0.111	Lepidoptera sp.1	33	0.034	0.011
Tenebrionidae sp.	7	0.009	0.244	Lepidoptera sp.2	34	2.095	0.128
Coleoptera sp.2	8	-	0.006	Lepidoptera sp.3 larvae	35	0.043	0.811
Coleoptera sp.3	9	-	0.011	Sphingidae sp.	36	0.328	0.011
DERMAPTERA				Lepidoptera sp.4	37	-	0.006
Forficulidae sp.	10	-	0.206	Sphingidae sp. larvae	38	0.017	-
DIPTERA				Lepidoptera sp.5	39	0.052	-
Drosophilidae sp.	11	0.017	0.006	Lepidoptera sp.6	40	0.017	-
Asilidae sp.	12	0.043	-	ORTHOPTERA			
Stratiomyidae sp.	13	0.034	-	Acrididae sp.	41	0.078	0.083
Tachinidae sp.	14	0.103	0.006	Gryllidae sp.	42	0.164	0.006
Diptera sp.	15	-	0.011	Mogoplistidae sp.	43	0.052	-
Pipunclidae sp.	16	0.19	-	ISOPODA			
Dolichopodidae sp.	17	0.396	-	Isopoda sp.1	44	-	0.4
Therevidae sp.	18	0.017	-	Isopoda sp.2	45	0.5	14.38
EMBIIDINA				Armadillidae sp.	46	0.017	1.767
Oligotomidae sp.	19	0.052	0.117	ARANEAE			
HEMIPTERA				Araneae sp.1	47	0.069	0.106
Anthocoridae sp.	20	0.112	0.011	Heteropodidae sp.	48	-	0.022
Cicadellidae spp.	21	2.043	0.628	Araneae sp.2	49	0.026	-
Delphacidae spp.	22	0.034	-	Lycosidae sp.	50	-	0.017
Eurymelidae sp.	23	0.043	0.028	Araneidae sp.	51	-	0.011
Cydnidae sp.	24	-	0.033	PULMONATA			
Hemiptera sp.1	25	0.052	-	Pulmonata sp.	52	-	0.194
Hemiptera sp.2	26	0.043	-	DECAPODA			
Hemiptera sp.3	27	0.121	0.044	Paguroidea	53	-	0.022
				Unidentified larvae	54	0.06	-

*: IDs are used for Fig. 3a, b, c

DISCUSSION

Our results indicate that rodent eradication positively affected populations of skinks and terrestrial invertebrates, but did not affect flying insects. However, a closer examination of the data provides a slightly more complex picture.

The GLMM model with *Eradication*$_{year-1}$ as the response variable was selected as the best model, indicating that the response of skinks to eradication was observed with a 1-year time lag. Similar delayed responses to predator abundance have been reported for songbirds with varying predator pressure on eggs and chicks (Schmidt and Ostfeld 2003). Rodents may also primarily consume the eggs or juveniles of the skink, leading to the observed delayed response, although we lack observations of such events. There are some indications that tuatara (*Sphenodon punctatus*), an endemic reptile of New Zealand, is suppressed by the rats through predation of eggs or juveniles (Towns *et al.* 2006), although the tuatara is considerably larger than *C.*

haplorhinus. Another possibility is that recovery of the skink population lagged behind recovery of its food or habitat (i.e., invertebrates and vegetation). Further studies are needed to reveal the above processes. Although skink counts seemed to decrease after 2007 (Fig. 2), this might not have been caused by a decrease in the skink population, but by changes in skink detectability because of weather conditions. To test for this, we incorporated weather into the GLMM as a random factor. There were 2 and 1 days with non-sunny weather during the three surveys in 2007 and 2008, respectively; more skinks were observed on these days than on sunny days. Indeed, the average (± SE) numbers of skinks per 25-m sub-transect in 2007–2008 under sunny and non-sunny days were 3.67 (± 0.67) and 13.0 (± 2.20) in forest patches, and 0.88 (± 0.24) and 7.80 (± 1.10) in plain patches.

These results indicate that skinks were observed more frequently in forest patches and that their abundance increased in both forest and plain patches after rodent
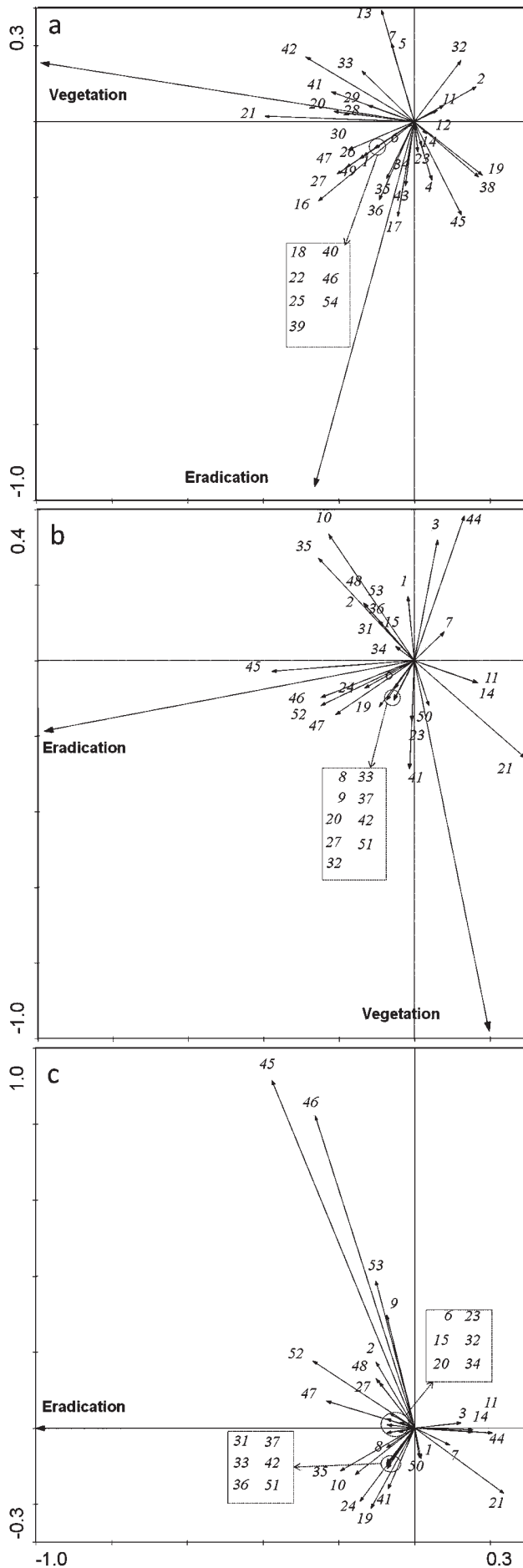
Fig. 3 RDA ordination diagrams of invertebrate community caught by a) surface traps, b) pitfall traps, and c) pitfall traps with the effect of vegetation type as a random factor. Numbers represent the ID of each species from Table 2. The horizontal and vertical axes are the first and the second RDA axes respectively. Species arrows directing toward the *Vegetation* and *Eradication* show that the species frequently occurred at the plain (vs. forest) and after eradication (vs. before eradication), respectively. For example, Fig. 3b indicates that species 21 occurs more frequently either at the plain patches or before eradication.
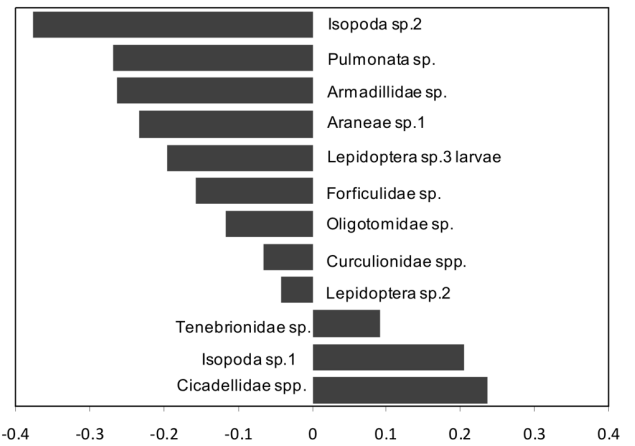
Fig. 4 RDA scores of 12 major species plotted against the first (horizontal) axis of Fig. 3c. Species with positive and negative RDA scores (i.e. species arrows directing away from, and toward the *Eradication* in Fig. 3c) indicate decreasing and increasing patterns following rodent eradication.

eradication. However, the extent to which skinks increased depended on vegetation type, with a greater increase in plain patches than in forest patches. This pattern can be explained by the positive relationship between skink abundance and vegetation ground cover (Norbury *et al.* 2009). Although ground vegetation at the study site has recovered since rodent eradication in both forest and plain patches (Courchamp *et al.* 2011, unpublished data), vegetation cover has also increased in areas that were once bare ground (Courchamp *et al.* unpublished data), likely leading to stronger bottom-up effects on the skink population.

We did not observe our predicted "surprise effects," where invertebrate abundance declined after rodent eradication, despite the expected increase in skink (mesopredator) abundance. In fact, ground-dwelling invertebrates from pitfall traps increased in abundance after rodent eradication, whereas the flying insects in surface traps showed a neutral response to the eradication. Therefore, the invertebrate communities generally benefited from the removal of their top predators (rodents), despite the increased abundance of their mesopredator (skinks). To thoroughly examine the effects of rodent eradication, we compared invertebrate community structure between years before and after rodent eradication. However, caution is required when interpreting such differences in invertebrate community composition, as they are likely to be caused not only by a balance of top-down predation effects between rodents and skinks, but also by other indirect effects. Furthermore, vegetation (food and habitat

resource) and seabirds (resource input from the sea) have clearly recovered since the rodent eradication on Surprise Island (Courchamp *et al.* 2011, unpublished data), which could, in turn, exert bottom-up effects on the invertebrate community (Fig. 5; Fukami *et al.* 2006; Norbury *et al.* 2009; Towns *et al.* 2009). How these responses might be induced requires further examination. In summary, any negative indirect effects of increased skink abundance (mesopredator increase) on the invertebrate community were likely overcome by the sum of the decreased direct effect of rodent predation and the positive indirect effects of the recoveries of seabirds with increased nutrient input and vegetation through decreased rodent consumption (Fig. 5). Moreover, the increase in invertebrate abundance may partially contribute to the increased skink abundance through a bottom-up cascade. We thus found that increased mesopredator abundance does not always exert negative impacts on the rest of the community, and while important to consider, should not be the sole reason for renouncing the benefits of eradicating alien predators (Bonnaud *et al.* 2010; Russell *et al.* 2009).

The responses of some invertebrates may reflect interspecies interactions within the invertebrate community. Among the three Isopoda species sampled in this study, Isopoda sp.2 showed the highest rate of recovery and Armadillidae showed the third-highest rate. Another Isopoda species, Isopoda sp.1, showed a negative response. A possible explanation for these different responses between species with similar traits is that these patterns were the result of competition among them. Two predatory invertebrates, the spiders Araneae sp.1 and Forficulidae sp., both became more common in our samples. These increases might have been caused by a reduction in top-down pressure and increased bottom-up effects through increases in other invertebrates.

Because we only analysed the abundances of skinks and invertebrates in this study, the relative contributions of possible mechanistic processes to the observed patterns in Fig. 5 remain unknown. Our next challenge will be to analyse the strengths of interactions in light of predator and prey densities, quantitative food habits, species traits, and interactions within invertebrate communities. Our study
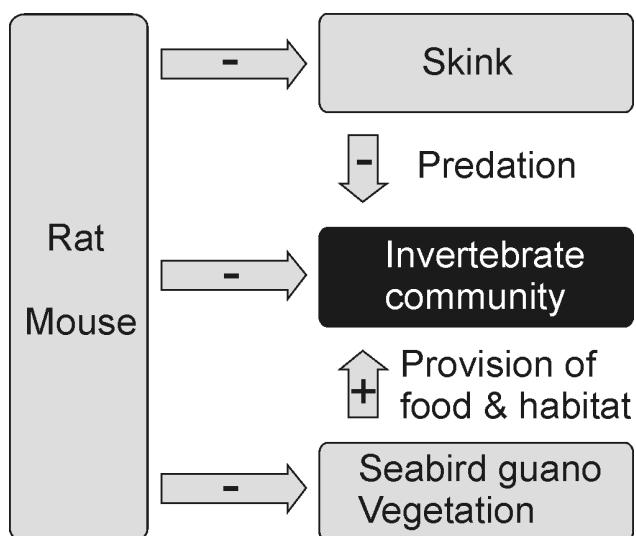
lacks replication because we only examined one island, and three nearby islands are ecologically very different. In addition, we only had invertebrate samples from 1 year before eradication. We thus cannot exclude the possibility that the above patterns resulted from factors other than the rodent eradication, such as annual climate variation, although the skink and invertebrate recoveries shown in this study are consistent with the results of other studies (e.g., Towns *et al.* 2006). Moreover, the lack of any information about ecosystem structure before rat and mice introductions to this island makes it difficult to assess the extent to which changes within communities after rodent eradication represent a recovery towards the initial state. Our study of Surprise Island communities after alien rodent eradications also reveals the difficulty of adequately understanding ecosystem processes, even in apparently very simple, small closed ecosystems. We must continue to carefully monitor the Surprise Island ecosystem. Nonetheless, our results and conclusions are important both ecologically and in terms of conservation efforts, particularly for highlighting some limitations of ecosystem studies.

ACKNOWLEDGEMENTS

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Fig. 5 Possible ecosystem processes related to rodent eradication and the invertebrate community.

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