

RESEARCH ARTICLE

# Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication

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Invasive rats have colonized most of the islands of the world, resulting in strong negative impacts on native biodiversity and on ecosystem functions. As prolific omnivores, invasive rats can cause local extirpation of a wide range of native species, with cascading consequences that can reshape communities and ecosystems. Eradication of rats on islands is now becoming a widespread approach to restore ecosystems, and many native island species show strong numerical responses to rat eradication. However, the effect of rat eradication on other consumers can extend beyond direct numerical effects, to changes in behavior, dietary composition, and other ecological parameters. These behavioral and trophic effects may have strong cascading impacts on the ecology of restored ecosystems, but they have rarely been examined. In this study, we explore how rat eradication has affected the trophic ecology of native land crab communities. Using stable isotope analysis of rats and crabs, we demonstrate that the diet or trophic position of most crabs changed subsequent to rat eradication. Combined with the numerical recovery of two carnivorous land crab species (*Geograpsus* spp.), this led to a dramatic widening of the crab trophic niche following rat eradication. Given the established importance of land crabs in structuring island communities, particularly plants, this suggests an unappreciated mechanism by which rat eradication may alter island ecology. This study also demonstrates the potential for stable isotope analysis as a complementary monitoring tool to traditional techniques, with the potential to provide more nuanced assessments of the community- and ecosystem-wide effects of restoration.

**Key words:** ecological niche, island, land crabs, *Rattus rattus*, SIBER, trophic ecology

## Implications for Practice

- Rat eradications strongly impact native land crab trophic structures in this island system.
- Stable isotope analyses reveal functional shifts in cryptic and hard-to-survey animal populations following eradication actions.
- Trophic studies using stable isotopes allow a frequently low-impact, low-effort, and relatively immediate way for restoration monitoring to move beyond single-species and numerical response surveys, bolstering evaluations of ecosystem restoration success.

## Introduction

Biological invasions are one of the greatest global anthropogenic impacts, influencing native species, biological communities, and ecosystem processes (Simberloff et al. 2013). The negative effects of invasive species are especially pronounced on islands, which, although they constitute only 3% of global land area, support 15–20% of all terrestrial biodiversity (Alcover et al. 1998; Myers et al. 2000). Approximately 75% of the total species extinctions in the last century have occurred on islands; over 50% of these are due to invasive species (Clavero & García-Berthou 2005; Woods 2008). The impacts of island invasive species go beyond species loss to influence community

interactions and ecosystem functioning (Vitousek et al. 1997; Tylianakis et al. 2008).

Although islands are the terrestrial ecosystems most threatened by invasive species, they are also the most feasible areas in which to completely eradicate unwanted species due to their well-defined boundaries and isolation from mainland species pools (Keitt et al. 2011). As such, island eradications are often conducted, with 1,100 successful eradications of invasive vertebrates on islands worldwide (DIISE 2015; Jones et al. 2016).

While eradication can be an effective and efficient technique for restoring native communities and functions (Mulder et al. 2008), eradications are not without shortcomings. Monitoring at large ecological and temporal scales is, as for many large-scale restoration efforts, often difficult to achieve. Eradications can

Author contributions: HSY, SAH conceived and designed the research; SAH, ASW, RNF, HSY, AM-tK collected field data; KMN processed lab samples; KMN, HSY analyzed the data; KMN, HSY, SAH, ASW, RNF, AM-tK wrote and edited the manuscript.

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doi: 10.1111/rec.12511

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.12511/supinfo>

cost millions of dollars, and monitoring, particularly of nontarget species and community and ecosystem responses, is usually only a small component (approximately 5%) of the overall budget of eradications (Holmes et al. 2015). Many ecologically important species are logistically difficult to monitor, and many critical community responses to eradication may not manifest as changes in species abundance, but rather in subtle behavior and interaction pattern changes (Zavaleta et al. 2001). Such monitoring limitations narrow the ability to accurately assess restoration success, as defined by a self-sustaining, predominantly native ecosystem that contains the necessary functional groups for development and stability (Clewell et al. 2004).

One technique that has not yet been used extensively as a tool in eradication monitoring (or other forms of restoration), but which is commonly employed in community ecology to determine community trophic (feeding) interactions, is stable isotope analysis (Post 2002; Layman et al. 2012). Isotopic ratios of carbon ( $^{12}\text{C}/^{13}\text{C}$ , annotated  $\delta^{13}\text{C}$ ) and nitrogen ( $^{14}\text{N}/^{15}\text{N}$ , annotated  $\delta^{15}\text{N}$ ) in organism tissues can be used to track the source of nutrients into a food web, the number of feeding links in the web, and the properties of ecological niches (“isotopic niche space”) of species or communities (Layman et al. 2012) in disturbed and restored ecosystems. In the context of invasive rats and rat eradication, stable isotopes have been used to estimate the impacts of rats on abundance or survivorship of specific consumer groups (Hobson et al. 1999; Caut et al. 2008). They have also been used to understand impacts of rats and rat eradication on nutrient subsidies (e.g. seabird subsidies) and nutrient dynamics (Mulder et al. 2011). However, they have rarely been employed as an explicit monitoring and management tool for community-scale recovery (Layman et al. 2007b). The use of stable isotopes to calculate isotopic niche space may provide valuable and relatively easily attainable information on the community-wide effects of eradication-based restoration, specifically related to how native biota fill the trophic voids left by eradicated species. Additionally, stable isotope analysis may minimize some drawbacks of traditional eradication monitoring by (1) offering the ability to monitor responses of rare or hard-to-survey taxa, (2) capturing shifts in behavior and interaction patterns following eradications, and (3) increasing monitoring cost- and time-effectiveness.

In this study, we examine the utility of stable isotopes in monitoring effects of rat eradication at Palmyra Atoll National Wildlife Refuge. Until their successful eradication in 2011, Palmyra supported a large population of invasive black rats (*Rattus rattus*), which was likely introduced during the U.S. military occupation of the island in World War II (Wegmann et al. 2012). Black rats are one of the most widespread and detrimental of invasive rat species (Townsend et al. 2006; Traveset et al. 2008; Harper & Bunbury 2015). Their diets are dominated by plants, which can limit seed and seedling survival and germination and alters plant community structure (Shiels & Drake 2010; Shiels et al. 2014). Although their diets are primarily plant based, rats are omnivorous and are known to impact island animals, most famously burrow-nesting seabirds that provide marine-derived nutrient subsidies to island ecosystems (Fukami et al. 2006; Caut et al. 2008; Jones et al. 2008; Mulder et al. 2008). Two

primary restoration goals of the Palmyra Atoll rat eradication were increasing nesting success of native seabirds, and improving recruitment of native plants (U.S. Fish and Wildlife Service 2011). However, changes in these responses are likely to both influence and be influenced by other shifts in the atoll community (Young et al. 2016).

On Palmyra Atoll, as on many tropical islands, land crabs (order Decapoda) are a hyperabundant group of consumers likely to be both directly and indirectly affected by rat eradication (Pascal et al. 2004; Shiels et al. 2014). Land crabs are often keystone species in island ecosystems, transferring nutrients from marine to terrestrial environments, increasing soil turnover and litter breakdown, and shaping plant communities through seed dispersal and seed and seedling predation (O’Dowd & Lake 1989; Green et al. 1997; Lindquist et al. 2009; Young et al. 2013b). Introduced rats can alter crab population dynamics, disrupting these processes and creating feedbacks at the ecosystem level (Pitman et al. 2005). Rat predation and competition alter crab community composition by eliminating vulnerable species and releasing competition pressure for less vulnerable species (Samaniego-Herrera 2014). Smaller species and juvenile land crabs are vulnerable to predation by rats (Samaniego-Herrera & Bedolla-Guzman 2012; Harper & Bunbury 2015); at Palmyra, crab carapaces were frequently observed in rat middens (Wegmann 2009). Additionally, it is likely that land crab species of all sizes are strongly impacted by competition with black rats (Harper & Bunbury 2015).

To add to current understanding of the community-wide effects of black rat eradication, we assessed how rat removal influenced the foraging ecology of land crabs using stable isotope analysis. By comparing stable isotopes of crabs from both before and after rat eradication, we assessed the extent to which black rats historically competed with crabs for resources, and how ecological niches of crab species and crab communities responded to rat eradication. We expected crab community diets to shift following rat eradication, and were interested in species-specific responses, crab community-wide changes, and how different island environments might mediate these diet shifts. In addition to highlighting trophic shifts in competing consumers following an eradication, our study outlines how stable isotope analysis can be employed with a small set of samples to assess short-term responses in difficult-to-monitor species, and how this technique captures ecologically significant changes in behavior and interaction patterns in ecological communities over short time periods following eradications.

## Methods

### Study Site

Palmyra Atoll National Wildlife Refuge (5°53’N, 162°05’W) is a coral-derived atoll situated in the Central Tropical Pacific. The atoll supports an ecologically diverse community of land crabs including *Birgus latro* (coconut crab), *Coenobita brevipennis* (purple hermit crab), *Coenobita perlatus* (strawberry hermit crab), *Cardisoma carnifex* (orange land crab), *Cardisoma rotundum* (purple land crab), *Geograpsus crinipes* (beige tree

**Table 1.** Life history characteristics of common terrestrial crabs of Palmyra Atoll. \*Data from Palmyra.

Crab Species	Consumer Trophic Guild	Diet	Shelter	Maximum Body Mass (g)	Zoeal Stage Length	Lifespan	References
<i>Birgus latro</i>	Opportunistic omnivore	Fruits, plant matter, carrion	Rock shelters, shallow burrows	3,900*	3–4 weeks	>100 years	(Burggren & McMahon 1988; Briffa & Mowles 2008; Drew et al. 2010, 2013)
<i>Cardisoma carnifex</i>	Herbivorous	Leaf litter, detritus	Burrows	480*	22–25 days	—	(Silas & Sankarankutty 1960; Alexander 1979; Lee 1985; Burggren & McMahon 1988)
<i>Cardisoma rotundum</i>	Herbivorous	Plant matter	Burrows	285*	—	—	(Johnson 1965; Alexander 1979; McLay & Ryan 1990)( FAO.org)
<i>Coenobita brevipennis</i>	Scavenger, mainly herbivorous	Fruits, plant matter, detritus	External shell, crevices, buries in sand	185	3–7 weeks	>10 years	(Alexander 1979; Burggren & McMahon 1988; Greenaway 2003)
<i>Coenobita perlatus</i>	Scavenger, mainly herbivorous	Fruits, plant matter, detritus	External shell, crevices, buries in sand	80	3–7 weeks	>10 yrs	(Alexander 1979; Burggren & McMahon 1988; Greenaway 2003)
<i>Geograpsus crinipes</i>	Carnivorous scavenger/predator	Other arthropods, plant matter	Burrows	150	—	—	(Burggren & McMahon 1988; McLay & Ryan 1990; Paulay & Starmer 2011)
<i>Geograpsus grayi</i>	Carnivorous scavenger/predator	Other arthropods, plant matter	Crevices	50	—	—	(Alexander 1979; Burggren & McMahon 1988; Greenaway & Nakamura 1991)

crab), *Geograpsus grayi* (little nipper crab), *Geograpsus stormi* (red nipper crab), and *Ocypode cordimanus* (smooth-handed ghost crab) (life histories in Table 1). The atoll is composed of 25 smaller islets that vary in productivity due to variation in the density of nesting seabirds and their guano subsidies (Young et al. 2010). This gradient drives cascading changes in community composition (Young et al. 2016) with potential impacts on crab ecology. To capture the range of variability, we chose to sample one high- and one low-productivity islet (Eastern and Paradise Islets; Young et al. 2013a).

### Crab Community Surveys

We surveyed crabs on six Palmyra islets (Eastern, Paradise, Aviation, Kaula, Sand, and Strawn) in 2010, 2012, and 2013 along 5–8 habitat-stratified transects per islet. All surveys for each year were completed within a 30-day period between July and October. Transects were 10 m in width and 50 m in length, except on one islet (Strawn) that did not span 50 m across; in this case, the transects were split in half but still covered the same total area. We surveyed each transect 2–3 times per sampling period, always at night by a single observer using a high-powered headlamp in good weather conditions. If at least one individual of a crab species was detected on any of these 2–3 nights, we marked that species as present on the transect and assigned a value of 1. If a species was not observed during any of the nights, we marked it as absent and assigned it a

value of 0. These surveys provided a rough but conservative estimate of species presence across time periods. We pooled the post-eradication years (2012 and 2013) and performed Fisher's exact tests ( $\alpha = 0.05$ ) for each species to test for the relationship between eradication status and the number of transects on which we observed each species.

### Sample Collection

We collected tissue samples from all crab species, rats, and, as a baseline, plants, from both islets (Eastern and Paradise). We collected pre-eradication samples in 2009, and post-eradication samples in 2013 and 2015. For each sampling period and islet, we collected one full-sun, nonsenescent leaf from five individuals of all common tree species. We collected tissue from 2–16 individuals of each crab species (Table 2). We removed one of the second pereopods from each crab, which minimally impacts crab fitness (Herreid & Full 1986). For *B. latro* we removed only the tarsus of one leg. We obtained rat thigh muscle tissue samples from another project conducted in 2008 (Lafferty et al. 2010). All samples were frozen at  $-80^{\circ}\text{C}$  until analysis.

### Stable Isotope Processing

Plant leaves were washed in distilled water, dried at  $60^{\circ}\text{C}$ , ground, and homogenized per species per islet. We removed crab exoskeletons from crab legs and chopped, freeze dried, and

**Table 2.** Number of individuals sampled of all species used in stable isotope analysis.

Species	2009		2013		2015	
	Eastern	Paradise	Eastern	Paradise	Eastern	Paradise
<i>Birgus latro</i>	4	2	—	—	5	5
<i>Coenobita brevipennis</i>	9	7	10	10	6	6
<i>Cardisoma carnifex</i>	10	10	11	10	4	6
<i>Coenobita perlatus</i>	10	5	10	10	5	5
<i>Rattus rattus</i>	10	9	—	—	—	—
<i>Geograpsus crinipes</i>	—	—	16	10	6	6
<i>Geograpsus grayi</i>	—	—	10	10	5	5

powdered the muscle tissue; we processed rat tissue similarly. We then analyzed carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios at the UC Davis Stable Isotope Lab using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.), with a standard deviation of 0.2 per mil for carbon and 0.3 per mil for nitrogen.

On Palmyra, as in many systems, the baseline values of nitrogen isotope ratios can differ between sites and sampling periods. Thus, to compare across the two islets across years, we corrected for variation in baseline  $\delta^{15}\text{N}$  by subtracting the average  $\delta^{15}\text{N}$  signature of the plant samples taken for each island and year from the  $\delta^{15}\text{N}$  signature obtained for each crab. These values were used in all analyses in place of raw  $\delta^{15}\text{N}$  data (Takimoto et al. 2008).

#### Ecological Niche Quantified With Isotopic Niche Space

We analyzed both species-specific and whole crab community niche space before and after rat eradication using two different but similar approaches (species-specific: sample-size corrected standard ellipse values; community-wide: convex hull values; Layman et al. 2007a; Jackson et al. 2011).

#### Species-Specific Niche Space

We performed one-way analysis of variance (ANOVA) tests on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values among crab and rat species (both islets, pre- and post-eradication), and for each species separated by islet pre- and post-eradication, with Tukey honest significant difference (HSD) post hoc tests. We performed Welch's  $t$  tests comparing average isotopic values of crab species between islets pre- and post-eradication.

We developed generalized linear models (GLMs) for each crab species, with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values as response variables, and islet (Paradise or Eastern), rat status (pre- or post-eradication), and their interaction as explanatory variables. We used model averaging if multiple models received substantial support ( $\Delta\text{AIC}_c < 5$ ), calculating the relative importance of each term based on the sum of their Akaike weights in all models (MuMIn; Barton 2016). We calculated the proportion of variance explained by the best supported model (lowest  $\Delta\text{AIC}_c$  value) by measuring the adjusted  $D^2$  value (Guisan & Zimmermann 2000).

We created isotope space plots for black rat and all crab species and calculated their Bayesian metrics using the package “SIBER” in R. This Bayesian approach accounts for uncertainty in data sampling, and propagates the error through to derived metrics (Jackson et al. 2011). Specifically, “SIBER” calculates niches of species from variable and small sample sizes by measuring a sample-size corrected standard ellipse that encompasses 40% of the data for each species. We generated corrected standard ellipses using Markov chain Monte Carlo (MCMC) simulations (Jackson et al. 2011). We calculated niche overlap between species with the package “siar” in R (Parnell & Jackson 2013) using each species' sample size-corrected ellipse value.

#### Crab Community Niche Space

We performed Welch's  $t$  tests comparing average isotopic values of the crab community between islets (averaged over pre- and post-eradication). To quantify these values as the crab community niche before and after rat eradication, we used the six metrics of niche space proposed by Layman et al. (2007a), using average  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for each species. These metrics include the  $\delta^{15}\text{N}$  range (NR),  $\delta^{13}\text{C}$  range (CR), total convex hull area (TA), mean distance to the centroid (CD), mean nearest neighbor distance (MNND), and standard deviation of the nearest neighbor distance (SDNND). NR describes the number of trophic levels in the community, with larger values corresponding to a community with more trophic levels. CR describes the diversity of primary carbon sources of a community, with larger CR corresponding to dependence on a greater number of diverse carbon resources. TA represents the total niche area occupied by the community. CD is a measure of the trophic diversity among species in the community. MNND is a measure of the similarity of species' trophic ecologies in the community, and SDNND provides a measure of how evenly spaced species ecologies are within isotope space (Layman et al. 2007a; Fig. S1, Supporting Information).

## Results

#### Crab Community Surveys

In 2010 (pre-eradication), we recorded *Birgus latro*, *Cardisoma carnifex*, *Coenobita brevipennis*, and *Coenobita perlatus* on 70–100% of the transects surveyed across the entire atoll

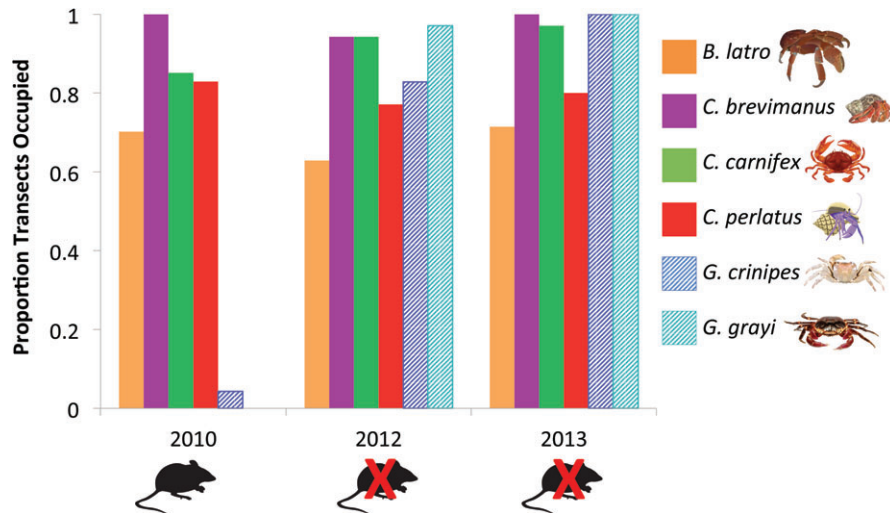


Figure 1. Proportion of transects on which each crab species was observed by year. Data for each species is pooled from all islets surveyed ( $n = 6$ ). In 2010, 47 transects were surveyed; in 2012 and 2013, 35 transects were surveyed each year. The two species that showed significant increases after rat eradication are denoted with diagonal marks.

(47 transects; Figs. 1 & S2), while the two carnivorous species, *Geograpsus crinipes* and *Geograpsus grayi*, were functionally absent (4.3 and 0% of transects, respectively), consistent with earlier surveys (Howald et al. 2004). During post-eradication (2012 and 2013) surveys, we observed the same four dominant crab species, and *G. crinipes* and *G. grayi* were observed on over 82% of transects (35 transects each year). We confirmed that *B. latro*, *Cardisoma carnifex*, *C. brevimanus*, and *C. perlatus* detection was not significantly different pre- and post-eradication using Fisher's exact tests ( $p = 0.84, 0.09, 0.52$ , and  $0.64$ , respectively). However, detection was significantly different for *G. crinipes* and *G. grayi* ( $p < 0.0001$ ).

Crab detection patterns for the two focal islets (Eastern and Paradise) mirrored the atoll-wide patterns. On Eastern pre-eradication, all crab species except *G. crinipes* and *G. grayi* were observed on 100% of the transects surveyed; the two *Geograpsus* species were never detected prior to eradication. On Eastern post-eradication, all crab species were detected on 100% of the transects surveyed. This was also true for Paradise with the exception that *B. latro* was detected on only 37.5% of transects pre-eradication and 83% of transects post-eradication and *G. crinipes* was detected on 83 and 100% of post-eradication transects in 2012 and 2013, respectively. *Cardisoma rotundum* were abundant all 3 years, but we did not collect pre-eradication samples for this species, so they were excluded from analyses. Based on life history, we expect they fill a similar niche to *C. carnifex* and this omission would not alter our results. Additionally, we observed only a single *Ocyropode cordimanus* and no *Geograpsus stormi* crabs through all sampling periods, so we excluded them from analyses.

#### Species-Specific Niche Space

One-way ANOVA comparisons revealed significant differences between species for average  $\delta^{13}\text{C}$  and corrected  $\delta^{15}\text{N}$  values

( $F = 42.43, p < 0.0001$ ; and  $F = 25.62, p < 0.0001$ ; Fig. 2), and Tukey HSD pairwise comparisons showed significant differences between some species pairs. Nitrogen isotope values divided the community into two significantly different groups of consumers: (1) *G. crinipes* and *G. grayi*; and (2) rats, *C. carnifex*, *C. perlatus*, *C. brevimanus*, and *B. latro*, with group 1 having higher corrected  $\delta^{15}\text{N}$  values (higher trophic levels) than group 2. Carbon isotope values divided the crab community into three significantly different consumer groups: (1) *G. crinipes* and *G. grayi*; (2) *C. brevimanus*; and (3) *C. carnifex*, *C. perlatus*, and *B. latro*. Consumers in group 1 had the least negative  $\delta^{13}\text{C}$  values (most marine) and group 3 had the most negative values (most terrestrial).

The rat  $\delta^{13}\text{C}$  signature differed from species in group 3, but not groups 1 and 2 (Table S1). When we analyzed rat and crab isotopic values by islet before rat eradication using Welch's  $t$  test, rats had a significantly lower  $\delta^{15}\text{N}$  value than all crabs on the low-productivity islet, a significantly higher  $\delta^{13}\text{C}$  value than some crabs on both islets, and crabs varied in isotopic values similar to those of pooled samples, with some variations (Table S2). After rat eradication,  $\delta^{15}\text{N}$  values for all crab species decreased (Welch's  $t$  test, *B. latro*:  $T = -2.90, p < 0.05$ ; *C. brevimanus*:  $T = -4.02, p < 0.001$ ; *C. perlatus*:  $T = -4.53, p < 0.0001$ ; *C. carnifex*:  $T = -5.24, p < 0.0001$ ). These effects were consistently stronger on the low-productivity than the high-productivity islet (average decreases of 64.9 and 18.8%; Fig. S3). Rat eradication led to variable increases and decreases in  $\delta^{13}\text{C}$  values for crab species across islets (Fig. S3). On the high-productivity islet, *C. perlatus*  $\delta^{13}\text{C}$  values significantly increased after eradication (Welch's  $t$  test,  $T = 2.12, p < 0.05$ ). At the low-productivity site,  $\delta^{13}\text{C}$  values significantly decreased for *C. brevimanus* and significantly increased for *C. carnifex* (Welch's  $t$  test,  $T = -3.05, p < 0.01$ ; and  $T = 2.83, p < 0.05$ , respectively).

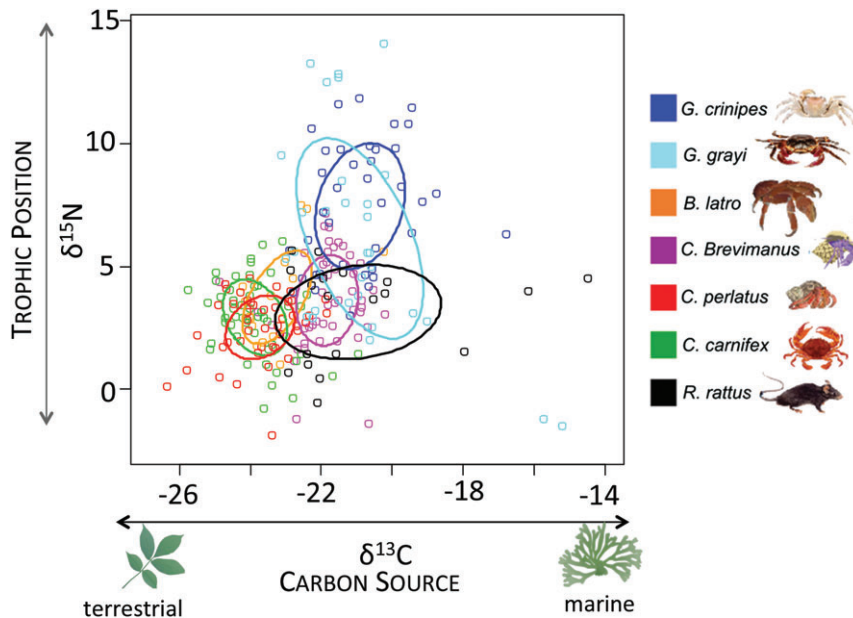


Figure 2. Isotope space plot depicting the isotopic niche of each crab species sampled and *R. rattus*. Data for each species is pooled from all years and islets sampled. Each point represents the carbon and corrected nitrogen isotopic signature of an individual crab. Each ellipse contains approximately 40% of the data from its respective species group.

Our GLM results for the effects of rat eradication illustrated that factors driving changes in crab  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values varied across species (Tables S3 and S4). For all species except *B. latro*, the variation in  $\delta^{15}\text{N}$  was best explained by the model including all factors (rat status, islet, and their interaction; Table S3), whereas the best supported model for  $\delta^{15}\text{N}$  of *B. latro* included rat status only. The best supported model explaining variation in  $\delta^{13}\text{C}$  was different for each species analyzed (Table S3).

We calculated corrected standard ellipse area (SEAc) values corresponding to the standard ellipse area of each species, based on maximum likelihood estimates and corrected for small sample sizes (Jackson et al. 2011). The probability that two SEAc values differed from each other was determined using Bayesian inference based on 10,000 draws. The SEAc values of rats, *G. crinipes*, and *G. grayi* were significantly greater than those of all other crab species ( $p > 0.99$  for all), with the SEAc value of *G. grayi* being the greatest of the three ( $p = 1.00$  for *G. crinipes* and 0.88 for rats). The SEAc value of rats was greater than that of *G. crinipes* ( $p = 0.90$ ). We compared the SEAc values for each species pre- and post-eradication using pairwise tests. The comparison revealed that the trophic niche widths of *C. carnifex*, *C. perlatus*, and *C. brevimanus* increased after rat eradication with  $p$ -values of 0.91, 1.00, and 0.94, respectively. *C. perlatus* crabs showed the largest increase (188.2%), while *C. carnifex* increased by 45.5% and *C. brevimanus* increased by 68.3%. The trophic niche area of *B. latro* decreased by 54.6% post-eradication, with a probability of 0.91.

We saw strong changes in trophic overlap among species. The percentage of niche overlap, measured as the amount of overlap between standard ellipses, of consumers (including crabs and rats) increased from 18.3% pre-eradication to 35.6%

post-eradication (Fig. 3). This was largely due to the addition of *G. crinipes* and *G. grayi* to the community, whose niches overlapped by 28.4%. However, the percentage of niche overlap between the four crab species present in both time periods also increased after eradication, from 25.8 to 46.5%.

#### Crab Community Niche Space

When we averaged isotope values by islet, the corrected  $\delta^{15}\text{N}$  value for the crab community was significantly higher on the high-productivity islet (Eastern Islet; Welch's  $t$  test,  $T = 6.54$ ,  $p < 0.0001$ ), but the  $\delta^{13}\text{C}$  value for the crab community did not differ significantly between low- and high-productivity islets (Welch's  $t$  test,  $T = 1.30$ ,  $p = 0.20$ ). The average  $\delta^{13}\text{C}$  of the entire crab community significantly increased after rat eradication (Welch's  $t$  test,  $T = 3.09$ ,  $p < 0.01$ ; Figs. 4 & S4). While the average  $\delta^{15}\text{N}$  of the community also increased post-eradication, the change was not significant (Welch's  $t$  test,  $T = 0.93$ ,  $p = 0.36$ ). Despite significant changes in average  $\delta^{13}\text{C}$ , the CR was only slightly higher after eradication ( $p = 0.86$ ), whereas NR was significantly greater in the land crab community after rat eradication ( $p = 1.0$ ; Fig. 5).

The combined addition of *G. crinipes* and *G. grayi* at higher trophic levels and the decrease in trophic position of the three other crabs caused substantial increases in land crab community trophic breadth. Due mainly to the NR expansion post-eradication, TA of the crab community on Palmyra increased significantly ( $p = 1.00$ ), as did CD ( $p = 1.00$ ). The MNND did not change significantly after rat eradication, but the SDNND was slightly lower ( $p = 0.81$ ), indicating a somewhat more even distribution of species within the crab community isotope space post-eradication (Figs. 4 & 5).

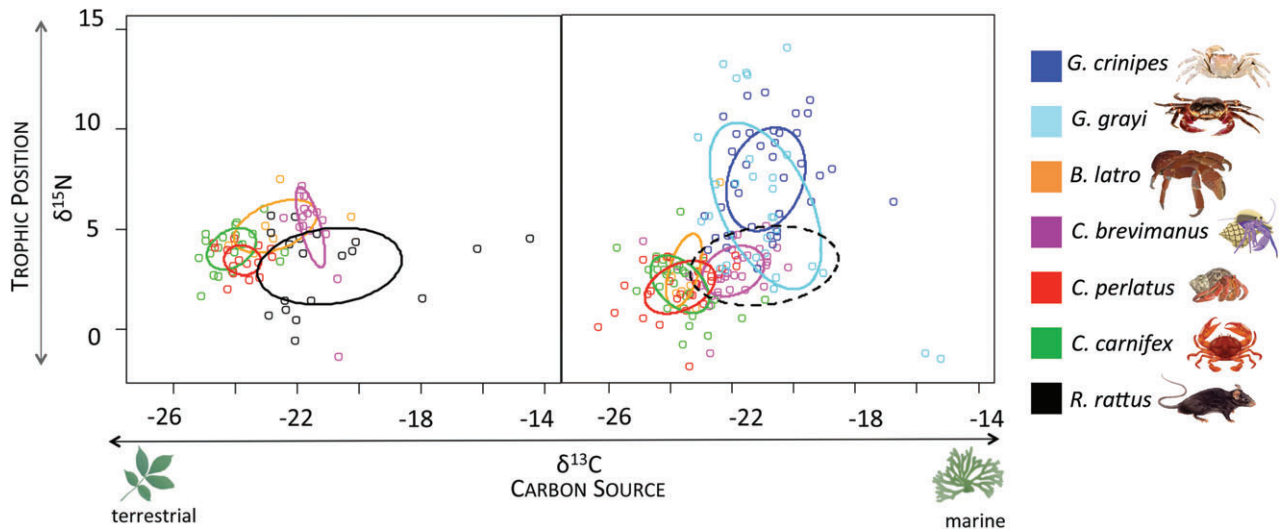


Figure 3. Isotope space plot depicting the isotopic niche of each species before and after *R. rattus* eradication. Each point represents the carbon and corrected nitrogen isotopic signature of an individual crab. Each ellipse contains approximately 40% of the data from its respective species group.

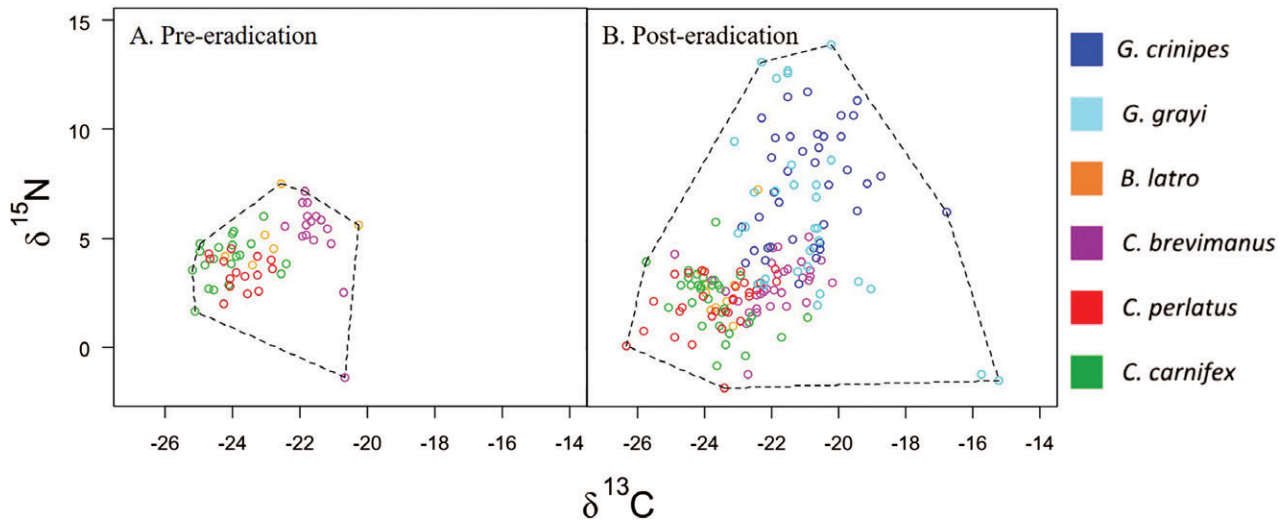


Figure 4. Isotope space plot depicting the crab community before (A) and after (B) *R. rattus* eradication. Each point represents the carbon and corrected nitrogen isotopic signature of an individual crab. The convex hull connects the isotopic values of the most extreme individuals in the community.

Analysis of the crab community excluding the two new crabs revealed opposite trends than those of the community as a whole. The post-eradication community of *B. latro*, *C. perlatus*, *C. brevimanus*, and *C. carnifex* had a smaller TA ( $p=0.88$ ), NR ( $p=0.96$ ), CR ( $p=0.94$ ), and CD ( $p=0.99$ ) than the pre-eradication community of those four species. The MNND was slightly lower ( $p=0.81$ ) and the SDNND was slightly higher ( $p=0.81$ ) in the post-eradication community.

## Discussion

### Crab Trophic Ecology

The eradication of black rats had a clear impact on Palmyra land crabs. When rats were removed, species composition and

species-specific and community-wide trophic ecology changed. The appearance of *Geograpsus crinipes* and *Geograpsus grayi* as top carnivores in the system illustrates that rats were suppressing some crab populations. The rat niche overlapped with that of the crab community, and the expansion of individual crab species' trophic niches into the space formerly occupied by rats following eradication suggests that rats may have prevented crabs from obtaining resources.

One of the most notable changes in crab communities following rat eradication was the reemergence of two species of *Geograpsus* crabs. Species of this genus have reappeared on other islands following rat eradications (Bellingham et al. 2010; Paulay & Starmer 2011). While highly carnivorous, these species are the smallest and least-armored of the Palmyra crabs, and were likely the most vulnerable to rat

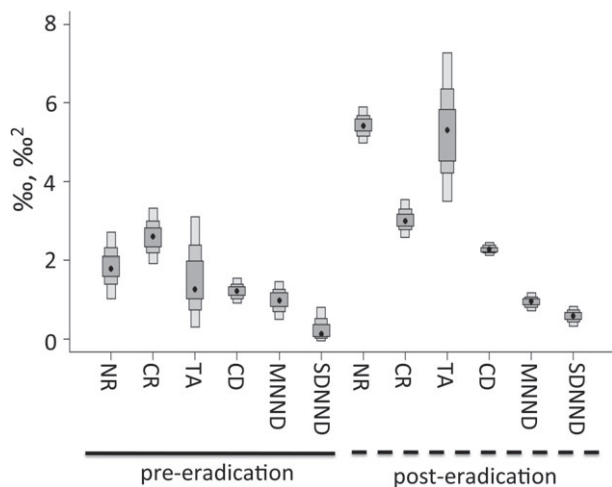


Figure 5. Uncertainty in the six Layman et al. (2007a) metrics associated with Figure 4. The mode of each metric is represented by a black dot with the 50, 75, and 95% credibility intervals shown as boxes shaded from dark to light gray. Range in  $\delta^{15}\text{N}$  (NR), range in  $\delta^{13}\text{C}$  (CR), total sample hull area (TA), distance to the centroid (CD), mean nearest neighbor distance (MNND), and standard deviation of mean nearest neighbor distance (SDNND) are shown for the crab communities before and after rat eradication.

competition and predation, especially as juveniles (Wegmann 2009; Samaniego-Herrera & Bedolla-Guzman 2012; Harper & Bunbury 2015). These carnivorous species represent the highest trophic level post-eradication species, and although we do not know their trophic levels prior to eradication, their post-eradication trophic levels likely increased due to increased abundance and consumption of conspecifics (Finke & Denno 2005). Rat trophic levels were much lower than those observed post-eradication for *Geograpsus* species, which suggests that rats were suppressing these species by consuming younger, lower trophic level individuals. Continued monitoring of crab population demographics, particularly body size distributions, will support or refute this explanation (Samaniego-Herrera 2014). More nuanced community dynamics may explain the resurgence of *Geograpsus* species on Palmyra following eradication (i.e. behavioral plasticity and direct and indirect effects of rat eradication on *Geograpsus* prey), although these also require further and broader community studies on Palmyra and in other rat-invaded tropical island systems.

It is interesting to note that while the niche spaces of *Coenobita brevimanus*, *Coenobita perlatus*, and *Cardisoma carnifex* increased following eradication, the niche space of *Birgus latro* decreased, which may illustrate nuanced ecological effects. The smaller-bodied species may now be foraging in areas where they would previously have been predated or out-competed by the larger-bodied black rat (Glen & Dickman 2005). This is suggested by significant shifts in both directions for  $\delta^{13}\text{C}$  values in these crab species across habitats—crabs are likely either expanding their food sources now that rats are gone, or these food sources have themselves become more varied (e.g. prey species have shifted food sources). Meanwhile, the diet of the larger-bodied and slower-moving *B. latro* suggests optimal

foraging—*B. latro* diet has likely become less general as they no longer forage for low-ranked food sources, and can instead feed on high-ranked food sources that would have otherwise been depleted when shared with rats (Pyke 1984). Rats are known to actively defend food items from *B. latro*; this active competition for resources no longer limits *B. latro* consumption of ideal resources like coconuts (Harper & Bunbury 2015). Alternatively, *B. latro* prey sources themselves may have declined in variability, although given the increases in niche width for other crab species, this seems unlikely.

An important caveat to note in interpreting changes in isotopic niche space across species is the limitations of isotopic analysis to fully identify variation in trophic niche, and particularly to note that isotopic niche space maps imperfectly across species and time onto true trophic niche. This is partly due to variation in the range of isotopic values of food sources (Newsome et al. 2007). For instance, a crab could undergo dramatic dietary shifts (e.g. complete shift from one plant species to another), which would go undetected with isotopic approaches because the food sources are themselves isotopically similar. In contrast another species that undergoes more subtle shifts (e.g. 10% increase in scavenging of seabird carcasses and parallel decreases in terrestrial plant material) may show stronger changes in niche space because these food sources are so isotopically dissimilar. Despite these and other challenges involved in isotopic interpretation of trophic ecology (Boecklen et al. 2011), isotopic niche area variability across species is a good indicator of differences among species, especially when combined with other methods.

Also notable is that crab and rat trophic ecology appears environment-dependent on Palmyra. While rats and crabs overlapped in their  $\delta^{15}\text{N}$  values on the high-productivity islet, their trophic levels differed significantly on the low-productivity islet, with rats filling an apparently almost completely herbivorous niche. This could be due to fewer seabirds or invertebrate prey on the low-productivity islet, or to the abundant and readily available herbaceous food provided by coconuts (*Cocos nucifera*), which are more abundant on the low-productivity islet (Caut et al. 2008; Young et al. 2010, 2013a). Additionally, while  $\delta^{15}\text{N}$  values for all crab species decreased across islets following rat eradication, this effect was stronger on low-productivity islets, where crabs may now be feeding on the easily accessible coconuts previously consumed by rats. These varying shifts across habitats suggest that interference competition can depend on environmental context.

Following eradication, the total niche area of the crab community increased due to the appearance of *G. crinipes* and *G. grayi*. However, the niche space of the suite of crabs present both pre- and post-eradication contracted, and their individual species niches had greater overlap following rat eradication. Rat populations were estimated to be 90 rats per hectare prior to eradication, and the release of resources due to their eradication likely allowed the crab community as a whole to alter its foraging behavior toward more optimal resources (Wegmann 2009). Given that rats are homeothermic with higher metabolisms than crabs, which are poikilothermic, their feeding rates were presumably higher than those of crabs



(Gillooly et al. 2001). Therefore, all crab species individually, and potentially combined, equal the feeding capacity of the rat population, allowing the community's trophic space to contract and for species niches to overlap.

### Crabs and Community Restoration

While crab population health was not the main priority of the Palmyra Atoll rat eradication, shifts in crab communities are evidence that restoration has affected the broader atoll community. The resurgence of two new species in the crab community following rat eradication increased the community's total ecological niche breadth, reflecting a movement toward native species filling the community's ecological roles. Although, as in most eradication efforts, we lack data prior to the colonization by rats, the land crab community on Palmyra is likely moving toward a more restored state (Clewell et al. 2004; Towns et al. 2006).

In addition, land crabs are likely to alter their influence on the rest of the Palmyra ecosystem. While we have no data on population numbers of land crabs pre- or post-eradication, the reestablishment of two species as significant components of the land crab community suggests that the populations of at least some crabs are expanding. As agents of nutrient transfer and soil turnover, increased populations of crabs are likely to alter ecosystem cycles, transferring more nutrients from marine to terrestrial environments and altering litter decomposition patterns (O'Dowd & Lake 1989; Lindquist & Carroll 2004; Lindquist et al. 2009; Young et al. 2013b). As seed predators, larger and altered land crab communities have the potential to influence forest species composition and structure through increased and selective seed and seedling predation (Wegmann 2009; Young et al. 2013b).

### Stable Isotopes as a Monitoring Tool

Stable isotope analysis revealed that the effects of rat eradication on Palmyra are likely to cascade throughout the atoll community and alter ecosystem-level structures and processes. This technique captured ecologically significant changes in consumer behavior and interactions that would not have been observed with species surveys alone. While land crabs are important consumers on Palmyra, they are also cryptic—crabs hide in litter, burrows, and trees during the day, have variable and sometimes large home ranges, and must be surveyed at night. Monitoring population abundance of these animals would thus be difficult, time-intensive, and expensive. Using stable isotopes, we were able to glean information about community-wide patterns from a sub-population of organisms. Our analyses suggest that traditional restoration monitoring approaches likely underestimate the impacts of restoration on recovering ecosystems by missing these trophic effects. We suggest that, used to complement traditional monitoring approaches, isotopic approaches for non-target or cryptic species may yield important new insight on complex, and sometimes unexpected, results of ecological restoration.

While land crabs are common and often dominant consumer groups on tropical islands, the type of stable isotope monitoring

used here could be equally valuable for common taxa in other ecosystems (e.g. passerine birds, reptiles, amphibians, terrestrial invertebrates; Harper & Bunbury 2015). They are likely to be particularly useful for monitoring either (1) consumers with flexible diets that respond trophically to rat eradication, or (2) higher level consumers whose diets may reflect community wide shifts in trophic structure (e.g. top predators). While this study was confined to a single taxonomic group (land crabs), these monitoring approaches could equally well target a broader range of taxa constrained by ecological characteristics (e.g. all large omnivores and predators).

### Trophic Ecology: Restoration Tool of the Future

Restoration ecology as a science recognizes that restoration is only successful when restored communities are self-sustaining, resilient, and supportive of functional diversity (Clewell et al. 2004). Restoration goals, then, should encompass a comprehensive monitoring plan that captures not just population responses, but also changes in species behaviors and community interactions. As the indirect effects of invasive species removal can greatly alter ecosystems, especially systems with multiple invaders, many restoration efforts would benefit from a greater understanding of community interaction patterns and how they might change with species removals (Zavaleta et al. 2001; Bergstrom et al. 2009). Trophic interactions have the potential to change not only when introduced predators and competitors are removed, but also as plant communities and habitat are restored. Studying how these shifts occur will lead to a greater understanding of the ecology of restoration, and will lead to more successful restoration efforts.

### Acknowledgments

Funding support for this project came from the National Science Foundation (DEB # 1457371) and the National Geographic Society, who supported the data collection and writing of this report but had no other involvement in the results presented above. We thank USGS Ecosystems Mission Area for funding and project support. Mention of trade names, firm names or commercial products does not constitute their endorsement by the U.S. Government or the National Fish and Wildlife Foundation. For field and laboratory assistance we thank Amanda Meyer, Ben Boyce, Maggie Klope, Elizabeth Gallegos, Jeff Tracey, Cheryl Brehme, Denise Clark, Dam Nguyen and Douglas McCauley. We thank U.S. Fish and Wildlife Service, The Nature Conservancy, Island Conservation, and the Palmyra Atoll Research Consortium for their critical logistical and technical support for this project (PARC Publication number 122). Finally we thank Dr Jacob Bowman and four anonymous reviewers for their helpful feedback in reviewing this manuscript.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Visualization of isotopic niche space metrics.

**Figure S2.** Frequency of crab presence before and after eradication for two focal islets only.

**Figure S3.** Average isotopic values before and after eradication for all crab species at both high and low productivity islets.

**Figure S4.** Isotope space plot depicting the consumer community before and after eradication including rats in pre-eradication isotopic space.

**Table S1.** Carbon and nitrogen values for all crab species and rats, pooled across years and islets.

**Table S2.** Carbon and nitrogen values of each species, for both high and low productivity islets, pre and post *R. rattus* eradication.

**Table S3.** Factors explaining isotopic variation in carbon and nitrogen for each species pre and post *R. rattus* eradication.

**Table S4.** Relative importance of each factor in explaining isotopic change after eradication.

Coordinating Editor: Jacob Bowman

Received: 5 October, 2016; First decision: 16 November, 2016; Revised: 24 January, 2017; Accepted: 26 January, 2017