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Coqui frog invasions change invertebrate communities in Hawaii

Ryan T. Choi · Karen H. Beard

Abstract The Puerto Rican coqui frog (*Eleutherodactylus coqui*) invaded Hawaii in the late 1980s. Because the coqui reaches high densities and consumes large quantities of invertebrates, it was hypothesized to change invertebrate communities where it invades. Previous research found that coquis can change invertebrate communities, but these studies used highly manipulative, small-scale experiments. The objective of this research was to determine whether coquis create community-level changes in invertebrate communities at the landscape scale. We collected leaf litter, flying, and foliage invertebrates on both sides of 15 coqui invasion fronts across the island of Hawaii. Multivariate analyses show that coquis are associated with changes in leaf-litter communities, primarily reductions in Acari, but are not associated with overall changes in flying or foliage communities. Across sites, coquis reduced the total number of leaf-litter invertebrates by 27%, specifically by reducing Acari by 36%. Across sites, coquis increased flying Diptera by 19%. Changes were greater where coqui densities were higher. We suggest that coquis changed leaf-litter communities primarily through direct predation, but that they increased Diptera through the addition of frog carcasses and excrement. Results support previous studies conducted in more controlled settings, but add to our understanding of the invasion by showing that coqui effects on invertebrate communities are measurable at the landscape scale.

Keywords Amphibian · Anuran · Community impacts · Eleutherodactylus coqui · Invasive species · Non-native species

Introduction

When species establish outside their native range, they often have complex interactions with and change the native community. Introduced species can change native communities by extirpating (Clavero and Garcia-Berthou 2005; Fritts and Rodda 1998), reducing (Lodge 1993; Porter and Savignano 1990; Sanders et al. 2003), and even increasing native species (Barber et al. 2008; Cohen and Carlton 1998; Roemer et al. 2002). However, community-level changes induced by some non-natives can be difficult to observe, especially if the changes occur to communities that have high spatial and temporal variability, such as invertebrate communities.

Compared to other non-native taxa, the impacts of non-native amphibians, especially on invertebrate communities, are only moderately known. Of 183 known globally introduced amphibians, studies on

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ecological impacts have been conducted only on a handful of species, primarily cane toads (*Chaunus marinus*), American bullfrogs (*Lithobates catesbeianus*), and African clawed frogs (*Xenopus laevis*) (Kraus 2009). These studies show that non-native amphibians reduce prey (Greenlees et al. 2006; Lafferty and Page 1997), reduce predators (Catling et al. 1999; Doody et al. 2006; Phillips et al. 2003), and cause cascading effects on other species (Kiesecker and Blaustein 1998). Thus, studies conducted on the effects of invasive amphibians indicate they have community-level impacts.

The Puerto Rican coqui frog (*Eleutherodactylus coqui*) has rapidly colonized and established in Hawaii (Kraus and Campbell 2002). It is especially widespread on the island of Hawaii while it has been greatly controlled on the other islands (Beard et al. 2009). Since its introduction, researchers have proposed that coquis may impact invertebrate communities (Beard and Pitt 2005; Kraus et al. 1999), largely because of their high densities, up to 91,000 frogs/ha (Beard et al. 2008; Woolbright et al. 2006), and ability to consume up to 690,000 prey items/ha/night (Beard et al. 2008). This potential impact is of concern because Hawaiian invertebrates constitute the largest component of Hawaii's biological diversity, with the majority of species occurring as single-island endemics (Howarth and Mull 1992).

Previous studies using enclosures found that coquis have the ability to change invertebrate communities in controlled, manipulated settings (Beard et al. 2003; Sin et al. 2008; Tuttle et al. 2009). However, the implications of these studies at the landscape level are uncertain. Previous studies suggest that coquis forage primarily on leaf-litter invertebrates, but also on foliage invertebrates, and that leaf-litter invertebrates are the most likely to be reduced (Beard 2007; Sin et al. 2008). Previous work also suggests that coquis may increase some flying invertebrates (Tuttle et al. 2009). Thus, various components of the invertebrate community may be directly or indirectly impacted, and the impacts may be greater where coqui density is higher. Lastly, high abundances of prey may bolster and support higher coqui densities, which may facilitate further invasion (Beard et al. 2008).

The objective of this study was to determine whether coqui invasions create community-level changes in invertebrate communities at the landscape scale. We compared invertebrate communities in adjacent invaded and non-invaded plots because this method allowed us to control for environmental variability between plots and to observe the impacts of the invasion in a variety of habitats. We also assessed site-specific diet composition to determine how well invertebrate sampling captured available prey and to better understand the direct and indirect effects of the coquis on invertebrates. Finally, we investigated how coqui density influences and is affected by invertebrate communities.

Methods

Study sites

Research was conducted at 15 sites along coqui invasion fronts on the island of Hawaii, USA, from May to August 2009 (Fig. 1). Sites were selected to capture a diversity of elevation (range 35–912 m), climate, geological history, and vegetation. Mean annual temperatures across study sites ranged from 18 to 23°C (Nullet and Sanderson 1993), and mean precipitation ranged from 1,000 to 6,000 mm/year (Price 1983). Volcanic parent material across all sites
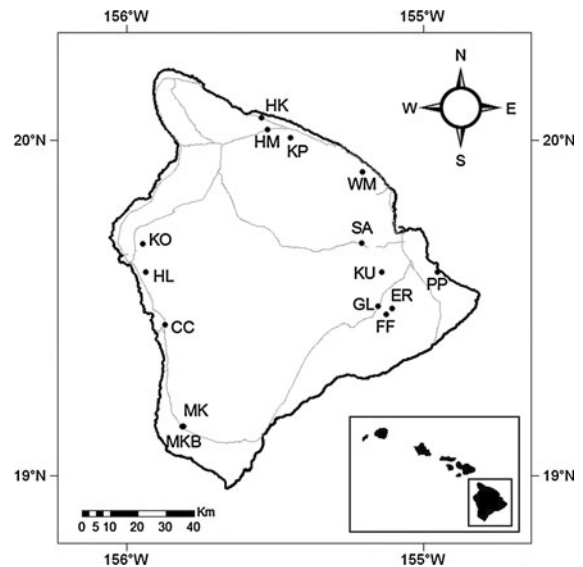

Fig. 1 Fifteen coqui sampling sites in the present study on the island of Hawaii. Site abbreviations are Captain Cook (*CC*); Eden Roc (*ER*); Fern Forest (*FF*); Glenwood (*GL*); Honokaa (*HK*); Holualoa (*HL*); Hamakua (*HM*); Kaloko (*KO*); Kalopa (*KP*); Kulani (*KU*); Manuka (*MK*); Manuka B (*MKB*); Paradise Park (*PP*); Saddle Road (*SA*); and Waikaumalo (*WK*). *Gray lines* indicate state routes

ranged from 155 to >10,000 years in age (Trusdell et al. 2005). Dominant overstory differed among sites and included *Aleurites moluccana* (site: MK, site abbreviations are in Fig. 1), *Bambusa vulgaris* (GL and MV), *Eucalyptus* sp. (CA, HK, HM, KP and WP), *Macadamia integrifolia* (CC and KE), *Metrosideros polymorpha* (ER, FF, KO, MKB, PP and SA), *Musa* sp. (HL), *Psidium cattleianum* (KU), *Schinus terebinthifolius* (PB), and *Spathodea campanulata* (WM). Dominant understory also differed among sites: *Coffea arabica* (CC, HL and KE), *Dicranopteris linearis* (ER, FF and SA), *Freycinetia arborea* (KO), *Hedychium* sp. (GL, MV and WM), *Melastoma malabathricum* (PP), *Psidium cattleianum* (CA, HM and KU), *Psydrax odorata* (MK), *Psychotria mariniana* (KP), *Schinus terebinthifolius* (MKB and PB), and *Urochloa maxima* (HK and WP).

Site selection

Presence and absence of coquis on each side of the front were determined by listening for 20 min between 1,900 and 0200 h, peak hours of calling (Woolbright 1985), for the loud (70 dB at 0.5 m) two-note mating call on three separate nights over a 1-week period (Beard and Pitt 2005). Designations were also confirmed during subsequent sampling. No frogs other than coqui were ever seen or heard at any of the sites. A mean distance of 380 m separated plots on either side of the invasion front (57–1,000 m). The coqui is known to be very territorial and individuals remain within 20 m × 20 m areas for many years (Woolbright 1985, 2005); however, they do move each night and can home up to 100 m (Gonser and Woolbright 1995). Therefore, all data for plots on either side of a front were collected within a 48 h period to minimize the likelihood of dispersal between plots during our period of observation.

To address our objective, plots on either side of a front needed to differ only by the presence of coqui. To determine whether there were other environmental characteristics that differed between plots on either side of a front, we collected and compared environmental variables (canopy cover, ground cover, stem density, understory density, and dominant canopy and understory composition). All measurements, including invertebrate sampling and frog surveys described below, were taken within 30 m × 30 m plots located on each side of each front.

Of the original 20 sites selected for this study, 15 did not differ (*P* > 0.05) for any of the environmental variables measured and were considered in the rest of the study. Five sites that had significant differences between plots on either side of the front for one or more environmental measurement were removed from further analyses.

Invertebrate sampling

Invertebrates were sampled after 2,200 h using three collection methods. All invertebrate samples were collected at the center of the plot and 10.6 m from the center at 45 degrees from the cardinal axes, for a total of five samples for each collection method per plot. Leaf litter was collected from 0.25 m × 0.25 m areas, dried in Berlese-Tullgren funnels, and invertebrates were extracted and stored in 70% ethanol (leaf-litter samples). Flying invertebrates were collected using yellow 10 cm × 18 cm sticky traps (Chevron Ortho, Marysville, OH, USA) hung vertically from the dominant vegetation with a 10 cm side 1 m from the ground and left out for 48 h (sticky trap samples). Finally, invertebrates were collected from trunks and leaves of the dominant vegetation using a modified hand-held vacuum (Black & Decker, Towson, MD, USA) for 30 s at each point. Vacuumed invertebrates were collected and immediately stored in 70% ethanol (vacuum samples). All invertebrates were later counted and identified to lowest recognizable taxonomic unit (RTU), mostly to scientific order, but in some cases family, using a dissecting microscope.

Coqui survey and sampling

Because we hypothesized that changes in invertebrate communities may be greater where coqui density was higher, we estimated coqui density in each invaded plot using distance-sampling surveys (Buckland et al. 2001; Fogarty and Vilella 2001). Surveys were conducted only on nights for which the relative humidity was greater than 80% to ensure favorable conditions frog activity. Beginning at 1,930 h, two researchers surveyed with headlamps one of six adjoining 5-m wide, 30-m long parallel transects, slowly walking and searching for frogs for 45 min. When a frog was either seen or heard, the distance from the observer and height from the forest floor were recorded. At the end of each transect, researchers

moved to the next adjoining transect, until the entire plot and total of six transects were surveyed for coquis, for a total time of 270 min per plot.

The night following distance sampling, starting at 2,000 h, we collected coquis for stomach-content analysis. Two researchers searched for frogs via headlamp each of six (5 m × 30 m) transects for 30 min across the entire plot. Observed frogs were hand-captured and euthanized. In the laboratory, individuals were dissected, and pierced stomachs were stored in vials of 70% ethanol until analysis. Snout-vent length (SVL) for each individual was measured to the nearest 0.1 mm using dial calipers and placed into a stage class (adult or preadult) based on visual inspection of gonads. Later, stomach contents were counted and identified to lowest RTU using a dissecting microscope.

Statistical analysis

To determine the effect of frog treatment (coqui vs. non-coqui) and site (15 sites) on invertebrate community composition as a whole, we used permutational multivariate analysis of variance (perMANOVA) (Anderson 2001) with the Adonis function in the Vegan package in R 2.0.1 (Oksanen et al. 2008). Adonis builds a dissimilarity matrix describing the multivariate community and tests for treatment effects by identifying spatial community centroids and calculating the squared distance of dissimilarity. Adonis generates non-parametric ANOVA results by building the null distribution of the test statistic calculated through 1,000 data permutations (Oksanen et al. 2008). We evaluated invertebrate community composition using matrices of taxon-abundance data, and constructed distance matrices using a Bray-Curtis index. We analyzed each of the collection methods (leaf litter, sticky traps, vacuum sampling) separately. When results yielded significant frog treatment (coqui vs. non-coqui) and site (15 sites) differences for the perMANOVA, we conducted principal components analyses (PCA) using the pca function with a covariance matrix in the labdsv library in R 2.0.1 to visualize the results.

To determine the effect of frog treatment (coqui vs. non-coqui) and site (15 sites) on: (1) the abundance of total invertebrates; and (2) the abundance of each taxon comprising more than 5% of each environmental collection, we conducted a two-way factorial ANOVA. We analyzed each of the three invertebrate collection methods separately. For all ANOVAs, we treated treatment and site as fixed factors. Data were modeled using a negative binomial distribution to handle the count data (O'Hara and Kotze 2010).

To estimate coqui densities at each site, we used Program DISTANCE (Thomas et al. 2010), which fits distance sampling data to specific detection functions and evaluates the models using Akaike's Information Criterion (AIC). We fit the data to key detection functions (uniform, half-normal, or hazard-rate) and series expansions (cosine, simple polynomial, or hermite polynomial). Program DISTANCE was unable to estimate site-specific densities for two sites (KP and KU) because of low detectability for frogs. For these sites, we estimated density using the linear relationship between observed frogs and frog densities for the other sites ($R^2 = 0.9602$).

We could not use density as a covariate in the ANOVAs because density and site were confounded factors. Instead, we used site-specific coqui densities to determine the relationship between coquis and invertebrate abundances. More specifically, to investigate the relationship between coqui abundance and differences in invertebrates across invasion fronts, we assumed that the non-coqui sites represented invertebrate communities pre-invasion and analyzed relationships between site-specific coqui densities and the difference in invertebrate abundance between paired coqui and non-coqui sites. We also analyzed the relationship between site-specific coqui densities and total invertebrate abundance in paired non-coqui sites to investigate the relationship between prey availability and coqui abundance. Correlations were analyzed for invertebrate taxa comprising >5% of environmental collections or coqui diet. Out of all 15 sites, one site (CC) had a much higher coqui density than the other sites. We conducted analyses with and without this site, but findings were never different, and therefore all sites were included in the analysis.

We also used two-way ANOVAs to investigate differences in dietary taxa between stage classes, for which we treated stage class (adult and preadult) and site as fixed factors, and treated individuals within site as sub-samples. Taxa that comprised >5% of coqui diet were analyzed from eight sites where there were sufficient numbers for comparison of both adults and preadults (i.e. ≥5 individuals). Data were modeled

using a negative-binomial distribution (O'Hara and Kotze 2010).

For this study, we were mostly interested in treatment effects (effects of the coqui) including whether they were consistent or differed across sites. Thus, while we could have analyzed the data using site as a random effect instead of a fixed effect, we chose to use site as a fixed effect because it gave us more insight into coqui impacts (treatment effects) that varied across sites. From a management perspective, the analysis allowed us to highlight taxa that might not always be impacted by the invasion but may be impacted in some areas.

In the multivariate and ANOVA analyses, site was significant in 96% of the analyses. This suggests that sites had different invertebrate communities, which was expected because sites were chosen to capture a high degree of landscape variability. Because site was almost always significant, significant site effects are not discussed unless we observed an interaction with coqui treatment effects. We conducted ANOVAs using PROC GLIMMIX and Spearman correlations using PROC CORR in SAS v. 9.1.3 for Windows (SAS Institute, Cary, NC, USA). We considered tests significant when $P < 0.05$ and presented values where appropriate.

Results

Invertebrate communities

We collected and identified a total of 21,382 invertebrates from the 15 coqui sites and 28,184 invertebrates from the 15 non-coqui sites. Of the collected invertebrates, leaf-litter samples made up 90.4%, sticky-trap samples made up 7.4%, and vacuum samples made up 2.2% of the total (Fig. 2). Samples across all collection types and treatments consisted primarily of Acari (50.6%), Collembola (21.1%), Hymenoptera (7.6%), and Isopoda (5.7%).

Multivariate analyses on leaf-litter invertebrate communities showed that coqui changed the composition of leaf-litter invertebrates; however, these changes varied by site (Table 1). PCAs on leaf-litter invertebrate communities showed that sites with frogs had fewer Acari, but effects on Collembola and Hymenoptera seemed to vary by site (Fig. 3). Overall, coqui sites had 26.9% fewer total leaf-litter invertebrates (treatment, $F_{1,120} = 10.89$, $P = 0.0013$). Taxon-specific ANOVAs supported the PCA ouput and showed that coqui
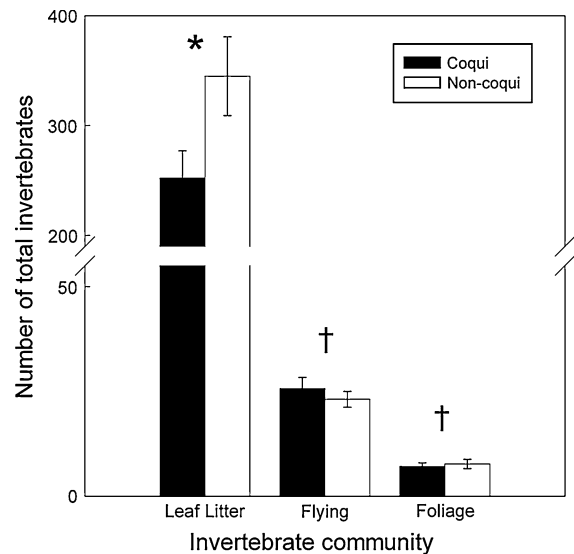

Fig. 2 Mean numbers of invertebrates (±SE) in three invertebrate communities with and without coqui frogs ($n = 15$). Significant treatment results are marked with *asterisk*, and significant treatment-site interactions are marked with *dagger* ($P < 0.05$)

sites also had 36.0% fewer leaf-litter Acari, but changes in leaf-litter Collembola, Hymenoptera, and Isopoda varied by site (Fig. 4a).

Multivariate analyses on flying invertebrate communities showed that coqui impacts on flying-invertebrate composition varied across sites (Table 1). ANOVAs supported this result and showed that coquis affected total flying-invertebrate abundance at some sites (Fig. 2). But taxon-specific ANOVAs showed that coquis increased flying Diptera abundance by 19.0% across sites, while effects on flying Hemiptera and Hymenoptera varied by site (Fig. 4b). Coquis had no effect on Collembola collected on sticky traps.

Multivariate analyses on foliage-invertebrate community composition also showed impacts varied across sites (Table 1). ANOVAs supported this showing that coquis affected total foliage-invertebrate abundance at some sites (Fig. 2), while taxon-specific ANOVAs showed that coquis affected foliage Hymenoptera at some sites, but did not change foliage Acari, Araneae, Collembola, or Diptera (Fig. 4c).

Coqui density and correlations

A total of 988 frogs was observed during distance sampling on all invaded plots (range 25–239). Site-

Table 1 Results from perMANOVA multivariate analysis of variance comparing the effects of treatment (coqui vs. no coqui) and site on invertebrate community abundance analyzed by taxa

Model	DF	Taxa	
		R^2	Pr(>F)
Leaf litter treatment	1	0.0114	0.017*
Leaf litter site	14	0.4017	<0.001*
Leaf litter treatment* site	14	0.0897	0.002*
Flying treatment	1	0.0069	0.100
Flying site	14	0.4037	<0.001*
Flying treatment* site	14	0.0989	<0.001*
Foliage treatment	1	0.0089	0.117
Foliage site	14	0.2412	<0.001*
Foliage treatment* site	14	0.1317	<0.001*

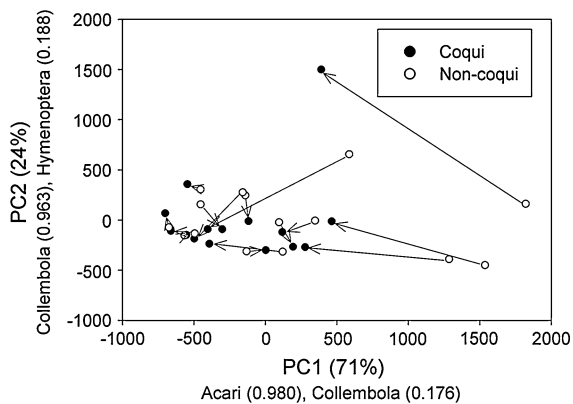* Indicates test significance ($P < 0.05$)

Fig. 3 Principal component analysis of leaf-litter invertebrate taxa at sites with and without coquis ($n = 15$ sites). Total variance explained by each axis in parentheses and two most important contributing taxa

specific population densities ranged from 347 to 6,983 frogs/ha.

When we compared coqui density to changes in invertebrate abundance (differences between non-coqui and coqui sites), coqui density was positively related to reductions in leaf litter and foliage Acari ($R^2 = 0.5250$, $P = 0.0445$; $R^2 = 0.5474$, $P = 0.0347$, respectively). In contrast, coqui density (from coqui sites) was positively correlated with some invertebrate groups from the non-coqui sites, specifically leaf-litter Araneae ($R^2 = 0.5738$, $P = 0.0253$) as well as flying and foliage Coleoptera abundance ($R^2 = 0.6289$, $P = 0.0120$; $R^2 = 0.5670$, $P = 0.0275$, respectively).

Coqui diet selection

We identified a total of 6,701 prey items from 874 coqui stomachs (range 30–122 stomachs per site). Across sites, dominant prey included Hymenoptera (32.80%), Coleoptera (12.10%), Amphipoda (8.73%), Collembola (7.89%), Acari (7.22%), and Isopoda (5.75%). At eight sites with both preadult and adult frogs, 233 preadult frogs consumed 402.2% more Acari and 213.1% more Collembola than 392 adult frogs, while effects of stage class on Amphipoda, Coleoptera, and Isopoda varied by site (Fig. 5).
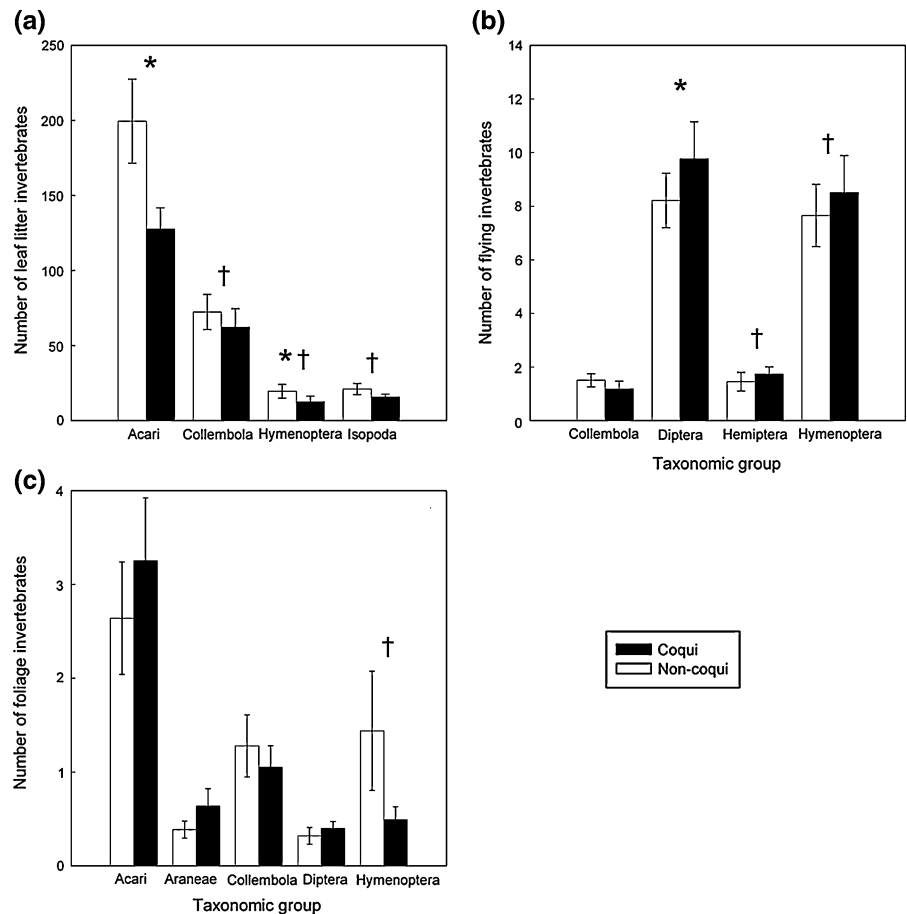
Discussion

Across 15 sites on the island of Hawaii, we found that coqui frogs were associated with a reduction in the total number of leaf-litter invertebrates, primarily Acari. While coqui sites had no overall consistent change in foliage-invertebrate communities, Diptera abundances increased in flying communities across sites. Although enclosure experiments previously conducted in Hawaii suggested that coquis may reduce leaf-litter invertebrates and increase flying invertebrates (Sin et al. 2008; Tuttle et al. 2009), these patterns have not previously been measured at the landscape scale. Similar to other invasive amphibians, coquis have the potential to induce measurable changes in invertebrate communities at the landscape scale (Catling et al. 1999).

We expected to see the greatest change in the leaf-litter invertebrate community because coquis primarily consume leaf-litter invertebrates in Hawaii (Beard 2007). The observed reduction of total invertebrates in this community (27%) was largely driven by the reduction in highly abundant Acari by 36%. These results were similar to previously conducted enclosure studies that showed that coqui reduce total leaf-litter invertebrates by 14% (Sin et al. 2008) and microbivore (primarily Acari and Collembola) abundance by 40% (Tuttle et al. 2009).

Based on dietary studies alone, we might not expect the flying-invertebrate community to be greatly impacted by the coqui invasion (Beard 2007). However, we found a 19% increase in Diptera with coquis, which is similar to an enclosure study that found coquis increased Diptera by 27% (Tuttle et al. 2009). Tuttle et al. (2009) suggested that Diptera may

Fig. 4 Mean numbers of invertebrate (±SE) taxa comprising more than 5% of each collection method at sites with and without coqui frogs by: **a** leaf litter, **b** flying-, and **c** foliage-invertebrate communities (*n* = 15). Significant treatment results are marked with *asterisk* and significant treatment-site interactions are marked with *dagger* (*P* < 0.05)

increase with coqui because Diptera larvae may feed on readily available frog carcasses and excrement. When we investigated specific Diptera families in our samples, we found that Sciaridae was responsible for the greatest increase in Diptera abundance, and this family is known to feed on carcasses (Perotti et al. 2010). Thus, we propose that coquis increase Diptera by increasing nutrient availability in the system though excrement and carcasses (Beard et al. 2002).

We expected coquis to have the potential to change foliage invertebrates (Beard 2007); however, we found no consistent directional change in the foliage-invertebrate community composition with coquis. In Puerto Rico, foliage invertebrates are the dominant prey consumed by coquis (Stewart and Woolbright 1996), whereas in Hawaii they have not been found to be as important as leaf-litter invertebrates (Beard 2007). The lower abundance of foliage invertebrates compared to leaf-litter invertebrates (at least based on our sampling), as well as fewer coqui predators in the

leaf litter compared to the native range (Beard and Pitt 2005), might explain why the frogs consume more invertebrates in the leaf litter as opposed to the foliage in Hawaii. In addition, it is also possible that sites with younger a'a and pahoehoe lava substrates may provide an abundance of subterranean diurnal retreat sites and breeding spots, increasing the amount of time frogs spend on the ground foraging in the leaf litter.

Another potential explanation might be attributed to collection biases resulting from our invertebrate sampling techniques. Our methods were chosen to sample invertebrates available to foraging coqui and other taxa that may experience indirect change due to the coqui. However, some invertebrate taxa that were prominent in coqui diets were underrepresented in environmental collections. For example, some large-bodied and highly mobile cockroaches (Blattodea) and grasshoppers (Orthoptera) were frequently found in adult stomachs (62 and 48 items, respectively), but were not common in environmental samples. Because
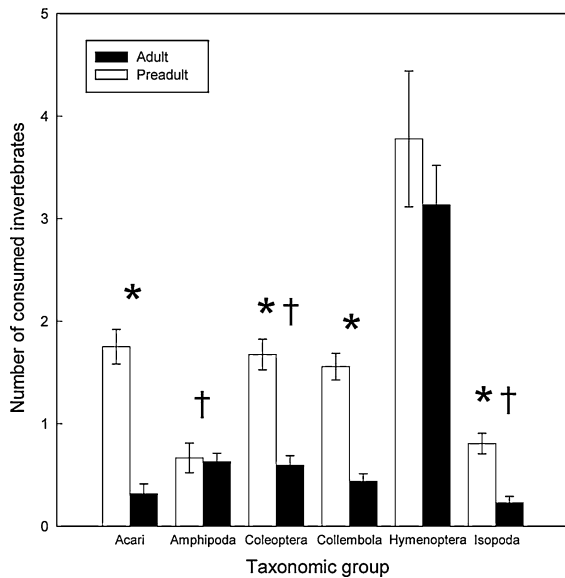
Fig. 5 Mean numbers of prey consumed (± 1 SE) by adult and preadult frogs ($n = 8$ sites). Significant treatment results are marked with *asterisk* and significant treatment-site interactions are marked with *dagger* ($P < 0.05$)

these taxa should have been collected on the foliage, this suggests that portions of foliage-invertebrate communities might have been impacted by coquis but were not measured in this study.

We found positive correlations between coqui density and reductions of leaf-litter Acari. This reduction is likely attributed to direct predation, especially because Acari are prominent prey items in preadult diets. Preadult to adult ratios in Hawaii are estimated at 2.5:1 (± 1.7 SD) (Beard et al. 2008), and it has been shown that preadults consume more, smaller prey items than adults (primarily Acari, Collembola) (Beard 2007). Because prey size is positively correlated with body size (Woolbright and Stewart 1987) and smaller prey items compose a large percentage of preadult diets, preadult frogs are likely affecting smaller-bodied taxa like Acari and Collembola, while adults are more likely affecting larger invertebrates like Amphipoda and Coleoptera. In addition, we found positive correlations between coqui density and the relative abundance of prominent, large-bodied prey taxa in the environment (Araneae, Coleoptera), which suggests that greater large-bodied prey abundance may support higher densities of coquis (Beard et al. 2008).

Findings from our dietary analysis concur with the same six prominent taxonomic orders found in a

previous dietary study conducted in Hawaii (Beard 2007): Acari, Amphipoda, Isopoda, Coleoptera, Collembola, and Araneae. These taxa were not only common in the coqui diet but were also common in our invertebrate-community samples, which suggests that coqui prey selection reflects prey availability. Although dietary studies are temporal snapshots of consumed prey items, this dietary analysis was conducted across a number of different environments and habitats, which further supports that these taxa are both the dominant prey and abundant invertebrates in Hawaii.

It is reasonable to assume that different habitats result in different invertebrate communities and prey availability to coquis. This discussion focused on the effects that were consistent across sites, but several taxa had significant treatment and site interactions. For example, Collembola, Hymenoptera, and Isopoda in the leaf litter, and Hymenoptera in the foliage, were primarily reduced by coqui at sites. However, these results were inconsistent, and at some sites these taxa increased with coqui. In contrast, flying Hemiptera and Hymenoptera, similar to the response in Diptera, increased with coqui at most sites, but at some sites these taxa showed the opposite pattern. Unfortunately, we could not identify any environmental or biological factor that might have driven these site-level responses. But, the result is important because it suggests that some coqui effects are not uniform but vary among sites. Furthermore, we can use these results to identify orders (such as Collembola) containing endemic species that may be impacted by coquis at some sites. When considering the community-level impacts of coqui, it is important to also consider the effects on these other taxa that had site-specific responses.

One concern with these types of observational studies is that measured effects may not be a result of the invasive species but some other environmental factor that is associated with the invasive species. To account for this possibility, we used strict requirements regarding what sites could be included in our study, and the invaded and un-invaded sites could not differ in any environment parameter that we measured. This prevented us from including all of our original sites in the analysis. Although we cannot rule out the possibility that there were other factors contributing to the results, the fact that these results support both other dietary and enclosure studies suggests the changes that we observed can be attributed to the coqui.

Because we measured impacts of the coqui at sites along the invasion front, these results may represent short-term or only partial impacts of the invasion due to the recent nature of the invasion and potential lag-time responses by the invertebrate community (Krushelnycky and Gillespie 2010). Alternatively, densities of invaders could be higher as they invade new areas before they deplete resources, and short-term effects might be greater than long-term effects (Morrison 2002). Over time, a predator–prey dynamic equilibrium may be reached, possibly different than what is found at the invasion front (Buckley et al. 2005). In addition, because sites were not sampled over time, there could be unobserved seasonal differences in invertebrate communities and coqui activity.

In conclusion, our findings show that coqui frogs change invertebrate communities at 15 sites in Hawaii, and especially reduce highly abundant prey taxa, such as Acari. We observed some consistent changes in invertebrate communities, such as reductions in Acari and increases in Diptera, that will likely occur in most invaded sites. We found some other results that were only present at some sites, such as changes in Collembola, Hymenoptera, and Isopoda. These results are more daunting because it is difficult to know at what sites these changes might be present. We suggest that future research monitor the temporal response by invertebrate communities to the coqui invasion at these sites over time. Because coquis have measurable effects on invertebrate communities, this should be taken into consideration as control measures are evaluated.

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