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An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii

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Abstract A frog endemic to Puerto Rico, *Eleutherodactylus coqui*, invaded Hawaii in the late 1980s, where it can reach densities of 50,000 individuals ha^{-1}. Effects of this introduced insectivore on invertebrate communities and ecosystem processes, such as nutrient cycling, are largely unknown. In two study sites on the Island of Hawaii, we studied the top-down effects of *E. coqui* on aerial, herbivorous, and leaf litter invertebrates; herbivory, plant growth, and leaf litter decomposition rates; and leaf litter and throughfall chemistry over 6 months. We found that *E. coqui* reduced all invertebrate communities at one of the two study sites. Across sites, *E. coqui* lowered herbivory rates, increased NH_4^+ and P concentrations in throughfall, increased Mg, N, P, and K in decomposing leaf litter, increased new leaf production of *Psidium cattleianum*, and increased leaf litter decomposition rates of *Metrosideros polymorpha*. In summary, *E. coqui* effects on invertebrates differed by site, but *E. coqui* effects on ecosystem processes were similar across sites. Path analyses suggest that *E. coqui* increased the number of new *P. cattleianum* leaves and leaf litter decomposition rates of *M. polymorpha* by making nutrients more available to plants and microbes rather than through changes in the invertebrate community. Results suggest that *E. coqui* in Hawaii has the potential to reduce endemic invertebrates and increase nutrient cycling rates, which may confer a competitive advantage to invasive plants in an ecosystem where native species have evolved in nutrient-poor conditions.

Keywords Amphibian · Decomposition rate · *Eleutherodactylus coqui* · Invasive · Non-native · Productivity · Tropics

Introduction

Invasive species are more likely to reduce native species and alter ecosystems when they represent new trophic levels or functional groups, and attain high densities (Chapin et al. 1996; Parker et al. 1999). Invaders on island ecosystems are of particular concern because they often meet these criteria, and islands are often hotspots of endemics (Grenyer et al. 2006). With few notable exceptions (e.g., the brown tree snake [*Boiga irregularis*], *Anolis* lizards, and cane toad [*Bufo marinus*]), reptile and amphibian invasions on islands have been poorly studied, even though many islands lack native herptofauna and these species often attain high densities (Kraus and Campbell 2002). This may be because reptiles and

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amphibians are not thought capable of changing food web structure and ecosystem functioning, even though several studies show that they can (e.g., Fritts and Rodda 1998; Schoener and Spiller 1999; Whiles et al. 2006).

For example, 27 species of reptiles and amphibians have established in Hawaii, where there are no native reptiles or amphibians (Kraus 2003), but few, if any, studies have been conducted to describe their ecological impacts. The objective of this research was to identify the top-down effects of the Puerto Rican frog, *Eleutherodactylus coqui*, in Hawaii. This terrestrial frog became established on the Hawaiian Islands via the horticulture trade in the late 1980s (Kraus et al. 1999). Since its introduction, it has rapidly expanded its range. There are now over 250 known populations on all four main islands, located mostly in lowland forests on the windward sides of the islands of Hawaii and Maui (from 0 to 1,100 m). This invasion has received attention because *E. coqui* has a loud mating call, 80–90 dB (at 0.5 m), and has affected Hawaii economically (Kraus and Campbell 2002).

Eleutherodactylus coqui density in some areas in Hawaii is estimated to be > 50,000 ha^{-1} (Woolbright et al. 2006). In these areas, *E. coqui* is consuming an estimated 350,000 invertebrate prey items per hectare per night (Beard 2007). Because research from Puerto Rico (PR) suggests that *E. coqui* can reduce invertebrate prey (Stewart and Woolbright 1996; Beard et al. 2003), its predation effects are of concern in Hawaii, where there are 44 endangered invertebrates and invertebrates comprise the large majority of the endemic fauna (Beard and Pitt 2005). *E. coqui* is known to be a generalist predator, consuming invertebrates mostly on vegetation at night and in the litter during the day while in retreat sites located near the forest floor (Stewart and Woolbright 1996; Beard 2007). However, the predation effects of *E. coqui* on invertebrate communities in Hawaii have not yet been studied.

Eleutherodactylus coqui could also indirectly affect ecosystem processes involving invertebrates (Beard and Pitt 2005). In a study conducted in PR, *E. coqui* reduced herbivory rates, increased plant growth rates (leaf surface area, number of new leaves, stem height, and biomass), and increased nutrient (NH_4^+, P, and K) concentrations in throughfall chemistry (Beard et al. 2002, 2003). *E. coqui* also increased nutrient (P and K) availability in decomposing leaf litter and increased leaf litter decomposition rates (Beard et al. 2002). Beard et al. (2002) suggested that it was the increase in plant- and microbe-limiting nutrients with *E. coqui*, which resulted from converting invertebrates into more available nutrient forms, as opposed to reductions in invertebrates, that increased plant growth and leaf litter decomposition rates. It may be that *E. coqui* affects these processes through a similar mechanism in Hawaii.

To determine the top-down effects of *E. coqui* in Hawaii, we measured *E. coqui* effects on (1) the abundance of invertebrates (aerial, herbivorous, and leaf litter), (2) herbivory rates, (3) nutrient concentrations in throughfall chemistry and decomposing leaf litter, (4) leaf litter decomposition rates, and (5) plant growth rates. In addition, we used path analyses to determine whether changes in plant growth measures and leaf litter decomposition rates with *E. coqui* resulted from changes in nutrient availability or from changes in invertebrate abundances.

Very few studies have compared terrestrial vertebrate predator effects in introduced and native ranges using similar methods. This study provided a unique opportunity to make such a comparison because it was conducted using methods similar to those used in PR for the study described above. We also included previously published PR data in our path analyses, analyses that had not been previously conducted, to determine whether the mechanisms through which *E. coqui* influences ecosystem processes were similar in the two ranges.

Methods

Experimental design

Experiments were conducted at two sites: Bryson's Cinder Cone (BRY, 19°26′N 154°55′W; elevation 270 m) and Nanawale Forest Reserve (NFR, 19°28′N 154°54′W; elevation 230 m), 4 km apart on the eastern side of the Island of Hawaii. Both sites occur in lowland rain forests with a mean annual precipitation of 3,000–4,000 mm $year^{-1}$ (Giambelluca et al. 1986) and mean monthly temperatures of 23°C (Juvik and Juvik 1998). Both sites are located on a shallow, 300–400-year-old substrate (Wolfe and Morris 1996).

Both sites have native species, *Metrosideros polymorpha* (Gaud.) in the overstory, and *Psychotria hawaiiensis* (A. Gray) and *Cibotium* sp. in the understory. However, non-native plant composition and density differ. While both BRY and NFR have *Psidium cattleianum* (Sabine) in the understory, NFR also has *Melastoma candidum* (D. Don) and *Clidemia hirta* (L.) D. Don. Understory density was estimated to be 5.8 times lower at BRY than at NFR (determined as in Nudds 1977). An *E. coqui* population was not established at BRY, but one was established at NFR for >1 year prior to the initiation of the experiment.

At each site, 20 enclosures (1 × 1 × 1 m^3) were placed on the forest floor in pairs, constructed using a 2.5 cm diameter PVC pipe frame and completely covered by plastic mesh material with 0.76×0.76 cm^2 mesh size. This mesh size prevents passage of *E. coqui* >26.2 mm snout-vent length but allows passage of >99% of invertebrates found on site (K.H. Beard, unpublished data). One enclosure in each enclosure pair contained no frogs while the other was stocked with an average density of five male frogs, an approximation of natural densities, based on Hawaii estimates (Woolbright et al. 2006). Only males were used to ensure that frogs could not establish new populations. Frogs were added bimonthly as required to maintain experimental densities; dead frogs were left in enclosures. Frog loss rate did not change over the course of the experiment. The only plants in enclosures were potted plants (described below). The experiment was conducted for 6 months, from September 2004 to February 2005.

Invertebrate communities

One 10 × 18 cm^2 sticky trap (Seabright Laboratories, Emeryville, CA, USA) was suspended from the top center of the enclosure and one was placed as a bridge between potted plants. Sticky traps were collected and replaced every 2 weeks. Plastic trays (16 × 26 × 6 cm^3: l × w × h), filled with 20 g of mixed, air-dried leaf litter from the forest floor, were placed in each enclosure. Once a month the contents of each tray were collected and invertebrates were extracted using Berlese–Tullgren funnels within 2 h of collection. Collected litter was immediately replaced with 20 g of new mixed, air-dried leaf litter.

Invertebrates on sticky traps and extracted invertebrates were identified to order. Invertebrates with wings found on sticky traps suspended from enclosure tops were treated as aerial invertebrates. Invertebrates with plant feeding mouth parts on sticky traps placed between potted plants were treated as herbivorous invertebrates. Invertebrates from trays were treated as leaf litter invertebrates and sorted by feeding guild: microbivores (Acari and Collembola), fragmenters (Amphipoda, Coleoptera, Dermaptera, Diplopoda, Isopoda, and Psocoptera), and predators (Aranaea and Hymenoptera).

Plant herbivory and growth

Native (*M. polymorpha* and *P. hawaiiensis*) and non-native seedlings (*M. candidum* and *P. cattleianum*) were collected on-site. We placed four randomly selected individuals of each species in 3.8 L pots in each enclosure ($n = 16$ plants per enclosure). Soils in pots consisted of peat moss, topsoil (0–5 cm), and lava cinder in a 35-9-56 mass ratio. At the initiation and termination of the experiment, the following measurements were recorded for each plant: stem height, stem diameter, number of (new) leaves, total leaf surface area, and total herbivory. Herbivory during the experiment was determined as percent herbivory, and calculated by dividing the surface area loss to herbivory minus herbivory measured at the initiation of the experiment by total leaf surface area, which included the new leaf surface area. At the end of the experiment, above- and belowground biomass was determined for all plants. Biomass was determined by measuring total aboveground and belowground biomass dried at 70°C until constant weight.

Leaf washes

To measure changes in throughfall chemistry, four leaf wash samples were collected from each enclosure monthly, with each sample being a composite sample collected from one plant species. For each sample, a total of 50 ml of distilled water was sprayed over all leaves on each plant of one species and leachate was collected using a funnel. Collections were made within 72 h of a rain event. Samples were stored in a freezer and filtered with Whatman GF/A glass fiber filters prior to analysis. All samples were analyzed using a Thermo Electron Iris Advantage

Inductively coupled Plasma (ICP) Spectrophotometer (Thermo Electron Corporation, Waltham, MA, USA) for Ca, Mg, P, and K. *P. cattleianum* samples were analyzed using a Lachat Quickchem 8000 Flow Injection Analyzer (Lachat Instruments, Loveland, CO, USA) for dissolved NH_4^+ and NO_3^-.

Leaf litter

Six leaf litterbags were placed on the floor of each experimental enclosure. Each litterbag (15×15 cm^2, mesh size: 0.23×0.23 cm^2) contained 5 g of newly senesced air-dried *M. polymorpha* leaves. Subsamples of air-dried leaves were separately processed after every fifth litterbag was constructed to develop an air-dried to oven-dried (70°C) conversion factor. Half the litterbags were removed after 3 mo and half after 6 mo. Each retrieved litterbag was brushed to remove organic debris, oven-dried at 70°C, and weighed. Samples were ground and homogenized with a 2-mm mesh screen. A subsample from each was ashed overnight at 500°C to develop an ash-free conversion factor (Harmon and Lajtha 1999).

Both 3 and 6 mo leaf litter samples were analyzed for elemental (Ca, Mg, P, and K) concentrations, total C, and total N. Leaf litter samples were digested using the procedure outlined in Mills and Jones (1997) and analyzed for elemental concentrations using the ICP, and analyzed for C and N by the LECO TruSpec CN Analyzer (LECO, St. Joseph, MI, USA). To adjust for soil C and N contamination, three soil samples were collected from each site, sieved with a 2-mm mesh screen, oven-dried, and analyzed for C and N.

Statistical analyses

We used an ANOVA of a three-way factorial in a split–split plot design to evaluate the interactions of the fixed effects of site (the whole plot factor with two levels: BRY and NFR), treatment (the subplot factor with two levels: enclosures with and without *E. coqui*); and the third factor (the sub-subplot factor) varied with the response variable: (1) plant species for plant growth variables and percent herbivory, and (2) time for invertebrates: totals (aerial, herbivorous, and leaf litter) and leaf litter feeding guilds, throughfall nutrient concentrations, leaf litter nutrient concentrations and contents, and leaf litter decomposition rates. The split–split plot model uses compound symmetry covariance structures for repeated measures both on the whole plots and the subplots. The two sites were examined as fixed effects so treatment effects could be evaluated by site.

To better meet assumptions of normality and homogeneity of variance, invertebrate abundances, plant growth variables, percent herbivory, and leaf litter nutrient concentrations (Mg, K) were square root-transformed; throughfall nutrient concentrations (NH_4^+, Ca, Mg, and P), leaf litter decomposition rates, and leaf litter P concentration were log-transformed. For all other variables, no transformation was needed. We considered $P < 0.05$ significant except for invertebrate analyses where we considered $P < 0.10$ significant due to the high-variability associated with invertebrate sampling (as in Holmes and Schultz 1988). Only significant interactions are reported. ANOVAs were calculated using PROC MIXED in SAS Version 9.1 for Windows (SAS Institute, Cary, NC, USA). Mean ± 1 standard error (SE) are presented throughout.

To test the relative importance of nutrient cycling effects and indirect effects via invertebrate communities on ecosystem processes, we used path analysis, a multivariate technique that uses structural equation modeling to identify causation among intercorrelated variables based on a priori hypotheses. The technique uses partial regressions along with insights from graph theory to quantify interaction strengths between pairs of variables while also accounting for other relationships within the model.

We had two path analysis models: a new leaves model and a leaf litter decomposition model. Due to sample size limitations only four variables could be used in each model (Hatcher 1994). The new leaves model assessed the effects of *E. coqui* on the number of new leaves produced, through *E. coqui* effects on herbivory rates and leaf wash NH_4^+ concentrations. We used new leaves and herbivory rates for *P. cattleianum* because NH_4^+ concentrations in leaf washes were from *P. cattleianum* samples. The leaf litter decomposition model determined the effects of *E. coqui* on leaf litter decomposition rates through effects on leaf litter invertebrates and leaf wash NH_4^+ concentrations. For the PR data, variables were the same except new leaves and herbivory were for *Piper glabrescens* (Miq.) C. DC. and leaf litter decomposition rates were for *Dacryodes excelsa* Vahl.

The overall exogenous variable in the models was the number of *E. coqui* in each enclosure. This was either 0 (no *E. coqui* enclosures) or between 4 and 6 (mean number of frogs during the experiment for *E. coqui* enclosures). Each of the models was run for each Hawaii site and the PR site. Final coefficients were standardized (SD 1) to allow comparisons between relationships with different measurement units. Unexplained variance (U) was calculated by the square root of ($1 - R^2$). Path coefficients, unexplained variances, and goodness-of-fit statistics were calculated using PROC CALIS in SAS Version 9.1 for Windows.

Results

Invertebrate communities

Aerial invertebrates collected across sites were mostly Diptera (58%), Homoptera (28%), Hymenoptera (6%), and Coleoptera (2%). We found no difference by treatment at BRY, but *E. coqui* reduced aerial invertebrates by 16% at NFR (Table 1). BRY had fewer aerial invertebrates than NFR ($F_{1,18} = 76.43$, $P < 0.0001$).

Herbivorous invertebrates collected across sites were mostly Homoptera (83%), Heteroptera (10%), and Coleoptera (4%). We found no difference by treatment at BRY, but *E. coqui* reduced herbivorous invertebrates by 11% at NFR (Table 1). BRY had fewer herbivorous invertebrates than NFR ($F_{1,36.1} = 451.62$, $P < 0.0001$).

Leaf litter invertebrates collected across sites were mostly Isopoda (34%), Collembola (29%), Acari (16%), Hymenoptera (8%), Amphipoda (5%), and Homoptera (2%). We found no difference by treatment at BRY, but *E. coqui* reduced leaf litter invertebrates by 20% at NFR (Table 1). There were no differences by treatment for microbivores, fragmenters, or predators (Table 1). BRY had fewer litter invertebrates than NFR ($F_{1,18.4} = 6.91$, $P = 0.017$).

Plant herbivory and growth

During the 6-month experiment, *M. candidum*, *P. cattleianum*, and *P. hawaiiensis* had 87, 99, and 65% survivorship, respectively, while no *M. polymorpha* survived. *M. polymorpha* are not considered further.

Total herbivory was comprised of 80% leaf area missing and 20% leaf miner damage. Mean percent herbivory was lower with *E. coqui* than without *E. coqui* (Fig. 1). No herbivory differences were found between sites ($F_{1,18} = 0.05$, $P = 0.83$) or species ($F_{2,72} = 2.32$, $P = 0.11$).

Number of new leaves for *P. cattleianum* increased with *E. coqui* (Table 2). Plants at BRY produced fewer new leaves than at NFR ($F_{1,18} = 10.07$, $P = 0.0053$). Other measures of plant growth (leaf surface area, stem height and diameter, above- and belowground biomass) did not differ by treatment at either site or across sites (Table 2). However, leaf surface area increases ($F_{1,18} = 4.76$, $P = 0.043$) and stem height increases ($F_{1,18} = 11.68$, $P = 0.0031$) were smaller at BRY than at NFR.

Table 1 Mean invertebrate totals (±1 SE) measured in enclosures with and without *Eleutherodactylus coqui* across sampling periods at two sites on the Island of Hawaii, USA ($n = 10$ enclosures per treatment per site)

Site	Invertebrate groups					
	Aerial	Herbivorous	Leaf litter	Leaf litter functional groups		
Treatment				Microbivores	Fragmenters	Predators
Bryson's Cinder Cone						
E. coqui	13.59 (0.58)	6.61 (0.47)	56.68 (4.11)	26.81 (3.35)	21.10 (1.80)	4.68 (0.61)
No *E. coqui*	13.69 (0.70)	5.61 (0.38)	54.14 (4.83)	27.74 (4.27)	18.31 (1.70)	5.38 (0.85)
Nanawale Forest Reserve						
E. coqui	29.61 (1.13)[a]	18.14 (1.19)[a]	62.79 (4.38)[a]	24.25 (2.69)	27.42 (2.38)	7.02 (1.18)
No *E. coqui*	35.40 (1.55)	20.20 (1.42)	73.57 (4.81)	26.57 (3.02)	34.08 (2.87)	7.33 (1.03)

[a] Mean values are significantly different when comparing across treatments by site ($P < 0.10$)

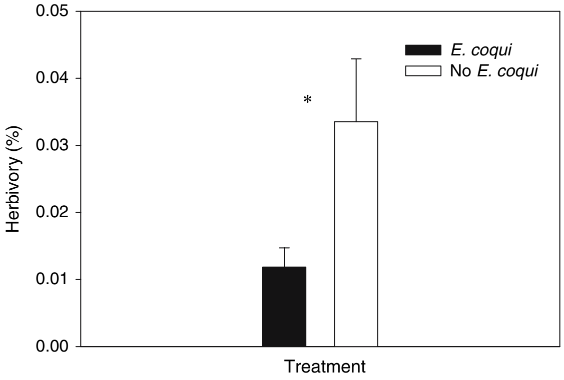

Fig. 1 Mean percent herbivory (+1 SE) in enclosures with and without *Eleutherodactylus coqui* across two sites on the Island of Hawaii. $n = 20$ per treatment. $^{*}P < 0.01$

Leaf wash chemistry

Concentrations of NH_4^+ in leaf wash increased by 47% and P increased by 8% with *E. coqui* (Fig. 2a). There was a 9% decrease in NO_3^- concentrations with *E. coqui* (Fig. 2a). Other elemental (Ca, Mg, and K) concentrations in leaf washes did not differ by treatment. Concentrations of NO_3^- ($F_{1,17.9} = 5.26$, $P = 0.034$) and Ca ($F_{1,37.6} = 4.62$, $P = 0.038$) in leaf washes were lower at BRY than NFR; no other elemental concentrations differed by site.

Leaf litter chemistry and decomposition rates

Concentrations of Mg, N, and K in decomposing leaf litter were 36, 6, and 44%, respectively, greater with *E. coqui* than without *E. coqui* (Fig. 2b). Concentrations of Ca, P, and N in decomposing leaf litter were lower at BRY than NFR; while Mg concentrations were greater at BRY than NFR ($F_{1,18} = 10.08$, $P = 0.0052$).

There was no treatment difference for N content (measured as mg of nutrient) in decomposing litter by site or treatment; however, P content was 8% higher with *E. coqui* than without *E. coqui* (0.94 ± 0.02 vs. 1.01 ± 0.04; $F_{1,52.5} = 5.09$, $P = 0.028$). CN ratios in decomposing leaf litter were 6% lower with *E. coqui* than without (90.3 ± 2.8 vs. 96.5 ± 3.0, $F_{1,54} = 0.74$, $P < 0.0001$). CN ratios were lower at 3 mo than at 6 mo ($F_{1,36} = 299.22$, $P < 0.0001$). CN ratios were 19% greater at BRY than NFR ($F_{1,18} = 49.36$, $P < 0.0001$).

Leaf litter decomposition rates were 3% faster with *E. coqui*, with a greater difference at 6 mo than at 3 mo (Fig. 3). Decomposition rates were 8% slower at BRY than at NFR ($F_{1,17.1} = 17.42$, $P = 0.0006$).

Path analyses

We found that *E. coqui* had a negative effect on herbivory at each site, and a positive effect on NH_4^+

Table 2 Mean plant measurements (±1 SE) of *Melastoma candidum*, *Psidium cattleianum*, and *Psychotria hawaiiensis* in enclosures with and without *Eleutherodactylus coqui* across two sites on the Island of Hawaii, USA ($n = 20$ enclosures per treatment)

Species	Plant measurements					
Treatment	Stem height growth (cm)	Number of new leaves (#)	Stem diameter growth (cm)	Leaf surface area growth (cm^2)	Aboveground biomass (g)	Belowground biomass (g)
M. candidum						
E. coqui	5.82 (0.91)	7.75 (0.40)	0.043 (0.0070)	253.81 (45.54)	0.35 (0.059)	0.10 (0.015)
No *E. coqui*	5.92 (1.06)	7.75 (0.50)	0.033 (0.0060)	240.16 (48.09)	0.35 (0.046)	0.09 (0.012)
P. cattleianum						
E. coqui	2.71 (0.39)	16.52 (1.040)[a]	0.029 (0.0050)	296.24 (33.50)	1.10 (0.10)	0.72 (0.076)
No *E. coqui*	3.51 (0.51)	13.11 (1.19)	0.029 (0.0040)	254.94 (32.71)	1.09 (0.073)	0.71 (0.079)
P. hawaiiensis						
E. coqui	0.74 (0.12)	3.12 (0.23)	0.013 (0.0020)	36.76 (4.36)	0.27 (0.030)	0.19 (0.024)
No *E. coqui*	0.70 (0.19)	2.81 (0.26)	0.013 (0.0040)	27.21 (5.58)	0.31 (0.049)	0.22 (0.033)

[a] Mean values are significantly different when comparing across treatment by plant species ($P < 0.001$)

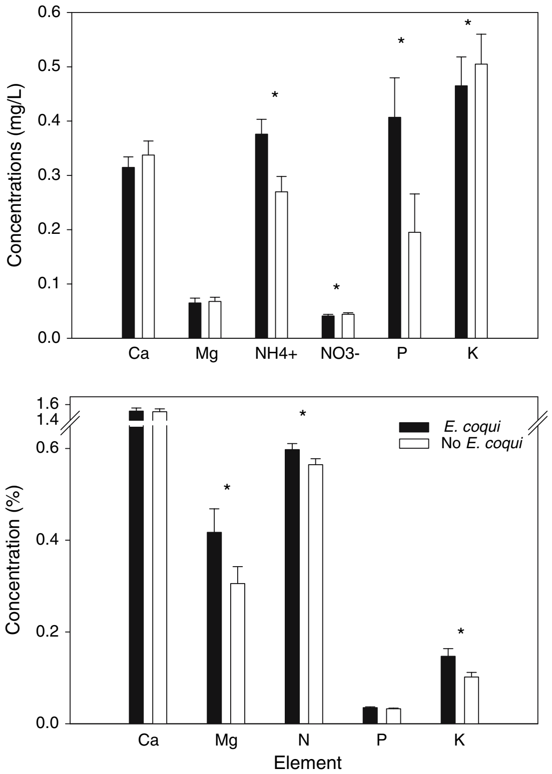

Fig. 2 **a** Mean concentrations (+1 SE) of NH_4^+, NO_3^-, Ca, Mg, P, and K in leaf washes in enclosures with and without *Eleutherodactylus coqui*. NH_4^+ and NO_3^- values are from *Psidium cattleianum* samples averaged across sampling periods, while Ca, Mg, P, and K values are averaged across plant species and sampling periods. **b** Mean concentrations (+SE) of Ca, Mg, N, P, and K in decomposing leaf litter in enclosures with and without *Eleutherodactylus coqui* across sites and sampling periods. *$P < 0.05$

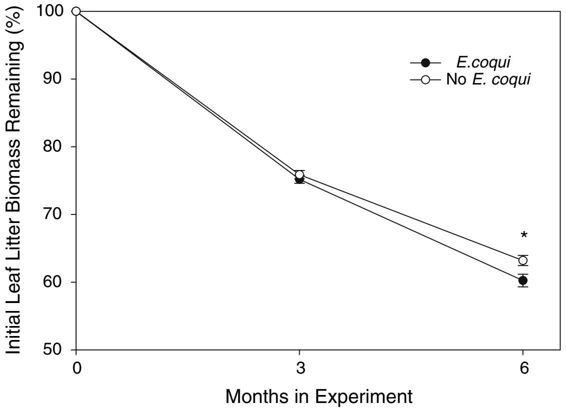

Fig. 3 Percent leaf litter biomass remaining (±1 SE) with and without *Eleutherodactylus coqui* across two sites on the Island of Hawaii at 3 and 6 months. *$P < 0.05$

concentrations in leaf washes at each site (Fig. 4a). At NFR and PR, NH_4^+ concentrations in leaf washes had a positive effect on the number of new leaves. Herbivory rates did not affect the number of new leaves at any site. *E. coqui* was found to have a negative effect on total leaf litter invertebrates at NFR only (Fig. 4b). At NFR and PR, NH_4^+ concentrations in leaf washes had a positive effect on leaf litter decomposition rates. Leaf litter invertebrates did not affect leaf litter decomposition rates at any site. Unexplained variance values were typical of these types of models (Mothershead and Marquis 2000; Price et al. 2005).

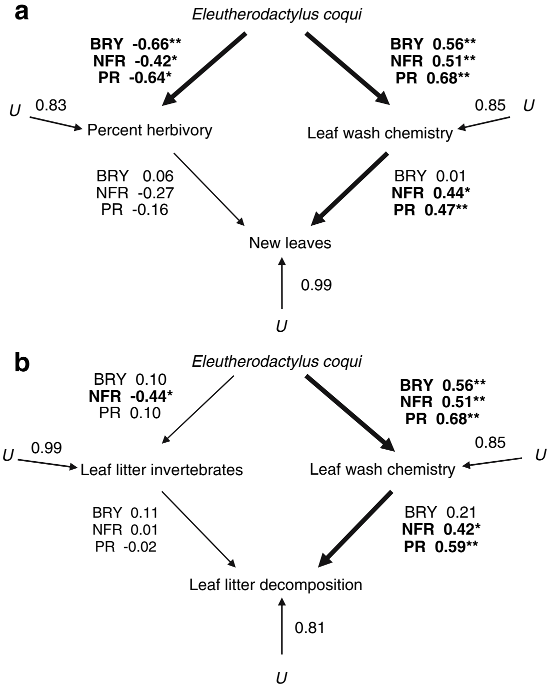

Fig. 4 **a** Path diagram of *Eleutherodactylus coqui* effects on the number of new leaves, as affected by percent herbivory and NH_4^+ concentrations in leaf washes. **b** Path diagram of *E. coqui* effects on leaf litter decomposition rates, as affected by leaf litter invertebrates abundance and NH_4^+ concentrations in leaf washes. Path coefficient values are for (1) Bryson's Cinder Cone (*BRY*), Hawaii, (2) Nanawale Forest Reserve (*NFR*), Hawaii, and (3) Luquillo Experimental Forest, Puerto Rico (*PR*). Unexplained variance (*U*) for endogenous variables is for (1 and 2 combined). *Bold arrows* indicate significant path coefficients for at least two sites. *Bolded sites* are significant for that pathway, *$P < 0.05$, and **$P < 0.01$

Discussion

In a 6-month enclosure experiment conducted in two lowland rain forest sites on the Island of Hawaii, we found that the invasive frog, *E. coqui*, lowers herbivory rates, and increases concentrations of several nutrients in leaf wash chemistry and decomposing leaf litter, leaf litter decomposition rates, and the number of new leaves on an invasive plant species. In general, *E. coqui* effects on ecosystem processes were consistent between the two study sites. However, the top-down effects of *E. coqui* on invertebrates greatly differed between the two sites. More specifically, we found that *E. coqui* reduced aerial, herbivorous, and leaf litter invertebrates at NFR and not at BRY.

There are several potential explanations for this site difference. First, NFR had higher invertebrate abundances (aerial, herbivorous, and leaf litter) than BRY. Perhaps we were unable to statistically discover a treatment effect at BRY due to the low number of invertebrates collected at this site, often approaching the zero bound (Table 1). Second, the established *E. coqui* population outside enclosures at NFR, and the lack of *E. coqui* at BRY, could have created a treatment effect at NFR if invertebrates outside enclosures sought refuge in enclosures without *E. coqui* (Pitt 1999; Schmitz and Suttle 2001). Alternatively, the established *E. coqui* population at NFR could have reduced the migration of invertebrates into enclosures, creating a treatment effect if invertebrates were not replaced as quickly at NFR as at BRY. We did not determine whether the reduction of invertebrates at NFR with *E. coqui* was through trait-mediated or density-mediated mechanisms. It would be important in future studies to determine whether invertebrates have behavioral responses to *E. coqui*.

New leaf and leaf litter decomposition models

We found that the top-down effect of *E. coqui* on both new leaves produced and leaf litter decomposition rates was better explained by a nutrient cycling effect than either a reduction in herbivory rates or invertebrate abundances. While top-down effects on ecosystem productivity through nutrient cycling by a vertebrate predator has been demonstrated in aquatic ecosystems (Schindler 1992; Vanni and Layne 1997), we do not know of any other study that has demonstrated this mechanism for vertebrate predators in terrestrial ecosystems. An exception to this may be in the case of allochthonous nutrient sources (Polis and Hurd 1996; Maron et al. 2006); however, in this study, we found that the effect of *E. coqui* was through autochthonous sources.

More specifically, in the new leaves model, we found positive relationships between *E. coqui* and leaf wash NH_4^+ concentrations, and leaf wash NH_4^+ concentrations and the number of new leaves on *P. cattleianum* seedlings (Fig. 2a). This suggests that there was a direct effect of *E. coqui* on the number of new *P. cattleianum* leaves through nutrient cycling, at least at NFR. This result is consistent with studies showing that *P. cattleianum* grows better in sites with elevated nutrient levels (Hughes and Denslow 2005). While we found that herbivory rates were lower with *E. coqui* across sites, as has been found in other studies of herptofauna effects on herbivory (Dial and Roughgarden 1995; Schoener and Spiller 1999), path analyses showed no relationship between herbivory and the number of new leaves, suggesting that this pathway was unimportant. If the nutrient cycling mechanism had not been investigated, we may have assumed that the increase in new leaves with *E. coqui* was due to reduced herbivory. As expected for islands (Angulo-Sandoval and Aide 2000), herbivory rates are low in Hawaii compared to continental areas, especially for non-native species (DeWalt et al. 2004), which may reduce the importance of herbivory on plant growth rates (Shurin et al. 2006). We do not, however, think that herbivory rates were artificially low because monthly herbivory rates on these plants were similar during the experiment and prior to the experiment when these plants were located outside the enclosures.

In the leaf litter decomposition model, we similarly found that nutrient cycling was a more important top-down mechanism than reduced abundance of leaf litter invertebrates in influencing leaf litter decomposition rates (Fig. 4b). If there was an indirect effect, we would have observed both a significant relationship between *E. coqui* and litter invertebrates and between litter invertebrates and leaf litter decomposition rates. The lack of an indirect effect in influencing leaf litter decomposition rates is not surprising because *E. coqui* is a generalist in the litter invertebrate community, and different feeding guilds are known to influence decomposition rates in contrasting ways. Alternatively, we found positive relationships between *E. coqui* and leaf wash NH_4^+ concentrations, and between leaf wash NH_4^+ concentrations and *M. polymorpha* decomposition rates, at least at NFR. This result is supported by studies suggesting that *M. polymorpha* decomposition rates increase with NP and P additions (Vitousek 1998).

Despite ANOVAs indicating an overall increase in the number of new leaves and leaf litter decomposition rates with *E. coqui* across sites in Hawaii, the path model only showed significant relationships between NH_4^+ concentrations in leaf washes and these variables at NFR. The path model only addresses the importance of two factors in explaining both the production rate of new leaves and leaf litter decomposition rates. Other factors are clearly important in influencing these processes, as indicated by the unexplained variance in the model, and other factors (e.g., P concentrations in leaf washes) likely contributed to increasing these rates with *E. coqui* at BRY.

Nutrient cycling mechanism

We attribute increased NH_4^+ and P concentrations in leaf washes at least in part to excrement because *E. coqui* was observed foraging on and above foliage, and excrement was observed on the foliage when leaf washes were collected. We attribute increased Mg, N, P, and K in decomposing leaf litter at least in part to *E. coqui* excrement and carcasses. As an example, increased P in decomposing litter was likely a direct effect of excrement and carcasses, and an indirect effect of fungal growth, stimulated by excrement and carcasses, which translocated P into leaf litter bags. Similar pathways likely increased Mg, N, and K concentrations in decomposing leaf litter. We did not distinguish between nutrients directly or indirectly from *E. coqui* in this study.

We found that *E. coqui* has important nutrient cycling effects. In this study system, nutrient cycling effects may be important because frog nitrogenous waste products are usually in the form of urea, while invertebrate waste products are in the least soluble form of nitrogenous waste, uric acid (Beard et al. 2002). Similarly, frog carcasses are more likely to decompose faster, and thus release nutrients faster, than invertebrate remains, which can act as a nutrient sink due to slow decomposition of chitinous exoskeletons (Seastedt and Tate 1981). Predator-mediated nutrient cycling effects will likely only be observed in ecosystems where predators convert nutrients to forms readily available to microbes and plants at a rate faster than their prey.

Comparison of results across ranges

Beard et al. (2002, 2003) found similar effects of *E. coqui* on ecosystem processes in PR. The path analyses conducted using PR data also showed that increases in new leaf production and leaf litter decomposition rates with *E. coqui* resulted from increased nutrient availability rather than from reduced herbivory rates and invertebrate abundances, respectively (Fig. 4a, b). The effect of *E. coqui* on invertebrate communities in PR differed from the effects found at either site in this study; in PR, only aerial invertebrates were found to be reduced with *E. coqui* (Beard et al. 2003); although, the present study also found site differences in the effect of *E. coqui* on invertebrates in Hawaii. In conclusion, results across ranges suggest that *E. coqui* effects on invertebrate communities will vary by site, but nutrient cycling effects will be similar regardless of site.

Implications

Because *E. coqui* reduced invertebrates at one study site, this study supports the idea that *E. coqui* can reduce endemic invertebrates in Hawaii. While *E. coqui* are mostly consuming non-native invertebrates, such as Amphipoda, Isopoda, and Hymenoptera: Formicidae, in Hawaii (Beard 2007), they have the ability to reduce invertebrate orders containing endemic species, such as Acari, Collembola, Diptera, and Homoptera. Furthermore, an increase in nutrient cycling rates in Hawaii could have a negative effect on native plant species that are slow-growing and that evolved in nutrient-poor conditions. As has been found in nutrient addition studies (Ostertag and Verville 2002), we found that *E. coqui* increased a plant growth response only for a non-native species. The native species had no response to *E. coqui*. By increasing nutrient cycling, *E. coqui* may confer a competitive advantage to invasive plants, and it would be important to test this hypothesis in future studies.

For this experiment, we used enclosures rather than a larger scale exclosures (i.e., *E. coqui* removal plots). While enclosures are viewed as a useful and potentially powerful way to understand mechanisms of trophic control of ecosystems (Schmitz 2004), their applicability to larger scale processes has been questioned (Carpenter 1999; MacNally 2000; Skelly 2002). We used enclosures because we wanted the results to be comparable to those from PR. To address concerns surrounding the use of enclosures, densities of *E. coqui* were natural (Woolbright et al. 2006); enclosure size was similar to *E. coqui* territory size, which *E. coqui* can remain in for several years (Woolbright 1985); invertebrate communities inside enclosures were determined to resemble those outside enclosures (Beard 2007); and enclosures contained seedlings of species that occurred on site. Furthermore, a 20 × 20 m^2 exclosure experiment was conducted in PR at the same time as the enclosure experiment described in this paper. The effects of *E. coqui* on invertebrate abundance, herbivory rates, and leaf litter decomposition rates were found to be similar across the two spatial scales (Beard et al. 2003). The smaller numbers of replicates and differences in collection methods were thought to contribute to the lack of significant differences by treatment at the larger spatial scale for plant growth rate and nutrient cycling variables (Beard et al. 2003). Thus, while enclosures do have limitations, we believe that enclosure studies conducted with this species provide insights into processes occurring at larger spatial scales. However, experiments conducted at larger spatial scales would further our understanding of the effects of *E. coqui* in Hawaii.

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References

Angulo-Sandoval P, Aide TM (2000) Leaf phenology and leaf damage of saplings in the Luquillo experimental forest, Puerto Rico. Biotropica 32:415–422

Beard KH (2007) Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii. Copeia 2007:281–291

Beard KH, Eschtruth AK, Vogt KA, Vogt DJ, Scatena FN (2003) The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. J Trop Ecol 19:607–617

Beard KH, Pitt WC (2005) Potential consequences of the coqui frog invasion in Hawaii. Divers Distrib 11:427–433

Beard KH, Vogt KA, Kulmatiski A (2002) Top-down effects of a terrestrial frog on nutrient dynamics. Oecologia 133:583–593

Carpenter SR (1999) Microcosm experiments have limited relevance for community and ecosystem ecology: reply. Ecology 80:1085–1088

Chapin FS, Reynolds HL, D'Antonio CM, Eckhart V (1996) The functional role of species in terrestrial ecosystems. In: Walker B, Steffen W (eds) Global change in terrestrial ecosystems. Cambridge University Press, New York

DeWalt SJ, Denslow JS, Ickes K (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85:471–483

Dial R, Roughgarden J (1995) Experimental removal of insectivores from rain forest canopy: direct and indirect effects. Ecology 76:1821–1834

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annu Rev Ecol Syst 29:113–140

Giambelluca TW, Nullet MA, Schroeder TA (1986) Rainfall atlas of Hawaii. Department of Land and Natural Resources, Division of Water and Land Development, Honolulu

Grenyer R, Orme C, Jackson S, Thomas G, Davies R, Davies T, Jones K, Olson V, Ridgely R, Rasmussen P, Ding T, Bennett P, Blackburn T, Gaston K, Gittleman J, Owens I (2006) Global distribution and conservation of rare and threatened vertebrates. Nature 444:93–96

Harmon ME, Lajtha K (1999) Analysis of detritus and organic horizons for mineral and organic constituents. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) Standard soil methods for long-term ecological research. Oxford University Press, New York

Hatcher L (1994) A step-by-step approach to using SAS for factor analysis and structural equation modeling. SAS Institute Inc., Cary, NC, USA

Holmes RT, Schultz JC (1988) Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Can J Zool 66:720–728

Hughes RF, Denslow JS (2005) Invasion by a N-2-fixing tree alters function and structure in wet lowland forests of Hawaii. Ecol Appl 15:1615–1628

Juvik SP, Juvik JO (1998) Atlas of Hawaii. University of Hawaii Press, Honolulu

Kraus F (2003) Invasion pathways of terrestrial vertebrates. In: Ruiz GM, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington, DC

Kraus F, Campbell EW (2002) Human-mediated escalation of a formerly eradicable problem: the invasion of Caribbean frogs in the Hawaiian Islands. Biol Invest 4:327–332

Kraus F, Campbell EW, Allison A, Pratt T (1999) *Eleutherodactylus* frog introductions to Hawaii. Herpetol Rev 30:21–25

MacNally R (2000) Modeling confinement experiments in community ecology: differential mobility among competitors. Ecol Model 129:65–85

Maron JL, Estes JA, Croll DA, Danner EM, Elmendorf SC, Buckelew SL (2006) An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. Ecol Monogr 76:3–24

Mills HA, Jones JB Jr (1997) Plant analysis handbook II. MicroMacro Publishing, Intl, Athens

Mothershead K, Marquis RJ (2000) Fitness impacts of herbivory through indirect effects on plant-pollinator interactions in *Oenothera macrocarpa*. Ecology 81:30–40

Nudds TD (1977) Quantifying the vegetative structure of wildlife cover. Wildl Soc B 5:113–117

Ostertag R, Verville JH (2002) Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. Plant Ecol 162:77–90

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Holle BV, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invest 1:3–19

Pitt WC (1999) Effects of multiple vertebrate predators on grasshopper habitat selection: trade-offs due to predation risk, foraging, and thermoregulation. Evol Ecol 13:499–515

Polis GA, Hurd SD (1996) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am Nat 147:396–423

Price M, Waser N, Irwin R, Campbell D, Brodya A (2005) Temporal and spatial variation in pollination of a montane herb: a seven-year study. Ecology 86:2106–2116

Schindler DE (1992) Nutrient regeneration by sockeye-salmon (*Oncorhynchus nerka*) fry and subsequent effects on zooplankton and phytoplankton. Can J Fish Aquat Sci 49:2498–2506

Schmitz OJ (2004) From mesocosms to the field: the role and value of cage experiments in understanding top-down effects in ecosystems. In: Weisser WW, Siemann E (eds) Insects and ecosystem function. Springer, Berlin, Germany

Schmitz OJ, Suttle KB (2001) Effects of top predator species on direct and indirect interactions in a food web. Ecology 82:2072–2081

Schoener TW, Spiller DA (1999) Indirect effects in an experimentally staged invasion by a major predator. Am Nat 153:347–358

Seastedt TR, Tate CM (1981) Decomposition rates and nutrient contents of arthropod remains in forest litter. Ecology 62:13–19

Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? real differences between aquatic and terrestrial food webs. Proc R Soc Lond 273:1–9

Skelly DK (2002) Experimental venue and estimation of interaction strength. Ecology 83:2097–2101

Stewart MM, Woolbright LL (1996) Amphibians. In: Reagan DP, Waide RB (eds) The food web of a tropical rain forest. University of Chicago Press, Chicago

Vanni MJ, Layne CD (1997) Nutrient recycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. Ecology 78:21–40

Vitousek PM (1998) The structure and functioning of montane tropical forests: control by climate, soils, and disturbance. Ecology 79:1–2

Whiles MR, Lips KR, Pringle CM, Kilham SS, Bixby RJ, Brenes R, Connelly S, Colon-Gaud JC, Hunte-Brown M, Huryn AD, Montgomery C, Peterson S (2006) The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Front Ecol Environ 4:27–34

Wolfe EW, Morris J (1996) Geologic map of the Island of Hawaii. US Dept. of the Interior, US Geological Survey, Honolulu

Woolbright LL (1985) Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. Herpetologica 41:1–9

Woolbright LL, Hara AH, Jacobsen CM, Mautz WJ, Benevides FL (2006) Population densities of the Coqui, *Eleutherodactylus coqui* (Anura: Leptodactylidae) in newly invaded Hawaii and in native Puerto Rico. J Herpetol 40:122–126