

Invasive litter, not an invasive insectivore, determines invertebrate communities in Hawaiian forests

Nathania C. Tuttle · Karen H. Beard ·
William C. Pitt

Received: 17 December 2007 / Accepted: 5 June 2008 / Published online: 21 June 2008
© Springer Science+Business Media B.V. 2008

Abstract In Hawaii, invasive plants have the ability to alter litter-based food chains because they often have litter traits that differ from native species. Additionally, abundant invasive predators, especially those representing new trophic levels, can reduce prey. The relative importance of these two processes on the litter invertebrate community in Hawaii is important, because they could affect the large number of endemic and endangered invertebrates. We determined the relative importance of litter resources, represented by leaf litter of two trees, an invasive nitrogen-fixer, *Falcataria moluccana*, and a native tree, *Metrosideros polymorpha*, and predation of an invasive terrestrial frog, *Eleutherodactylus coqui*, on leaf litter invertebrate abundance and composition. Principle component analysis revealed that *F. moluccana* litter creates an invertebrate community that greatly differs from that found in *M. polymorpha* litter. We found that *F. moluccana* increased the abundance of non-native fragmenters (Amphipoda and Isopoda) by 400% and non-native predaceous ants (Hymenoptera: Formicidae) by

200%. *E. coqui* had less effect on the litter invertebrate community; it reduced microbivores by 40% in *F. moluccana* and non-native ants by 30% across litter types. *E. coqui* stomach contents were similar in abundance and composition in both litter treatments, despite dramatic differences in the invertebrate community. Additionally, our results suggest that invertebrate community differences between litter types did not cascade to influence *E. coqui* growth or survivorship. In conclusion, it appears that an invasive nitrogen-fixing tree species has a greater influence on litter invertebrate community abundance and composition than the invasive predator, *E. coqui*.

Keywords Biological invasions · Bottom-up control · *Eleutherodactylus coqui* · Leaf litter · Top-down control · Trophic cascade

Introduction

Invasive plant species, which have traits that are distinctly different than those of native species, can greatly change community structure and ecosystem processes where they invade (Chapin et al. 1996; Vitousek 1986). These changes are particularly likely to occur in Hawaii, where native species have evolved in soils with very low nitrogen (N) concentrations (Goergen and Daehler 2001). Indeed, N-fixers have been extremely successful invaders on infertile soils in

N. C. Tuttle · K. H. Beard (✉)
Department of Wildland Resources and the Ecology
Center, Utah State University, Logan, UT 84322-5230,
USA
e-mail: karen.beard@usu.edu

W. C. Pitt
USDA/APHIS/WS/National Wildlife Research Center,
Hilo Field Station, Hilo, HI 96721, USA

Hawaii, where they have increased N inputs and cycling rates (Hughes and Denslow 2005; Vitousek and Walker 1989). The associated increase in N availability has been found to increase the growth, establishment, and spread of non-natives (Hughes and Denslow 2005; Vitousek and Walker 1989), and change the composition and activity of microbial communities (Allison et al. 2006). All of these changes can occur at the detriment of some native plant species, which are relatively unresponsive to N and phosphorus (P) addition (Ostertag and Verville 2002).

As an example, *Falcataria moluccana* [(Miquel) Barneby and Grimes] is a rapid-growing, N-fixing tree that was introduced from Indonesia in 1917 (Wagner et al. 1990). This tree is currently invading the few remaining native-dominated wet lowland forests in eastern Hawaii (Hughes and Uowolo 2006). As a result of the invasion, there has been an increase in N and P availability in the soil (Hughes and Denslow 2005), litterfall rates (Hughes and Denslow 2005), and leaf litter decomposition rates (Hughes and Uowolo 2006). Also, non-native N-fixing plants might alter litter-based food chains, which are thought to be classic examples of extreme bottom-up control (Ponsard et al. 2000). Many studies have found that different plants support different litter invertebrate organisms (Wardle 2002); therefore, non-native plant invasions should alter invertebrate community abundance and composition. However, relatively few studies have examined changes in litter invertebrate community composition as a result of non-native plant invasions, and this could be particularly important in Hawaii, where there are more than 5,000 endemic arthropod species (Eldredge and Evenhuis 2002).

Bottom-up influences, however, do not prevent the possibility of top-down influences at higher trophic levels (Ponsard et al. 2000). *Eleutherodactylus coqui* Thomas, a terrestrial frog endemic to Puerto Rico, was accidentally introduced into Hawaii around 1988 via the horticulture trade (Kraus et al. 1999). This species is of concern because it is able to reach densities up to 89,000/ha in some locations in Hawaii (Woolbright et al. 2006), and thus could be consuming an estimated 675,000 invertebrates (mostly litter invertebrates) $\text{ha}^{-1} \text{night}^{-1}$ (Beard 2007). Additionally, research suggests that *E. coqui* can reduce invertebrate prey (Beard et al. 2003; Sin et al. 2008; Stewart and Woolbright 1996). Thus, its predation effects on native invertebrates are of concern, and

need to be determined. Alternatively, invasive plants that alter the leaf litter invertebrate community (Ponsard et al. 2000; Rosemond et al. 2001; Wallace et al. 1999) may improve the prey base for *E. coqui*. Thus, it also should be determined if litter resources are an important factor contributing to the establishment and abundance of *E. coqui*.

The objective of this study was to compare the relative importance of litter resources, represented by leaf litter of the non-native, *F. moluccana*, and the native tree, *Metrosideros polymorpha*, and predation of *E. coqui* on leaf litter invertebrate abundance and composition in a Hawaiian lowland forest. Because litter resources are expected to exert extreme bottom-up control, we also investigate whether potential changes in the invertebrate community cascade to influence the growth and survivorship of *E. coqui*. We also determine the relative importance of the two leaf litter types and *E. coqui* on leaf litter decomposition rates.

Methods

Study site

We conducted the experiment in a tropical wet forest in the Nanawale Forest Reserve (NFR) on the Island of Hawaii, USA (19 28' N, 154 54' W, 230 m elevation). The site receives 3,000–4,000 mm of precipitation annually, with peak rainfall occurring between November and April (Giambelluca et al. 1986). The mean annual temperature is 23°C (Nullet and Sanderson 1993) with little seasonal variation (Price 1983). The site occurs on a rough a'ua lava flow substrate that is 400 years old (Wolfe and Morris 1996). Dominant overstory vegetation includes *Psidium cattleianum* Sabine, *M. polymorpha* Gaud, and *F. moluccana*. Understory dominants include *Cibotium* sp., *Melastoma candidum* D. Don, and *Clidemia hirta* (L.) D. Don.

Experimental design

To control the source pool of invertebrates and environmental factors, we conducted a common garden experiment, with a 2×2 full factorial design, with leaf litter of overstory plants (*F. moluccana* or *M. polymorpha*) and *E. coqui* (presence or absence)

as the main factors ($n = 10$ for each treatment combination). We conducted the experiment for 5 months, August through December 2005. We deemed this length of time as sufficient because invertebrate community responses to litter treatments in tropical wet lowland forests (Heneghan et al. 1999) and differences in leaf litter decomposition rates between *F. moluccana* and *M. polymorpha* in Hawaiian wet lowland forests (Hughes and Uowolo 2006) have been observed within this time period.

We randomly placed a total of 40, 1-m³ enclosures constructed of PVC frame (2.5 cm diameter) and covered on all sides with plastic mesh with 0.76×0.76 -cm openings, (BF Products, Harrisburg, Pennsylvania) in a 35×65 -m area on the forest floor. The mesh size allows passage of all leaf litter invertebrates found on site (Beard, unpubl. data) and prevents passage of adult *E. coqui* >26.2-mm SVL (snout-vent length). There were smaller frogs at the study site that could freely move into and out of the enclosures. We could not exclude these frogs from moving into the enclosures because they are similar in size to many invertebrates found at the study site. However, we found very few small frogs (often 6–10 mm SVL) in the enclosures over the course of the experiment. Light levels and temperature inside the enclosures were not different from the surrounding environment. We deemed the enclosure size appropriate because *E. coqui* have small territory sizes and do not disperse over the course of several years (Woolbright 1985), and studies have found this enclosure size appropriate for measuring invertebrate responses to frogs (Beard et al. 2003; Sin et al. 2008) and leaf litter (Hansen 2000).

Leaf litter treatment

We collected newly senesced leaf litter from the forest floor under *F. moluccana* and *M. polymorpha* trees <1 km from the experimental site. We considered yellow or red *M. polymorpha* leaves (Austin and Vitousek 2000) and yellow *F. moluccana* leaves on the forest floor newly senesced. *M. polymorpha* leaf size tends to be 5–10 cm² (Joel et al. 1994). *F. moluccana* has bipinnately compound leaves; leaflets (0.18–0.60 cm²), rachises, and petioles were all considered part of the leaf (22–30 cm long) (Jensen 1999). We placed air-dried leaf litter of each species on the floor of 20 randomly selected

enclosures. Because *M. polymorpha* decomposes slower than *F. moluccana*, we initially placed 150 g of air-dried litter (136 g oven-dried) on the floor of each enclosure, which is within the range of naturally occurring *M. polymorpha* litter on the forest floor on the Island of Hawaii (oven-dried mass: 92–432 g m⁻²) (Crews et al. 2000). We added additional litter (16 g, air-dried mass) weekly to the floor of the enclosures, corresponding to a mean annual leaf litterfall rate for *F. moluccana* of 7 Mg ha⁻¹ year⁻¹, which is a faster rate than that for *M. polymorpha* (0.25 Mg ha⁻¹ year⁻¹) (Hughes and Denslow 2005).

Frog treatment

We hand-captured frogs <1 km from the experimental site. We placed seven frogs in each of 10 enclosures of each litter type to approximate natural densities [from a recent Hawaiian estimate of 28,000–89,000 frogs/ha (Woolbright et al. 2006)]. To standardize treatments and because male frogs are easier to identify than female frogs, we used adult male frogs to control for greater female growth rates (Woolbright 1989) and prey consumption rates (Beard 2007). We marked each frog uniquely using toe clipping, and weighed and measured each frog. We removed all live frogs from each enclosure between 2000 h and 2200 h at the end of each month, and restocked the enclosures with seven adult male frogs. We left dead frogs in enclosures. We recorded growth [SVL to the nearest 0.01 mm using a digital caliper and biomass to the nearest 0.01 g] and survivorship of *E. coqui* on a monthly basis. We preserved removed frogs for subsequent stomach content analysis, in which we identified the invertebrates found in stomachs to order (family when possible).

Invertebrate community sampling

We collected invertebrates from a leaf litter tray (16 × 26 cm in area and 6 cm in height) every 2 weeks, and refilled the tray with an additional 20 g of air-dried leaf litter (the species assigned to the enclosure) in each enclosure. Trays had open tops, 15 openings (8 × 34 mm in area) on the sides, nine openings on the ends (8 × 34 mm in area), and 72 holes (4.5 mm diameter) arranged in a 6 × 12 grid on the bottom. The openings and holes were larger than all leaf litter invertebrates. We extracted invertebrates

from the leaf litter with Berlese-Tullgren funnels in the laboratory within 2 h. We identified all invertebrates collected to order (family when possible) and functional group for analysis: fragmenters (Amphipoda, Blattodea, Coleoptera, Dermaptera, Diplopoda, Gastropoda, Isopoda, and Psocoptera), microbivores (Acari, Collembola, and Diptera: Sciaridae), predators (Araneae, Chilopoda, Coleoptera: Staphylinidae, and Hymenoptera: Formicidae), and others (Coleoptera/Diptera larvae, Coleoptera: Scolytidae, Diptera, Heteroptera, Homoptera, Hymenoptera: other, Lepidoptera, Oligochaeta, Orthoptera, and Thysanoptera). We based identifications on Borror et al. (1989).

Leaf litter decomposition rates and chemistry

We placed six decomposition bags ($n = 240$ total, 15×15 cm, 0.23×0.23 cm mesh size), containing either 5 g of air-dried *M. polymorpha* leaves or 5 g of air-dried *F. moluccana* leaves, on the forest floor in each enclosure containing the same litter type. We oven-dried 20 initial subsamples (5 g, air-dried) of each litter type ($n = 40$ total) at 70°C and weighed the subsamples to establish the relationship between air-dried and oven-dried mass. After five months, we removed the decomposition bags from the enclosures, brushed them free of organic debris, oven-dried them at 70°C , and weighed them. We then hand-collected invertebrates from each decomposition bag, preserved the invertebrates, and identified them to order (family when possible) and functional group. We ground decomposition bag contents and homogenized them with a 2-mm mesh screen. We ashed a 0.5 g subsample from each decomposition bag overnight at 500°C to develop an ash-free conversion factor (Harmon and Lajtha 1999). We analyzed two additional 0.5 g subsamples from each decomposition bag ($n = 480$) for total C and N using a LECO TruSpec CN analyzer (LECO, St. Joseph, Michigan, USA), and we corrected them for C and N contamination from soil. We also analyzed the initial subsamples of each litter type for total C and N, and lignin using the 72% sulfuric acid procedure (Effland 1977).

Statistical analysis

To determine the effects of the treatments, litter (*M. polymorpha* and *F. moluccana*) and *E. coqui* (presence and absence), on the invertebrate

community in leaf litter trays and decomposition bags, we used a two-way factorial ANOVA with repeated measures through time and a compound symmetry covariance structure in a completely randomized, split-plot design. We used a similar analysis for *E. coqui* stomach contents, except we used a one-way ANOVA without an *E. coqui* treatment. Response variables for these analyses were abundances of invertebrate orders (only data for those comprising more than 3% of samples are presented throughout), invertebrate functional group abundances, and principal component (PC) values from principal components analyses (PCA), when appropriate. We conducted a PCA on invertebrate taxa abundances to reduce the dimensions of leaf litter invertebrate samples, decomposition bag invertebrates, and *E. coqui* stomach contents. We tested ordinations with a random permutation test. When the test was significant, we present PC scores for axes explaining >75% of the variation and loadings between -0.1 and 0.1 . We also conducted ANOVAs using these PC scores as response variables. For all ANOVAs, leaf litter type and frog (presence and absence), as appropriate, were fixed factors and enclosure was a random factor.

To determine *E. coqui* selection for each prey taxon relative to the abundance of each prey taxon in the environment (represented by leaf litter tray samples), we used Jacobs' prey electivity formula: $e_i = (p_i - p_k) / ((p_i + p_k) - (2p_i p_k))$, where p_i is the proportion of each prey taxon in stomachs, and p_k is the proportion of each prey taxon in the environment (Jacobs 1974). Electivity values range from -1 to $+1$, where negative values indicate avoidance of a prey taxon, and positive values indicate preference. Mean e_i values < -0.70 and > 0.70 for invertebrate taxa are presented. We did not include adult Diptera in this analysis because leaf litter trays are not likely to adequately sample this order and results could show a biased preference.

To test for differences in *E. coqui* growth, we used a 2×5 factorial ANOVA with litter type as a fixed effect and enclosures were subjects measured repeatedly over time; month (1–5) was a within subject factor. The response variables were initial SVL and initial biomass expressed as a proportion of SVL and biomass, respectively, after one month; analyses conducted on differences in SVL and biomass not as a proportion showed similar results. We used a

generalized linear model with a binomial distribution to test for differences in *E. coqui* survivorship. The response variable was the proportion of frogs that survived one month.

To test for differences in the fraction of leaf litter biomass remaining in decomposition bags, C and N concentrations, and CN ratio of decomposed litter, we used a two-way factorial ANOVA with a heterogeneous variance structure. We compared the C and N concentration and CN ratio of initial subsamples to that of decomposing litter using a one-way ANOVA for each litter type, with litter state (initial and decomposed) as fixed factors. We used a two tailed *t*-test to compare C, N, and lignin concentrations, percent moisture, and CN ratio between litter types in initial subsamples.

We conducted ANOVAs using PROC MIXED for all variables except for frog survivorship, which we conducted using PROC GLIMMIX, and we conducted *t*-tests using PROC TTEST in SAS/STAT v. 9.1.3 for Windows (SAS Institute 2006). We conducted PCAs using the *pca* function with a covariance matrix in the *labdsv* library R 2.0.1. To meet assumptions of normality and homogeneity, we logit-link transformed frog survivorship and inverse-square root transformed CN ratio. We considered $P < 0.05$ significant, except for invertebrate samples, where we considered $P < 0.10$ significant because we suspected high spatial and temporal variability (*sensu* Holmes and Schultz 1988).

Results

Invertebrate communities

We collected and identified a total of 97,541 invertebrates from enclosure leaf litter trays; samples across litter types and frog treatments mostly consisted of Isopoda (66%), Amphipoda (11%), Collembola (6%), Acari (5%), Coleoptera and Diptera larvae (5%), and Hymenoptera: Formicidae (3%). PCA showed there were differences among treatments (*ordtest*: $P = 0.0001$; Fig. 1). PC1 loaded negatively on Isopoda (-0.98) and Amphipoda (-0.17), and the ANOVA on PC1 scores showed that there were more Amphipoda and Isopoda in *F. moluccana* than *M. polymorpha* (litter, $F_{1,21.8} = 88.50$, $P < 0.0001$).

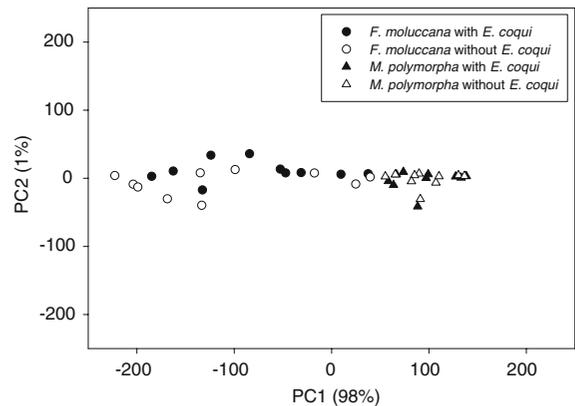
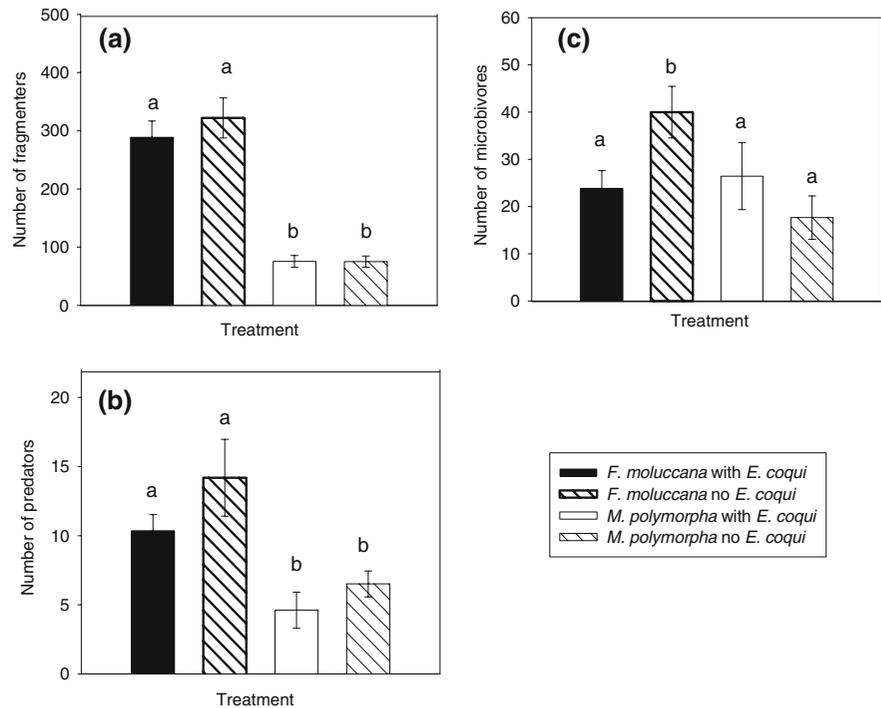


Fig. 1 Principal components analysis of invertebrates collected from semi-monthly leaf litter samples of *Falcataria moluccana* and *Metrosideros polymorpha* in enclosures with and without *Eleutherodactylus coqui*, Island of Hawaii, USA, 2005. Means were calculated by averaging samples across time (10 time periods) for each enclosure, and then averaging across treatments ($n = 10$ enclosures per treatment). Variance explained by PC1 and PC2 in parentheses

ANOVAs show that fragmenter (Fig. 2a; litter, $F_{1,36} = 97.45$; $P < 0.0001$) and predator abundance (Fig. 2b; litter, $F_{1,36} = 15.44$, $P = 0.0004$) was 400% and 200% greater, respectively, in *F. moluccana* than in *M. polymorpha*, but *E. coqui* had no effect on their abundance. We determined that 99% of the fragmenters were non-native (one Isopoda species, *Porcellio laevis*, and one Amphipoda species, *Talitroides topitotum*, D. Preston pers. comm.), and that 93% of the predators were non-native ants (Hymenoptera: Formicidae, R. Snelling, pers. comm.). When we repeated the predator analysis with only ants, we found that ant abundance was 200% greater in *F. moluccana* than in *M. polymorpha* (litter, $F_{1,36} = 15.32$, $P = 0.0004$), and 30% lower with *E. coqui* across litter types (frog, $F_{1,36} = 3.06$, $P = 0.091$). ANOVAs also show that there was a 40% microbivore reduction with *E. coqui* in *F. moluccana* (Fig. 2c; litter \times frog, $F_{1,36} = 4.52$, $P = 0.040$). Of the microbivores, 52% were Collembola and 46% were Acari, which both had origin status (native or non-native) that we were unable to determine.

Analyses conducted on individual orders suggest that Amphipoda, Collembola, Isopoda, and Coleoptera/Diptera larvae were all greater in *F. moluccana* than in *M. polymorpha*, and that *E. coqui* reduced Collembola in *F. moluccana* (litter \times frog, $F_{1,36} = 3.92$, $P = 0.056$), reduced Hymenoptera:

Fig. 2 Mean number of (a) fragmenters, (b) predators, and (c) microbivores (\pm SE) in *Falcataria moluccana* and *Metrosideros polymorpha* samples in enclosures with and without *Eleutherodactylus coqui*, Island of Hawaii, USA, 2005. Means were calculated by averaging samples across time for each enclosure (10 time periods), and then averaging across treatments ($n = 10$ enclosures per treatment). A different letter indicates a significant difference ($P < 0.05$)



Formicidae across litter types, and increased Coleoptera/Diptera larvae across litter types (Table 1).

Frog prey, growth, and survivorship

We identified 1,411 invertebrates from 358 *E. coqui* stomachs. Dominant prey items included Amphipoda (45%), Coleoptera: Scolytidae (10%), Hymenoptera: Formicidae (7%), Diptera (6%), Coleoptera (5%), and Isopoda (5%). PCA showed there were no differences among treatments (ordtest: $P = 0.68$;

Fig. 3). Furthermore, ANOVAs showed no differences between litter types for abundances of functional groups or invertebrate orders (Table 2).

Electivity analysis suggests *E. coqui* prefer Amphipoda in *F. moluccana* (0.72) and *M. polymorpha* (0.73), avoid Isopoda in *F. moluccana* (−0.94) and *M. polymorpha* (−0.95), and avoid Coleoptera/Diptera larvae in *F. moluccana* (−0.70).

Mean monthly *E. coqui* biomass decreased by 0.03 ± 0.009 g and SVL increased by 1.01 ± 0.001 mm, and the mean proportion surviving monthly

Table 1 Mean invertebrate abundance (\pm SE) for leaf litter invertebrate orders comprising >3% of total invertebrates in leaf litter samples from enclosures with *Falcataria moluccana* and *Metrosideros polymorpha*, with and without *Eleutherodactylus coqui*

Order: Family	<i>F. moluccana</i>		<i>M. polymorpha</i>	
	<i>E. coqui</i>	No <i>E. coqui</i>	<i>E. coqui</i>	No <i>E. coqui</i>
Acari	11.51(1.34) ^{A,A}	14.86(1.81) ^{A,A}	14.04(5.95) ^{A,A}	8.77(2.09) ^{A,A}
Amphipoda	48.45(7.65) ^{A,A}	41.14(4.20) ^{A,A}	9.76(1.26) ^{B,A}	8.15(1.38) ^{B,A}
Coleoptera/Diptera larvae	18.75(1.81) ^{A,A}	14.77(1.48) ^{A,B*}	6.52(0.59) ^{B,A}	5.75(0.75) ^{B,B*}
Collembola	11.58(3.15) ^{A,A}	24.62(5.85) ^{A,A}	11.84(5.29) ^{B*,A}	8.24(3.82) ^{B*,A}
Hymenoptera: Formicidae	9.68(1.12) ^{A,A}	13.64(2.79) ^{A,B*}	4.02(1.32) ^{B,A}	5.98(0.90) ^{B,B*}
Isopoda	237.14(23.24) ^{A,A}	278.41(31.27) ^{A,A}	63.84(9.37) ^{B,A}	64.69(8.89) ^{B,A}
Total	350.56(25.14) ^{A,A}	401.45(29.97) ^{A,A}	116.38(7.70) ^{B,A}	106.95(7.57) ^{B,A}

The first letter in superscript indicates a significant difference by litter treatment. The second letter indicates a significant difference by frog treatment. Significant interactions are discussed in the text. In all cases, $P < 0.05$, except when noted, * $P < 0.10$

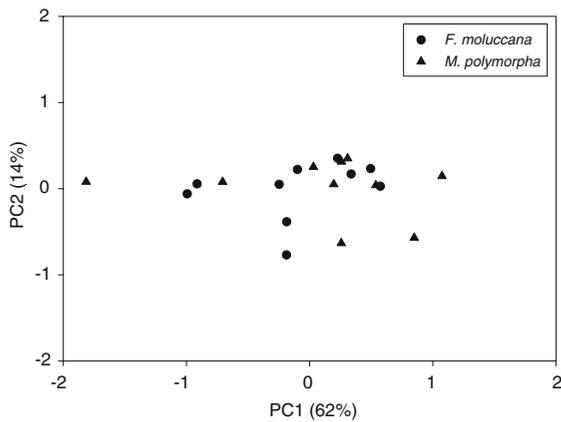


Fig. 3 Principal components analysis of invertebrates found in *Eleutherodactylus coqui* stomachs from enclosures with *Falcataria moluccana* ($n = 10$) and *Metrosideros polymorpha* ($n = 10$) leaf litter. Mean number of individuals in each invertebrate order was determined for all frogs surviving monthly ($n = 5$ months) in each enclosure, Island of Hawaii, USA, 2005. Means were calculated by averaging stomach contents across time for each enclosure, and then averaging across treatments. Variance explained by PC1 and PC2 in parentheses

Table 2 Mean invertebrate abundance (\pm SE) for leaf litter invertebrate functional groups and orders comprising $>3\%$ of total invertebrates in *Eleutherodactylus coqui* stomachs from enclosures with *Falcataria moluccana* and *Metrosideros polymorpha*

Functional group	<i>F. moluccana</i> $n = 177$	<i>M. polymorpha</i> $n = 182$
Order: Family		
Fragmenters	1.99(0.22) ^A	1.94(0.30) ^A
Amphipoda	1.67(0.21) ^A	1.50(0.26) ^A
Coleoptera	0.09(0.05) ^A	0.17(0.09) ^A
Isopoda	0.17(0.05) ^A	0.14(0.04) ^A
Microbivores	0.16(0.06) ^A	0.19(0.05) ^A
Collembola	0.09(0.04) ^A	0.15(0.05) ^A
Predators	0.43(0.22) ^A	0.23(0.06) ^A
Hymenoptera: Formicidae	0.37(0.22) ^A	0.20(0.06) ^A
Other	0.71(0.12) ^A	1.33(0.33) ^A
Coleoptera: Scolytidae	0.14(0.05) ^A	0.74(0.32) ^A
Diptera	0.20(0.06) ^A	0.28(0.08) ^A
Total	3.50(0.31) ^A	3.97(0.36) ^A

A different letter in superscript indicates a significant difference by litter treatment ($P < 0.10$)

was 0.51 ± 0.03 . There was no difference in proportional biomass change (litter, $F_{1,18} = 1.07$, $P = 0.31$), proportional SVL change (litter, $F_{1,18} = 0.19$, $P = 0.67$), or survivorship (litter, $F_{1,16.46} = 0.25$, $P = 0.62$) between frogs placed in the two litter types.

Leaf litter bag chemistry, invertebrates, and decomposition

Initial *F. moluccana* samples had a lower C concentration and CN ratio, and higher N and lignin concentration than initial *M. polymorpha* samples (Table 3). There was no difference between air-dried to oven-dried moisture content between the two litter types (Table 3). CN ratios were lower in decomposing litter than in initial subsamples in *F. moluccana* (litter state, $F_{1,38} = 312.81$, $P < 0.0001$) and *M. polymorpha* (litter state, $F_{1,38} = 803.54$, $P < 0.0001$).

We identified 18,178 invertebrates in the decomposition bags, which consisted primarily of Isopoda (52%), Acari, suborder Oribatida (19%), Amphipoda (10%), Hymenoptera: Formicidae (9%), and Coleoptera: Scolytidae (4%). PCA showed there were no differences among treatments (ordtest: $P = 0.52$). ANOVAs showed that there were more microbivores and predators, and more specifically, Acari: Oribatida, Coleoptera: Scolytidae, and Hymenoptera: Formicidae, in *M. polymorpha* decomposition bags than *F. moluccana* decomposition bags (Table 4). There were no differences in the invertebrate community with and without frogs by abundances of functional groups or invertebrate orders in the decomposition bags (Table 4).

F. moluccana leaf litter decomposed more rapidly than *M. polymorpha* (litter, $F_{1,20.1} = 18.10$, $P = 0.0004$). *M. polymorpha* decomposed faster with *E. coqui*, but there was no statistical support at our criterion level (litter \times frog, $F_{1,18} = 4.07$, $P = 0.059$), whereas decomposition for *F. moluccana* with and without *E. coqui* was non-significant (litter \times frog, $F_{1,18} = 0.02$; $P = 0.89$).

Table 3 Mean initial chemical characteristics of *Falcataria moluccana* and *Metrosideros polymorpha* litter

Litter chemistry	<i>F. moluccana</i> $n = 20$	<i>M. polymorpha</i> $n = 20$
%C	50.26(0.09) ^A	52.53(0.25) ^B
%N	1.82(0.03) ^A	0.42(0.006) ^B
C:N	27.77(0.42) ^A	126.10(1.98) ^B
% Lignin	39.57(0.68) ^A	32.83(0.56) ^B
% Moisture	10.84(0.42) ^A	9.63(0.65) ^A

A different letter in superscript indicates a significant difference ($P < 0.05$) between litter types

Table 4 Mean invertebrate abundance (\pm SE) for leaf litter invertebrate functional groups and orders comprising >3% of total invertebrates in decomposition bags from enclosures with*Falcataria moluccana* and *Metrosideros polymorpha*, with and without *Eleutherodactylus coqui*

Functional group	<i>F. moluccana</i>		<i>M. polymorpha</i>	
	<i>E. coqui</i>	No <i>E. coqui</i>	<i>E. coqui</i>	No <i>E. coqui</i>
Fragmenters	50.35(7.97) ^A	53.60(9.68) ^A	48.93(6.82) ^A	41.95(5.08) ^A
Amphipoda	7.13(0.78) ^A	7.83(1.29) ^A	9.28(1.43) ^A	7.28(1.25) ^A
Isopoda	41.82(7.71) ^A	44.93(8.96) ^A	38.42(6.40) ^A	33.55(4.37) ^A
Microbivores	12.40(2.02) ^A	10.37(3.29) ^A	20.34(3.54) ^B	16.85(2.55) ^B
Acari	12.31(2.02) ^A	10.05(3.30) ^A	20.16(3.52) ^B	16.73(2.57) ^B
Predators	5.20(1.06) ^A	4.02(1.01) ^A	14.12(4.21) ^B	8.59(2.07) ^B
Hymenoptera: Formicidae	4.52(0.96) ^A	3.47(0.91) ^A	13.28(4.11) ^B	7.99(2.09) ^B
Other	3.57(0.77) ^A	2.47(0.58) ^A	7.16(2.80) ^A	8.06(4.63) ^A
Coleoptera: Scolytidae	1.35(0.53) ^A	0.58(0.20) ^A	4.58(2.48) ^{B*}	6.52(4.57) ^{B*}
Total	71.20(9.48) ^A	70.47(13.40) ^A	83.85(11.14) ^A	74.24(9.73) ^A

A different letter in superscript indicates a significant difference by litter treatment. There are no differences by frog treatment. In all cases, $P < 0.05$, except when noted, * $P < 0.10$

Discussion

Our results suggest that litter resources of invasive plants have the potential to have a much greater impact on invertebrate abundance and community composition than the direct and indirect effects of a highly abundant invasive insectivore, such as *E. coqui*. More specifically, the findings show that *F. moluccana* leaf litter creates a very different invertebrate community than *M. polymorpha* leaf litter in the lowland forests of Hawaii, and that *E. coqui* did not have an effect of similar magnitude on the invertebrate community. In addition, we found that *F. moluccana* litter not only had the ability to change the invertebrate community, but also had the ability to greatly increase the abundance of non-native invertebrates.

More specifically, we found that *F. moluccana* increased litter fragmenter abundance by 400% (99% of which were non-native Isopoda and Amphipoda) and non-native predaceous ant (Hymenoptera: Formicidae) abundance by 200%. Because we controlled for initial litter biomass, and samples were collected frequently (every 2 weeks), the most parsimonious explanation for this increase is the greater N and P concentrations, lower CN ratio, and greater leaf surface area per unit of litter biomass of newly senesced *F. moluccana* leaf litter compared to *M. polymorpha* (Hughes and Uowolo 2006).

In general, *E. coqui* had little effect on the litter invertebrate community, even though a diet study suggests that they mostly consume litter invertebrates in Hawaii (Beard 2007). Exceptions include a 40% decrease in microbivore abundance in *F. moluccana*, which likely resulted from a 54% decrease in Collembola abundance, and a 30% decrease in non-native ant abundance across litter types. *E. coqui* also caused a 19% increase in Coleoptera/Diptera larvae across litter types. This may have occurred because this group largely feeds on frog carcasses.

Because there are many endemic invertebrates in Hawaii, it would be important to know whether these effects influence endemics. However, it is difficult to determine from our study the net effect of *E. coqui* on endemic Collembola in *F. moluccana* because, compared to *M. polymorpha*, *F. moluccana* increased Collembola abundance, and we could not determine the origin (i.e., native or non-native) of species in this order. *E. coqui* predation of non-native ants may benefit endemics, as ants are known to have a negative effect (i.e. predation and competition) on endemic invertebrates (Gillespie and Reimer 1993); however, our study did not permit such a comparison. Finally, we do not know the origin of Coleoptera and Diptera larvae, thus we do not know whether native or non-native larvae increased with *E. coqui*; although we could identify larvae in the family Culicidae (mosquitoes) because they are so distinct,

and know that none of the larvae in our samples were in this family, which would be a result of significance in Hawaii (Beard and Pitt 2005).

Frog prey, growth, and survivorship

Prey items in *E. coqui* stomachs were surprisingly similar in *F. moluccana* and *M. polymorpha* litter, despite dramatic differences in invertebrate abundances. The lack of an increase in prey items in *E. coqui* stomachs with increased invertebrates in *F. moluccana* may have occurred because prey were not limiting in the enclosures; *E. coqui* was not able to utilize the increase in resources; or prey preferences created similar diets in the two litter types. Because we found no difference in the invertebrate taxa in *E. coqui* stomachs across litter types, the 54% reduction of Collembola in *F. moluccana* with *E. coqui* is, in part, likely due to indirect effects, such as a behavior response of Collembola to *E. coqui* or through a trophic cascade with another prey item.

Electivity analyses suggest that *E. coqui* prefer Amphipoda and avoid Isopoda across litter types. We might have expected prey preferences (i.e. for Amphipoda) to translate to differences in invertebrate abundances across litter types with *E. coqui*. However, it is likely that litter type masked these effects because following Isopoda, Amphipoda was the order second most influenced by litter type. The other preference may not be expected to result in differences with *E. coqui* across litter types because it was an avoidance. For example, Isopoda was a small portion (5%) of their diet across litter types, even though it accounted for 66% of invertebrates collected from litter trays, and was four times more abundant in *F. moluccana* than *M. polymorpha* (Table 2).

Invertebrate community differences between litter types also did not influence *E. coqui* growth or survivorship. We expected that *E. coqui* growth and survivorship to be higher in *F. moluccana* because there were more invertebrates. There are several potential explanations for this finding. First, as previously mentioned, we found that *E. coqui* were not consuming more invertebrates in *F. moluccana* litter. Second, *M. polymorpha* leaves are much larger than *F. moluccana* leaflets, which might have provided *E. coqui* with more cover and reduced desiccation (Pough et al. 1983). Finally, because *E.*

coqui mass and SVL changes were small in both litter types, if there was a difference in *E. coqui* growth between treatments, it might have been difficult to detect.

Leaf litter bag invertebrates and decomposition

The litter invertebrate community in the decomposition bags represents the invertebrate community present after five months of decomposition. After five months, all invertebrate groups that differed between litter types had greater abundances in *M. polymorpha* than *F. moluccana*. This likely occurred because there was a greater proportion of *M. polymorpha* (55% \pm 0.64%) compared to *F. moluccana* (48% \pm 1.6%) remaining in the bags, or because the chemical quality of *M. polymorpha* compared to *F. moluccana* could have increased over time. The lack of an *E. coqui* effect on invertebrates inside decomposition bags might be attributed to their inability to directly predate on these invertebrates or indirectly influence their behavior.

Previous research has suggested that leaf litter decomposition rates of *F. moluccana* and *M. polymorpha* are more a function of the dominant species in the forest stand than initial chemical composition, and that decomposition rates are faster in stands dominated by *F. moluccana* than those dominated by *M. polymorpha* (Hughes and Uowolo 2006). Our results differ in that we found that *F. moluccana* decomposed at a faster rate than *M. polymorpha* in a forest stand that had both species in the canopy. However, our study provides a hypothesis for the pattern observed by Hughes and Uowolo (2006). Our study suggests that decomposition rates could change as a function of the dominant tree species because litter invertebrate communities differ. More specifically, the great initial increase in fragmenters, which were many times more abundant than the other functional groups, in newly senesced *F. moluccana* litter compared to *M. polymorpha* litter, might increase decomposition rates in *F. moluccana*-dominated stands compared to *M. polymorpha*-dominated stands.

We found a lack of statistical support for an *E. coqui* effect on decomposition rates over five months in both litter types, despite previous studies showing that *E. coqui* increases decomposition rate in both Hawaii and Puerto Rico (Beard et al. 2003; Sin et al.

2008). Although, the study showing that *E. coqui* increased *M. polymorpha* decomposition rates in Hawaii (Sin et al. 2008), only found a significant effect after 6 months, and not after 3 months, and this experiment was conducted for 5 months. The increase in decomposition rates with *E. coqui* has been attributed to an increase in nutrients in forms more available to microbes and fungi; more specifically, increased N and P availability from waste and carcasses (Beard et al. 2002). Thus, we expected that *E. coqui* would have a greater influence on decomposition rates of *M. polymorpha* than *F. moluccana* because *M. polymorpha* decomposition is more N- and P-limited (Vitousek 1998). Our results do suggest that *E. coqui* is more likely to affect *M. polymorpha* decomposition rates than *F. moluccana*, because *M. polymorpha* decomposition with *E. coqui* was nearly significantly faster, while decomposition for *F. moluccana* with and without *E. coqui* was non-significant.

Landscape-level implications

We chose to conduct this experiment in a common garden to control the source pool of invertebrates and environmental factors. However, we do not know if the results of this controlled experiment represent landscape conditions. For example, we found that *F. moluccana* supports more invertebrates based on litter resources alone, but *F. moluccana* may support even more invertebrates in the environment due to greater canopy cover and faster litterfall rates (Hughes and Denslow 2005). Litter resources alone do not appear to improve the diet, growth, or survivorship of *E. coqui*, but other characteristics of *F. moluccana*, such as additional habitat structure (e.g. larger boles, more vines on boles, and greater tree height) for foraging and calling, and more shade, might support more *E. coqui* on a landscape-scale. Furthermore, in *F. moluccana*-invaded forests, both litter types are often available, so *E. coqui* may benefit from increased invertebrate abundance as a result of *F. moluccana* invasion, and from the additional cover provided by *M. polymorpha* leaf litter on the forest floor. Future research could determine whether our results correlate with landscape conditions, and if traits other than litter characteristics of *F. moluccana* and *M. polymorpha* explain differences in the invertebrate community

and *E. coqui* densities in native and *F. moluccana*-invaded forests.

Acknowledgements Funding was provided by the Jack H. Berryman Institute and the Hawaii Invasive Species Council (Hawaii Department of Land and Natural Resources). We thank M. Higashi, M. Tuttle, A. Huff, J. Verlinde, K. Crowell, D. Grant, S. Bisrat, C. Richins, and S. Selamet for field and laboratory assistance; S. Durham for statistical advice; R. Ryel for vehicle use; and D. Preston and R. Snelling for invertebrate identification to species and origin. Procedures were performed with the approval of Utah State University's Institutional Animal Care and Use Committee permit number 1145R.

References

- Allison SD, Nielsen C, Hughes RF (2006) Elevated enzyme activities in soils under the invasive nitrogen-fixing tree *Falcataria moluccana*. *Soil Biol Biochem* 38:1537–1544. doi:10.1016/j.soilbio.2005.11.008
- Austin AT, Vitousek PM (2000) Precipitation, decomposition and litter decomposability of *Metrosideros polymorpha* in native forests on Hawai'i. *J Ecol* 88:129–138. doi: 10.1046/j.1365-2745.2000.00437.x
- Beard KH (2007) Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii. *Copeia* 2007:281–291. doi:10.1643/0045-8511(2007)7[281:DOTIFE]2.0.CO;2
- Beard KH, Pitt WC (2005) Potential consequences of the coqui frog invasion in Hawaii. *Divers Distrib* 11:427–433. doi: 10.1111/j.1366-9516.2005.00178.x
- Beard KH, Vogt KA, Kulmatiski A (2002) Top-down effects of a terrestrial frog on forest nutrient dynamics. *Oecologia* 133:583–593. doi:10.1007/s00442-002-1071-9
- 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. doi:10.1017/S0266467403006011
- Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects. Saunders College Publishing, Philadelphia
- Chapin FS III, Reynolds H, 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, Cambridge, pp 403–430
- Crews TE, Farrington H, Vitousek PM (2000) Changes in asymbiotic, heterotrophic nitrogen fixation on leaf litter of *Metrosideros polymorpha* with long-term ecosystem development in Hawaii. *Ecosystems* (N Y, Print) 3:386–385. doi:10.1007/s100210000034
- Effland MJ (1977) Modified procedure to determine acid insoluble lignin in wood and pulp. *TAPPI* 60:143–144
- Eldredge LG, Evenhuis NL (2002) Numbers of Hawaiian species for 2000. *Bish Mus Occas Pap* 68:71–78
- Giambelluca TW, Nullet MA, Schroeder PA (1986) Rainfall atlas of Hawai'i. Department of Land and Natural Resources, Honolulu

- Gillespie RG, Reimer N (1993) The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae:Tetragnathidae). *Pac Sci* 47:21–33
- Goergen E, Daehler CC (2001) Reproductive ecology of a native Hawaiian grass (*Heteropogon contortus*; Poaceae) versus its alien competitor (*Pennisetum setaceum*; Poaceae). *Int J Plant Sci* 162:317–326. doi:[10.1086/319587](https://doi.org/10.1086/319587)
- Hansen RA (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81:1120–1132
- 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, pp 143–165
- Heneghan L, Coleman DC, Zou X, Crossely DA Jr, Haines BL (1999) Soil microarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. *Ecology* 80:1873–1882
- 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 an N-2-fixing tree alters function and structure in wet lowland forests of Hawaii. *Ecol Appl* 15:1615–1628. doi:[10.1890/04-0874](https://doi.org/10.1890/04-0874)
- Hughes RF, Uowolo A (2006) Impacts of *Falcataria moluccana* invasion on decomposition in Hawaiian lowland wet forests: The importance of stand-level controls. *Ecosystems* (N Y, Print) 9:977–991. doi:[10.1007/s10021-005-0083-9](https://doi.org/10.1007/s10021-005-0083-9)
- Jacobs J (1974) Quantitative measurement of food selection. *Oecologia* 14:413–417. doi:[10.1007/BF00384581](https://doi.org/10.1007/BF00384581)
- Jensen M (1999) *Trees commonly cultivated in Southeast Asia: An illustrated field guide*. RAP Publication 13. Food and Agricultural Organization, Regional Office for Asia and the Pacific (RAP), Bangkok
- Joel G, Aplet G, Vitousek PM (1994) Leaf morphology along environmental gradients in Hawaiian *Metrosideros polymorpha*. *Biotropica* 26:17–22. doi:[10.2307/2389106](https://doi.org/10.2307/2389106)
- Kraus F, Cambell EW, Allison A, Pratt T (1999) *Eleutherodactylus* frog introductions to Hawaii. *Herpetol Rev* 30:21–25
- Nullet D, Sanderson M (1993) Radiation and energy balances and air temperatures. In: Sanderson M (ed) *Prevailing trade winds: weather and climate in Hawaii*. University of Hawaii Press, Honolulu, pp 37–55
- 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. doi:[10.1023/A:1020332824836](https://doi.org/10.1023/A:1020332824836)
- Ponsard S, Arditi R, Jost C (2000) Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain. *Oikos* 89:524–540. doi:[10.1034/j.1600-0706.2000.890312.x](https://doi.org/10.1034/j.1600-0706.2000.890312.x)
- Pough FH, Taigen TL, Stewart MM, Brussard PF (1983) Behavioral modification of evaporative water loss by a Puerto Rican frog. *Ecology* 64:244–252. doi:[10.2307/1937072](https://doi.org/10.2307/1937072)
- Price S (1983) Climate. In: Armstrong RW (ed) *Atlas of Hawaii*. University of Hawaii Press, Honolulu, pp 59–66
- Rosemond AD, Pringle CM, Ramirez A, Paul MJ (2001) A test of top-down and bottom-up control in a detritus based food web. *Ecology* 82:2279–2293
- Sin H, Beard KH, Pitt WC (2008) An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. *Biol Invasions* 10:335–345. doi:[10.1007/s10530-007-9133-x](https://doi.org/10.1007/s10530-007-9133-x)
- Stewart MM, Woolbright LL (1996) Amphibians. In: Reagan DP, Waide RB (eds) *The food web of a tropical rainforest*. The University of Chicago Press, Chicago, pp 273–320
- Vitousek PM (1986) Biological invasions and ecosystem properties: can species make a difference? In: Mooney HA, Drake JA (eds) *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, New York, pp 163–176
- Vitousek PM (1998) Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. *Ecosystems* (N Y, Print) 1:401–407. doi:[10.1007/s100219900033](https://doi.org/10.1007/s100219900033)
- Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecol Monogr* 59:247–265. doi:[10.2307/1942601](https://doi.org/10.2307/1942601)
- Wagner WL, Herbst DR, Sohmer SH (1990) *Manual of the flowering plants of Hawaii*. University of Hawaii Press, Honolulu
- Wallace JB, Eggert SL, Meyer JL, Webster JR (1999) Effects of resource limitation on a detrital-based ecosystem. *Ecol Monogr* 69:409–442
- Wardle DA (2002) *Communities and ecosystems: linking the aboveground and belowground components*. Princeton University Press, Princeton
- Wolfe EW, Morris J (1996) *Geologic map of the Island of Hawaii*. U.S. Geological Survey miscellaneous geologic investigations series map I-2524-A, scale 1:100, 000. USGS, Honolulu
- Woolbright LL (1985) Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. *Herpetologica* 41:1–9
- Woolbright LL (1989) Sexual dimorphism in *Eleutherodactylus coqui*: selection pressures and growth rates. *Herpetologica* 45:68–74
- Woolbright LL, Hara AH, Jacobsen CM, Mautz WJ, Benevides FL Jr (2006) Population densities of the Coqui, *Eleutherodactylus coqui* (Anura: Leptodactylidae) in newly invaded Hawaii and in native Puerto Rico. *J Herpetol* 40:122–126. doi:[10.1670/79-05W.1](https://doi.org/10.1670/79-05W.1)