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Different prey resources suggest little competition between non-native frogs and insectivorous birds despite isotopic niche overlap

Robyn L. Smith · Karen H. Beard · Aaron B. Shiels

Abstract Non-native amphibians often compete with native amphibians in their introduced range, but their competitive effects on other vertebrates are less well known. The Puerto Rican coqui frog (*Eleutherodactylus coqui*) has colonized the island of Hawaii, and has been hypothesized to compete with insectivorous birds and bats. To address if the coqui could compete with these vertebrates, we used stable isotope analyses to compare the trophic position and isotopic niche overlap between the coqui, three insectivorous bird species, and the Hawaiian hoary bat. Coquis shared similar trophic position to Hawaii amakihi, Japanese white-eye, and red-billed leiothrix. Coquis were about 3 ‰ less enriched in $\delta^{15}N$ than the Hawaiian hoary bat, suggesting the bats feed at a higher trophic level than coquis. Analyses of potential diet sources between coquis and each of the three bird species indicate that there was more dietary overlap between bird species than any of the birds and the coqui. Results suggest that Acari, Amphipoda, and Blattodea made up >90% of coqui diet, while Araneae made up only 2% of coqui diet, but approximately 25% of amakihi and white-eye diet. The three bird species shared similar proportions of Lepidoptera larvae, which were ~25% of their diet. Results suggest that coquis share few food resources with insectivorous birds, but occupy a similar trophic position, which could indicate weak competition. However, resource competition may not be the only way coquis impact insectivorous birds, and future research should examine whether coqui invasions are associated with changes in bird abundance.

Keywords Stable isotope analyses · ^{13}C · ^{15}N · Hawaiian Islands · Non-native amphibians

Introduction

Although most amphibian species are threatened worldwide (Stuart et al. 2004), some species are spreading globally and are significant threats to native wildlife (Kraus 2015). Because they can spread rapidly after introduction (Phillips et al. 2007) and attain high densities (Greenlees et al. 2006), amphibians can have strong ecological impacts in their new range. Non-native amphibians have been shown to change invertebrate communities (Choi and Beard 2012), and through resource competition, reduce

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native amphibian populations and change amphibian community composition (Kupferberg 1997; Richter-Boix et al. 2012; Smith 2005). However, few studies have examined whether non-native amphibians compete with other native vertebrate taxa (e.g., Boland 2004). Amphibian invasions are of particular concern on remote oceanic islands, because these islands rarely have native amphibian assemblages (Kraus 2015), and thus, endemic taxa often evolve without amphibian competitors. One such invasion is the Puerto Rican coqui frog (*Eleutherodactylus coqui*) to the Hawaiian Islands in the late 1980s (Kraus et al. 1999).

Coquis are now widespread on the island of Hawaii and have colonized many moist habitats, while they have been controlled or restricted on the other Hawaiian Islands (Beard et al. 2009; Bisrat et al. 2012; Olson et al. 2012). They reproduce through direct development (Stewart and Woolbright 1996), and are terrestrial throughout all life stages. At night, coquis climb onto understory vegetation from diurnal retreat sites to forage on invertebrates, and can change invertebrate community structure and reduce invertebrate numbers where they invade (Choi and Beard 2012). Because their populations can attain extremely high densities, up to 90,000 frogs/ha (Beard et al. 2008; Woolbright et al. 2006), they could reduce prey resources for Hawaii's native vertebrates. Kraus et al. (1999) first proposed that the coqui could compete with native insectivorous birds for invertebrate prey on the Hawaiian Islands. Coquis may also compete with non-native insectivorous birds, which are abundant in lowland forest habitats (Scott et al. 1986) and where most coqui populations are found (Olson et al. 2012). Beard and Pitt (2005) proposed that coquis could compete with the insectivorous native Hawaiian hoary bat (*Lasiurus cinereus semotus*) because they both feed nocturnally, and bats move into the lowlands during critical breeding periods (Menard 2001). To assess whether coquis compete with birds and bats for invertebrate prey, overlap between their trophic positions and food resources should be compared.

Methods for comparing the trophic position and food resources among different vertebrate taxa present some challenges. Stomach contents and fecal material may not be easily compared between all vertebrate taxa because of differing digestive systems (Bearhop et al. 2004), and stomach contents generally require lethal capture of target organisms, which is undesirable for species of conservation concern.

Stable isotope analyses provide a reasonable alternative to traditional stomach content and fecal analysis. For one, the trophic position and the diet of different taxa can be compared on standardized isotope axes (Bearhop et al. 2004), as long as one obtains estimates of the trophic base. Furthermore, stable isotopes reflect the assimilation of prey into the diet over time, in contrast to stomach contents, which do not persist long in the digestive tract. However, there are some limitations to using isotopes in diet analysis. Diet models can show high sensitivity depending on the trophic discrimination factors chosen (Bond and Diamond 2011); stable isotope diet analyses are less precise than stable isotope analyses in identifying prey items to species; and, when assessing competition between species, isotope analysis can have difficulty separating groups when the food web base has similar $\delta^{13}C$ signatures (Post 2002). However, for the purposes of comparing the trophic position and general overlap in prey resources, isotopes can help address the likelihood of competition between co-existing species (Beaulieu and Sockman 2012; Shiels et al. 2013).

Here we use stable isotope analyses to address three primary questions: (1) What is the relative trophic position, measured using $\delta^{15}N$ and $\delta^{13}C$, of coquis and their potential vertebrate competitors, (2) What is the degree of isotopic niche similarity between coquis and potential vertebrate competitors, and (3) What are the potential food sources and contribution of these sources to diet among coquis and potential vertebrate competitors? We use the results to address whether introduced coquis are likely to compete with insectivorous birds and bats in Hawaii.

Methods

Study site description

We conducted our research in a 30-ha area of lowland mesic forest in Manuka Natural Area Reserve (hereafter Manuka) on the island of Hawaii, USA (19°07′N, 155°49′W; elevation: 540 m). Mean annual temperature is 18 °C and mean annual precipitation is 838 mm, with a maximum mean monthly precipitation and temperature difference of 20 mm and 4 °C, respectively (Giambelluca et al. 2013). The four dominant tree species in the reserve include two

natives: *Metrosideros polymorpha* and *Psychotria hawaiiensis,* and two non-natives *Schinus terebinthifolius* and *Aleurites moluccana.* Dominant shrubs and additional trees in the understory include the native *Psydrax odorata* and non-natives *Psidium cattleianum* and *Ochna serrulata*.

We chose Manuka for this study because it has the highest density of coquis on record (Beard et al. 2008). Manuka also has a high abundance (>10 individuals/ha) of native birds, such as the apapane (*Himatione sanguinea*), Hawaii amakihi (*Chlorodrepanis virens*), and Hawaii elepaio (*Chasiempis sandwichensis*), and a high abundance of non-native birds such as the kalij pheasant (*Lophura leucomelanos*), house finch (*Haemorhous mexicanus*), northern cardinal (*Cardinalis cardinalis*), red-billed leothrix (*Leiothrix lutea*), and Japanese white-eye (*Zosterops japonicus*) (R.L. Smith and K.H. Beard unpubl. Data). Hoary bats have been observed foraging at Manuka (Jacobs 1994), and were observed during the course of our study.

We compared the isotopic composition of Hawaii amakihi, Japanese white-eye, and red-billed leiothrix to the coquis because they were the most abundant insectivorous birds in the study area (R. Smith and K.H. Beard, unpubl. data) and because they represent both native and non-native species. Hawaii amakihi, Japanese white-eye, and red-billed leiothrix are generalist insectivores, but they also consume nectar and fruit (Banko and Banko 2009; del Hoyo et al. 2008).

Sample collection

We collected all samples between 22 July and 19 August 2014. Five mist-nests were set up 200 m apart to collect independent bird samples in different areas of the reserve. All frogs, insects, and plant material were collected within 50 m of each of the five mist-net locations. With 50-m buffers around the mist-net locations; this made up a total study area of about 30-ha.

To capture the full range of prey that coquis consume, we targeted coqui of different ages and sex classes because they have been shown to have slightly different diets (Beard 2007). We hand-captured a total of 30 frogs [10 males, 10 females, and 10 pre-adults defined as <25 mm snout-vent-length (Woolbright 2005)] between 1930 and 0000 h. To euthanize frogs, we cooled and then froze them in an ice bath for 24 h (Shine et al. 2015), which ensured that decomposition

would not change their isotope ratios before drying (Krab et al. 2012). We sampled frog thigh muscle tissue because its tissue turnover rate is most similar to bird feathers and bat wing membranes (Caut et al. 2009).

We captured birds between 0600 to 1100 h and 1400 to 1800 h using an array of four 12 m × 3 m mist-nets, for a total of 336 net-hours. We checked nets a maximum of 20 min apart to minimize stress on captured birds. We removed tail feathers from the first 10 individuals captured of Hawaii amakihi, Japanese white-eye, and red-billed leiothrix. If we captured individuals of non-target species or beyond 10 individuals of the target species, these birds were released. We chose feathers as an isotope source because sampling feathers is a non-lethal, non-invasive way to collect tissue (Bearhop et al. 2004). Previous studies using feathers in stable isotope analyses have shown that ten individuals is a reasonable number to obtain good isotope estimates (Jackson et al. 2011). We took secondary feathers from a few Hawaii amakihi for which all their tail feathers were in pin, because it is unsafe to remove these feathers at this time (Spotswood et al. 2012). Minute differences in isotope signatures between feather tracts typically do not change interpretations of trophic position (Jaeger et al. 2009), unless species are highly migratory and molt over long periods of time (Zelanko et al. 2011), which are not characteristics of our study species.

We also obtained three individual Hawaiian hoary bats collected from various locations on the island of Hawaii. The US Department of Agriculture, Wildlife Services in Hawaii confirmed the species and sampled hoary bat wing membrane tissue. We could only compare their relative trophic position to that of the coqui and birds because the hoary bat is much more migratory in nature than the birds studied (del Hoyo et al. 2008) or the coqui. Therefore, regardless of where they were collected, bats would be less likely to reflect specific prey base signatures at a given site (Post 2002).

Frog muscle tissue turns over roughly 60–80 days (Cloyed et al. 2015), Hawaiian bird feather molt takes about 90–120 days (Freed and Cann 2012), and bat wing membrane tissue turnover is about 50 days (Roswag et al. 2015). Because the turnover rates for all these tissues are within 2–6 months, we felt that all samples collected for isotope analyses reflected the resource base for that year and should be comparable.

To obtain isotope signatures from a diverse potential prey base, we targeted invertebrate groups that our vertebrates likely consume. We extracted leaf litter invertebrates from leaf litter using 12 Burlese-Tullgren funnels three times over the collection period. We collected flying invertebrates every 2 days during the course of the study from four Malaise traps placed near four of the five mist-net locations. To capture non-flying canopy invertebrates, we placed a bag over branches of dominant plant species at heights of 0–2 m, vigorously shook, and vacuumed invertebrates out of the bag with an aspirator. We opportunistically hand-collected certain invertebrate groups, like large Araneae, Blattodea, and Coleoptera. We used a blacklight trap to capture nocturnal flying invertebrates between 1930 and 2300 h on four nights. We also hand-collected leaves, litter, fruit, and flower samples from the dominant canopy and understory plants. We included plant samples in our collections as an isotopic base for which to compare our invertebrate and vertebrate samples, and as potential food items for our birds (Table 1).

The samples were then stored dry in glass vials or paper bags before sorting, which ensured that preservatives did not change the isotopic signatures (Krab et al. 2012). All samples, except bird feathers, were thoroughly rinsed with water to eliminate any contaminants before drying. We rinsed feathers with acetone to remove oils and then rinsed them thoroughly with water to remove the acetone before drying (Bontempo et al. 2014). Once rinsed, we placed samples in a drying oven at 60 °C for 48 h. We ground each sample into a very fine, evenly-sized powder using a mortar and pestle, but in the case of the feather

samples, we cut feathers into very small (<1 mm in width and length) pieces with scissors (Bontempo et al. 2014). Samples were analyzed for $\delta^{15}N$ and $\delta^{13}C$ using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California Davis Stable Isotope Facility. Bat samples were analyzed with a Thermo-Finnegan Delta V IRMS Isotope Ratio Mass Spectrometer at the University of Hawaii, Hilo. Both machines were calibrated using peach tree leaves (NIST 1547), and values were standardized to the international standards of Vienna PeeDee Belemnite for $\delta^{13}C$ and Air for $\delta^{15}N$.

Statistical methods

Isotope discrimination correction

Prior to statistical analysis, we corrected the raw isotope values of the vertebrates using trophic discrimination factors as is typical for these analyses (see Jackson et al. 2011; Parnell et al. 2010). These corrections are needed because differences in raw isotope values between species could falsely be attributed to separate diets, yet could result from different isotopic discrimination rates on the same diet. Ideally, one would use a discrimination factor empirically determined via a controlled feeding study in the laboratory. However, these studies take considerable time and resources to conduct, particularly for species that are hard to rear in the laboratory, and may not ultimately reflect diet discrimination in natural systems. Because we did not determine trophic

Table 1 Known diet sources of study species

Species	Scientific name	Diet sources	Citations
Coqui frog	*Eleutherodactylus coqui*	Acari, Amphipoda, Araneae, Blattodea, Hymenoptera-Formicidae, Isopoda	Beard (2007), Wallis et al. (2016)
Hawaii Amakihi	*Chlorodrepanis virens*	Araneae, Homoptera, Lepidoptera Larvae, Neuroptera, Ohia Nectar	Baldwin (1953), Banko and Banko (2009), Banko et al. (2015)
Japanese White-eye	*Zosterops japonicus*	Araneae, Homoptera, Lepidoptera Larvae, Neuroptera, Orthoptera, Ohia Nectar, Fruit	Banko and Banko (2009), Banko et al. (2015), del Hoyo et al. (2008), Scott et al. (1986)
Red-billed Leiothrix	*Leiothrix lutea*	Diptera, Hymenoptera-Wasps, Lepidoptera Adult, Lepidoptera Larvae, Fruit	Banko et al. (2015), del Hoyo et al. (2008), Scott et al. (1986)

discrimination values ourselves, we used taxon- and tissue- specific values reported in the literature, as has been done in other studies (Gavrilchuk et al. 2014; Paez-Rosas et al. 2014). We corrected bird feathers by 2.18 $\Delta^{13}C$ and 3.84 $\Delta^{15}N$ (Caut et al. 2009), frog muscle tissues by 1.6 $\Delta^{13}C$ and 3.1 $\Delta^{15}N$ (Cloyed et al. 2015), and bat wing membrane tissues by 4.0 $\Delta^{13}C$ and 3.7 $\Delta^{15}N$ (Roswag et al. 2015).

Interspecific isotopic niche variation

We used t-tests with an alpha value of 0.05 to test for significant differences in $\delta^{13}C$ or $\delta^{15}N$ between all pairwise comparisons of coquis, birds, and bats. We considered trophic position significantly different if the isotope differences were >2–3 ‰ (DeNiro and Epstein 1981). Bats were limited to this analysis because we had a small sample size and the bats were not collected from the specific study area.

We calculated stable isotope standard ellipses to compare both overlap and niche width among coquis and the three bird species, and calculated Layman metrics (Layman et al. 2007) to compare the degree of their dietary specialization. We plotted maximum likelihood standard ellipses and visually compared them for overlap in core isotopic niche among species (Jackson et al. 2011). We estimated niche width for the coquis and three bird species using a Bayesian standard ellipses approach (Jackson et al. 2011), which is useful to calculate uncertainty in estimates based on differences in sample size (30 for frogs and 10 for each bird species). It should be noted that we tested whether the difference in sample size influenced the final results with randomly selected frog samples of 10 and using male, female, and sub-adult frogs separately; qualitative differences in results were not detected (see Figure S1 and Table S2). We simulated Bayesian ellipses 10^5 times to derive 95% Bayesian credible intervals for niche width sizes. We considered niche width sizes to be different if there was no overlap between credible intervals.

To compare dietary specialization among species, we calculated the Layman metrics of mean Euclidean distance to the centroid and mean nearest-neighbor Euclidean distance (Layman et al. 2007), which quantify the difference between individual isotope points within a population. We generated null distributions from residual permutation procedures to test for differences in these two metrics among species,

and we considered them significantly different if the difference did not overlap zero (Turner et al. 2010).

Diet variation

To determine the relative proportions of diet sources contributing to coqui and bird diet, we used Bayesian mixing models in the package siar in R (Parnell and Jackson 2013). This approach allows the incorporation of more dietary sources (recommended no more than five) into the models than n + 1 sources in traditional mixture models (Parnell et al. 2010). We used a literature search to determine a priori the most likely invertebrate and plant groups to contribute to coqui and bird diet, and specific diet sources included in the model differed among species (see Table 1). We tested sources for significant differences in isotopic signatures using Hotelling's t-tests and an alpha value of 0.05, and sources that were not different were combined into a single group in the diet analysis (Gavrilchuk et al. 2014). Diet sources that we combined were Acari, Amphipoda, and Blattodea for the coquis; Homoptera and Neuroptera for amakihi and white-eye; and Diptera and Hymenoptera-wasps for leiothrix. Concentrations of C and N in these diet sources were incorporated into the siar model to determine more accurately the contribution of each source (Phillips and Koch 2002), particularly because plant and animal tissues can have very different concentrations.

We ran model simulations a total of 10^8 times to derive credible intervals for diet proportions. We then compared the mean proportion of shared sources in the diets of coquis and the three bird species to assess the amount of overlap in diet. We considered proportional contributions of sources in the diets within and among species to be different if there was no overlap in the Bayesian credible intervals.

Results

Relative trophic position of coquis, birds, and bats

Bat tissue was the most enriched in $\delta^{15}N$ relative to the other vertebrate samples (two sample t test, all pairwise comparisons: $p < 0.001$) (Fig. 1). Bats were about 2–3 ‰ higher in $\delta^{15}N$ than the other vertebrates. Japanese white-eye and red-billed leiothrix were more
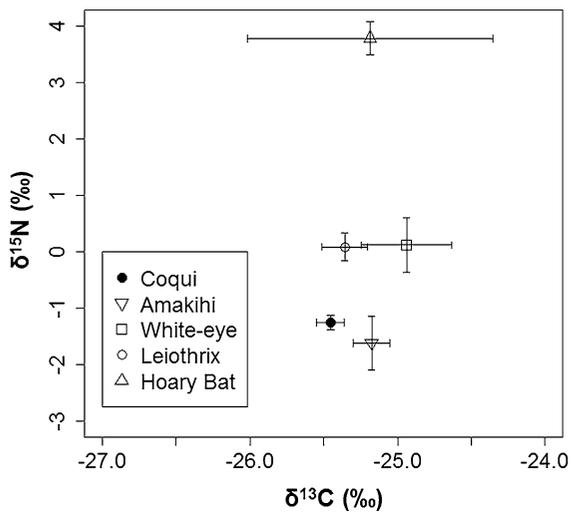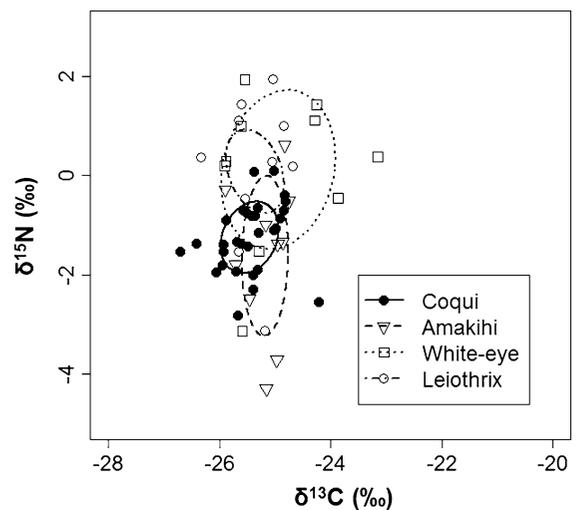
Fig. 1 Discrimination-corrected mean isotopic signatures of the coqui (n = 30), Hawaii amakihi (n = 10), Japanese white-eye (n = 10), red-billed leiothrix (n = 10), and Hawaiian hoary bat (n = 3). *Bars* indicate standard errors

Fig. 2 Discrimination-corrected core isotopic niches of Coqui (n = 30), Hawaii Amakihi (n = 10), Japanese White-eye (n = 10), and Red-billed Leiothrix (n = 10), represented by standard ellipse area

enriched in $\delta^{15}N$ than Hawaii amakihi and coquis (two sample t-test, $p < 0.05$), but were not different from one another (two sample t-test, t = 0.065, df = 13.63, $p = 0.47$). Coquis and amakihi also did not differ from one another in $\delta^{15}N$ (two sample t-test, t = 0.74, df = 10.33, $p = 0.76$). Pairwise comparisons of coqui, bird, and bat $\delta^{13}C$ signatures revealed no differences among species, except Hawaii amakihi, which were more enriched than coquis (two sample t-test, t = 1.79, df = 20.15, p value = 0.044) (Fig. 1).

Interspecific isotopic niche variation

Coquis overlapped the most in core isotopic niche space with Hawaii amakihi and Japanese white-eye, and showed less overlap in isotopic niche space with red-billed leiothrix (Fig. 2), but had some overlap with all three species. Core red-billed leiothrix niche space overlapped almost entirely with the Japanese white-eye, and both non-native birds had more overlap with one another than with the Hawaii amakihi. Japanese white-eyes had larger niche widths than coquis, but niche widths comparisons of all other species were not different (Table 2). There was no difference in distance to the centroid and mean nearest neighbor distance among any of the bird species or between the birds and the frogs (Table 2).

Bird and coqui diet inference

The mean proportion of each potential dietary source varied among the coqui and bird species (Fig. 3). Acari + Amphipoda + Blattodea contributed the most to coqui diet (>90%), and Araneae (~2%), Isopoda (~3%), and Formicidae (~4%) were less important (Fig. 3a). In contrast, Araneae contributed about 25% to both amakihi and white-eye diets (Fig. 3b, c). While the percentage of Homoptera + Neuroptera in amakihi diet was about two times higher than that of white-eyes (43% for amakihi, 22% for white-eye), there was wide overlap in credible intervals, and therefore no statistical difference. All bird species shared similar mean proportions of Lepidoptera larvae (19% for amakihi, 18% for white-eye, 17% for leiothrix). Diptera + Wasps accounted for 70% of leiothrix diet, and were a higher mean proportion than either fruit or adult Lepidoptera, though not Lepidoptera larvae (Fig. 3d).

Discussion

The similarity of $\delta^{15}N$ signatures, niche width size, and the overlap in isotopic niche space among coquis and the bird species in our study suggests that coquis occupy a similar trophic level to generalist

Table 2 Isotope niche metrics for coqui and bird species

Species	N	LOC (δ13C and δ15N)	CD	MNND	SEA_B
Coqui	30	−25.5, −1.25	0.61	1.21	1.31 (0.94, 1.91)
Hawaii amakihi	10	−25.2, −1.62	0.61	1.22	2.82 (1.64, 5.48)
Japanese white-eye	10	−24.9, 0.12	0.55	1.10	4.60 (2.67, 8.93)
Red-billed leiothrix	10	−25.4, 0.08	0.45	0.91	1.76 (1.02, 3.42)

The location of the centroid (LOC) indicates where the niche is centered in isotopic space. The mean Euclidean distance to the centroid (CD) and mean Euclidean nearest-neighbor distance (MNND) are estimates of trophic diversity within a species. The core isotopic niche width is represented by the median Bayesian standard ellipse area (SEA_B) and the 95% Bayesian credible intervals in parenthesis

insectivorous birds in Hawaii. These results were unexpected because all the birds we analyzed consume nectar and fruit as well as invertebrates (Table 1) while coquis feed only on invertebrates; thus, we expected that coquis would have more enriched $\delta^{15}N$ values than the birds, and that coquis would show greater dietary specialization. Coquis and amakihi did show a difference in $\delta^{13}C$, which could indicate that they feed on invertebrates from a slightly different plant base. The isotopic overlap between coquis and birds could indicate a shared trophic position and food resources, but the similar isotopic signatures could also be generated from divergent foraging strategies (Bearhop et al. 2004), or a C3 C base supporting multiple food webs (Fry 2006). Therefore, we cannot assess whether coquis and birds compete based on overlap in isotopic niche space alone. We did observe that the bats occupy a higher trophic level than either the birds or coqui. Other diet studies have shown that Hawaiian hoary bats feed predominantly on flying insects, such as Coleoptera and adult Lepidoptera (Bernard and Mautz 2016; Jacobs 1999), which had more enriched $\delta^{15}N$ than most other invertebrate groups we sampled (Table 3; Fig. 4). However, the bat samples were collected during different times and on different parts of the island, and therefore the isotopic values of the invertebrates in our study may not reflect the total range these bats consume.

Our more detailed diet source analyses suggest that there is little overlap in food resources between coquis and amakihi (Fig. 3a, b) and between coquis and white-eye (Fig. 3a, c), and essentially no shared food resources between coquis and leiothrix (Fig. 3a, d). This result is interesting because leiothrix primarily forage in the lower canopy and understory, where coquis likely obtain some prey. Amakihi and white-eye can forage in these zones, but mostly forage in the mid to upper canopy, where the coqui is thought less likely to forage (Banko and Banko 2009; Wallis et al. 2016). The credible intervals do overlap for the proportion of the only shared diet source, Araneae, between coqui, amakihi, and white-eyes; although the mean proportion is only 2% of the diet for coqui and it is ∼25% for amakihi and white-eye diet. Abundance of Araneae and other predatory insects in canopy foliage has been shown to increase with bird exclusion, which suggests that top-down control can limit their populations (Gruner 2004). Even though coquis can attain extremely high densities, foliage-collected Araneae have not been shown to differ across the invasion fronts on Hawaii (i.e., Araneae are not reduced in the areas where coquis have invaded compared to neighboring areas where they have not; Choi and Beard 2012).

The three bird species showed substantial overlap in isotopic niche space (Fig. 2), and there was more overlap in diet sources between the bird species than with the coqui, suggesting that there could be more interspecific competition among birds. Japanese white-eyes have similar proportions of invertebrate prey groups (Araneae, Homoptera, and Lepidoptera) and ohia flowers in their diet as Hawaii amakihi (Fig. 3b, c), which supports the conclusion of other studies in Hawaii that white-eyes could compete with amakihi and other native honeycreepers for food (Freed and Cann 2009; Mountainspring and Scott 1985). Alternately, similar proportions of prey resources between these generalist insectivore species could reflect the high relative abundance of these invertebrates in the environment (Banko et al. 2014, 2015). Of the birds, Japanese white-eyes had the widest mean isotopic niche space (Table 2), likely reflecting their high adaptability and generalized diet (Mountainspring and Scott 1985; Scott et al. 1986).

Table 3 Mean $\delta^{13}C$ and $\delta^{15}N$ values of invertebrate, vertebrate, and plant groups of interest in Manuka Natural Area Reserve

| Group	Order or Spp	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Invertebrate				
	Acari	3	−25.82 (0.88)	−1.35 (1.07)
	Amphipoda*	5	−25.06 (0.20)	−0.71 (0.14)
	Araneae (>10 mm)	5	−25.52 (0.44)	2.76 (0.55)
	Araneae (<10 mm)	5	−25.88 (0.23)	1.70 (0.55)
	Blattodea*	5	−25.77 (0.62)	−0.98 (0.35)
	Chilopoda	1	−24.27	2.05
	Coleoptera	5	−24.16 (1.32)	0.35 (1.59)
	Collembola	1	−26.53	−2.97
	Diplopoda	1	−21.6	−0.98
	Diptera	13	−25.21 (0.51)	2.27 (1.14)
	Gastropoda	4	−21.26 (1.52)	1.22 (0.78)
	Homoptera	9	−26.83 (0.50)	−1 (0.63)
	Hymenoptera: Formicidae*	6	−26.69 (0.19)	0.34 (0.56)
	Hymenoptera: Wasps	3	−25.22 (1.23)	−0.38 (1.57)
	Isopoda*	5	−24.15 (0.53)	1.31 (0.38)
	Isoptera	1	−26.76	−0.5
	Lepidoptera: Adult	10	−27.77 (1.08)	1.81 (0.55)
	Lepidoptera: Larvae	4	−27.16 (0.43)	0.26 (0.27)
	Neuroptera	2	−26.96 (1.05)	−1.81 (0.74)
	Oligochaeta*	1	−24.33	0.31
	Orthoptera	5	−26.73 (0.11)	0.54 (0.31)
Vertebrate				
Amphibia	*Eleutherodactylus coqui* *	30	−23.85 (0.09)	1.85 (0.13)
Aves	*Hemignathus virens*	10	−23.02 (0.12)	2.22 (0.48)
	Leiothrix lutea *	10	−23.20 (0.16)	3.92 (0.25)
	Zosterops japonicus *	10	−22.78 (0.31)	3.96 (0.48)
Mammalia	*Lasiurus cinereus semotus* (wing membrane)	3	−21.19 (0.83)	7.48 (0.29)
Plant				
Leaves	*Ageratina riparia* *	1	−30.94	0.43
	Diospyros sandwichensis	1	−29.22	−2.26
	Metrosideros polymorpha	6	−30.08 (0.31)	−2.72 (0.35)
	Ochna serrulata *	5	−31.44 (0.21)	−1.26 (0.4)
	Pipturus albidus	1	−29.81	0.22
	Psidium cattleianum *	5	−30.32 (0.32)	−0.29 (0.89)
	Psidium guajava *	1	−29.6	−1.66
	Schinus terebinthifolius	3	−30.15 (0.70)	−0.90 (0.18)
Flowers				
	Metrosideros polymorpha	5	−28.47 (0.64)	−2.74 (0.14)
	Schinus terebinthifolius *	1	−29.85	−3.67
Fruit				
	Ochna serrulata *	5	−28.06 (0.52)	−2.19 (0.95)
	Psidium cattleianum *	5	−28.82 (0.65)	−1.86 (0.50)
	Psidium guajava *	1	−32.64	−1.12

Table 3 continued

Group	Order or Spp	N	δ¹³C (‰)	δ¹⁵N (‰)
Litter				
	Metrosideros polymorpha	5	−28.76 (0.45)	−2.08 (0.27)
	*Ochna serrulata**	5	−30.46 (0.44)	−2.48 (0.24)
	Pipturus albidus	1	−29.32	0.91
	*Psidium cattleianum**	5	−29.09 (0.44)	−2.13 (0.083)
Wood				
	Metrosideros polymorpha	3	−27.94 (0.67)	−1.99 (0.53)
	*Schinus terebinthifolius**	1	−27.65	−0.45

SE added in parenthesis for groups with >1 observation

* Indicates all non-native taxa in Manuka Natural Area Reserve
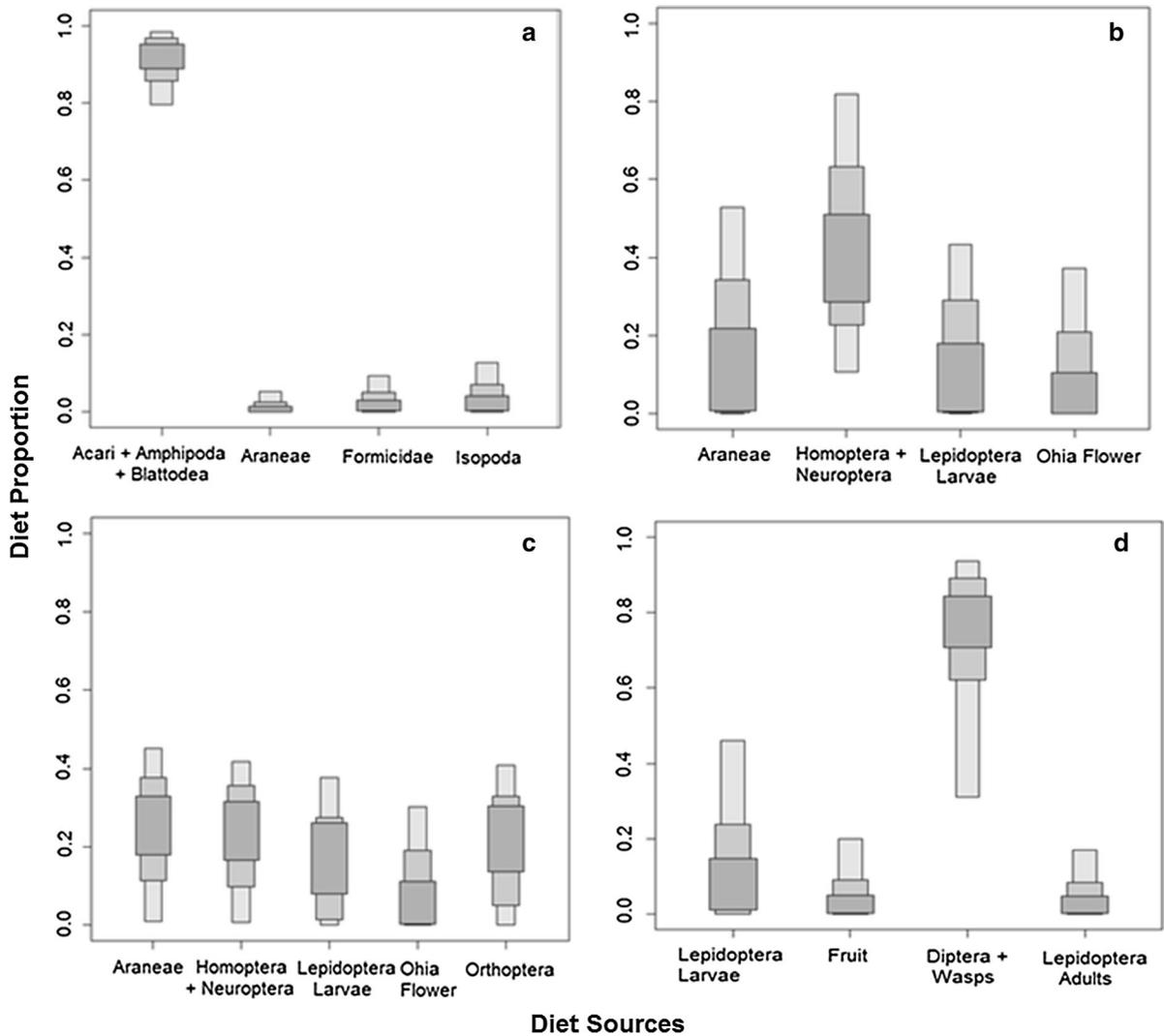
Fig. 3 Diet proportions of **a** coqui, **b** Hawaii amakihi, **c** Japanese white-eye, and **d** red-billed leiothrix dietary sources. *Darkest gray boxes* indicate 50% credible interval, *lighter gray* indicate 75% credible interval, and *lightest gray* indicate 95% credible interval
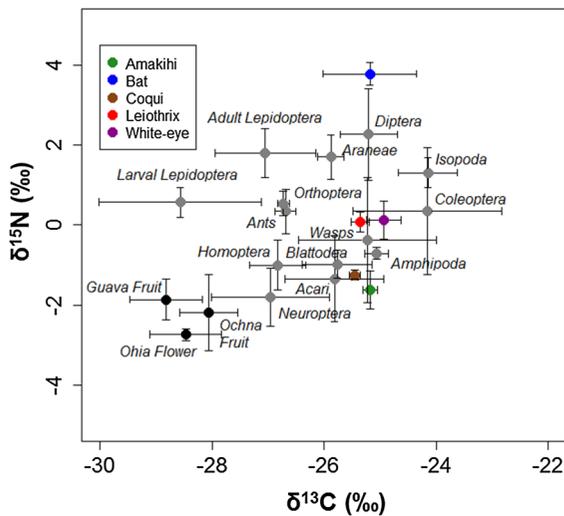
Fig. 4 Mean isotope values (±SE bars) for discrimination-corrected coqui, Hawaii amakihi, Japanese white-eye, red-billed leiothrix, and Hawaiian hoary bats plotted with invertebrates (*gray*) and plants (*black*)

Our results show that the three bird species shared similar proportions of Lepidoptera larvae (Fig. 3b–d), but at another sites on the island of Hawaii (Hakalau) amakihi have been found to consume twice as many Lepidoptera larvae as white-eye and leiothrix (Banko et al. 2015). Lepidoptera larvae are thought to be a limiting prey resource for native Hawaiian birds (Banko and Banko 2009), particularly during reproductive periods. Extremely high densities of Japanese white-eye and red-billed leiothrix could have negative consequences for native insectivorous birds if they reduce Lepidoptera populations.

The proportion of diet sources for coquis from our isotopic analyses are similar to the sources previously found in stomach content analyses conducted at Manuka (Beard 2007; Choi and Beard 2012). Both types of analyses suggest that the majority of the prey in their diet is from the leaf litter, in this study, identified as Acari, Blattodea, and Amphipoda. The only difference between these analyses is the notable exception that the mean proportion of Formicidae in the diet inferred from our analysis (4%) is less than the frequency of Formicidae found from stomach content analysis conducted at this site: 8% in Beard (2007) and 28% in Wallis et al. (2016). There are at least two possible explanations for this pattern. The first is that the frequency of prey items may not be as good an approximation of dietary assimilation as prey

volume. In Wallis et al. (2016), Formicidae only constitute 1.4% of the prey volume, while Amphipoda (25.8%) and Blattodea (42.5%) make up a greater proportion, a combined volume more similar to our isotope diet predictions (Fig. 3a). The second potential explanation is that specific items in the diet can assimilate at different rates into tissues (Bearhop et al. 2002), and there may be differences in biochemical digestibility between Formicidae and other prey groups that would result in less incorporation into coqui muscle tissue (Cardwell 1996).

Though we provide evidence that coquis largely do not share food resources with insectivorous birds in Hawaii, our results are limited. First, we only sampled one location within one time period, which may not reflect the full range of isotopic dynamics across years and seasons (Post 2002). Coquis have been in Manuka for over a decade (Beard 2007), and the diet of the bird species could have changed over the course of the coqui invasion. Because we do not have samples from before the invasion, we cannot address this. Secondly, by only sampling one location, we cannot eliminate the possibility that birds and coquis might compete for resources elsewhere on the island. Coqui diet can vary greatly across sites (Beard 2007; Choi and Beard 2012), and in some sites they consume a greater proportion of insect groups such as Hemiptera and Lepidoptera larvae (Wallis et al. 2016), which both amakihi and white-eyes in Hawaii consume (Banko et al. 2014, 2015). Finally, the bird diet sources from the literature that we used in this study were not collected from this site, but from other sites across Hawaii. We felt these sources were likely representative of what they consume at Manuka because the main diet sources for these birds are consistent across sites (Baldwin 1953; Banko et al. 2015) and present at this site.

Although coquis and insectivorous birds had substantial overlap in isotopic niche space, which could suggest competition, we did not find evidence that they share similar proportions of prey resources in our more detailed diet source analyses. Our diet results support previous findings that coquis forage mostly on leaf litter insects in Hawaii (Beard 2007), while amakihi, white-eye, and leiothrix primarily forage in foliage and on tree trunks (Banko and Banko 2009). Thus, birds and coquis likely forage on prey in different microhabitats. Furthermore, there is a general lack of larger scale geographic overlap between coquis and many native birds. Manuka is one of the

few mid-elevation areas where native birds are still abundant on the island of Hawaii. In many cases, native Hawaiian birds are restricted to elevations above 1500 m (Camp et al. 2009), where the coqui has not yet invaded or may be unable to invade because of colder temperatures (Bisrat et al. 2012; Olson et al. 2012).

It is important to note that while this study focused on whether birds and coquis compete, there are other ways that the coqui frog invasion may influence Hawaiian birds. First, they may provide a novel prey resource for predatory birds, which is typically the strongest trophic effect of invasive species (Sax and Gaines 2008). Our choice of bird species did not investigate this potential interaction. Second, coqui invasions could alter invertebrate communities in other ways that influence birds. For example, coquis have been shown to increase flying Diptera where they invade (Choi and Beard 2012), which could positively affect bird species that feed on these groups. Finally, coquis have been shown to increase leaf litter decomposition rates, rates of nutrient cycling, and non-native plant growth, but not native plant growth (Sin et al. 2008). An increase in non-native plant growth could result in increased food resources for non-native birds or alternatively decreased food resources for species dependent on native plants. To more fully understand the impact of the coqui on Hawaiian birds, future research should determine if bird population sizes change in response to coqui invasions.

Furthermore, other introduced vertebrate species on the island of Hawaii may be more important competitors of birds and coquis. Jackson's chameleon, as well as 19 other species of lizard (Kraus 2009), have been introduced to Hawaii, and may be more important competitors of birds because they are diurnal and feed in the lower canopy, and take some of the same prey groups (Kraus et al. 2012). Of the introduced rodents, house mice are the most insectivorous, and Lepidoptera larvae constitute a large proportion of their diet (Shiels et al. 2013). Of other introduced amphibians, greenhouse frogs are more likely competitors of the coquis because they forage in the leaf-litter (Olson and Beard 2012).

At this point in time, the coqui has not successfully invaded Pacific Islands outside the Hawaiian Islands. They were introduced to Guam, but did not establish (Christy et al. 2007). White-eyes, on the other hand, are widespread throughout the Pacific (van Riper 2000),

and may be a concern for sympatric birds on other Pacific Islands because of their generalist insectivorous habits and ability to exploit a variety of niches. However, competition with non-natives on islands often does not produce measurable population change, compared to predation and disease (Sax and Gaines 2008); therefore, such competition, if it exists, may be difficult to detect. Perhaps the most important way that white-eyes affect native birds on Pacific islands is as a reservoir for avian diseases to which natives have little to no immunity (Foster 2009; LaPointe et al. 2009). Whereas the most important way that coquis may affect vertebrate communities is as novel prey (Beard and Pitt 2005, 2006) or as a reservoir for disease (Beard and O'Neill 2005), and not as competitors.

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