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ABSTRACT

The global spread of invasive species has created significant challenges for avian conservation. Introduced predators and pathogens have long been recognized for their direct negative effects on birds, but introduced amphibians can reach high densities on islands with no native amphibians, where they interact with native species. The coqui frog (*Eleutherodactylus coqui*), introduced to the Hawaiian Islands in the late 1980s, could have significant impacts on birds because it is fully terrestrial and achieves high densities. Coquis have been hypothesized to compete with native birds for invertebrate prey, but could also serve as a novel food resource for birds that consume small vertebrates. To test whether coquis measurably affect bird abundance, we conducted point counts of birds in coqui-invaded and adjacent uninvaded plots across 15 sites on the island of Hawaii, USA. We used *N*-mixture models to estimate the effect of coqui presence and density on the abundances of both native and nonnative birds, while controlling for possible habitat differences between plots with and without coquis. We found that coquis were associated with ~35% higher abundance of nonnative birds in general, and more specifically generalist birds that sometimes consume small vertebrates. We suggest that generalist birds increase in abundance with coquis primarily because coquis serve as an abundant food resource. While 4 native bird species co-occurred with coquis, native bird abundance (20% of our total observations) did not show a difference across coqui-invaded and uninvaded plots. Coquis do not appear to be important competitors with native birds in Hawaii, but the frogs are associated with increased abundances of some nonnative birds, which could induce undesirable ecosystem impacts.

Keywords: Eleutherodactylus coqui, invasion fronts, Hawaiian birds, native birds, nonnative amphibian, *N*-mixture models, novel prey

La rana invasora coqui está asociada con mayores abundancias de aves no-nativas en Hawái

RESUMEN

La propagación global de las especies invasoras ha causado importantes desafíos a la conservación de las aves. Los depredadores y los patógenos introducidos han sido reconocidos desde hace mucho tiempo por sus efectos negativos directos sobre las aves, pero los anfibios introducidos pueden alcanzar altas densidades en islas en las que no hay anfibios nativos y donde interactúan con las especies nativas. La rana coqui (*Eleutherodactylus coqui*), introducida a las islas de Hawái a finales de 1980, podría tener impactos significativos en las aves debido a que es completamente terrestre y alcanza altas densidades. Se ha hipotetizado que la rana coqui compite con las aves nativas por presas de invertebrados, pero también podría ser una nueva presa para las aves que consumen pequeños vertebrados. Para evaluar si la rana coqui afecta de un modo medible la abundancia de las aves, realizamos conteos de aves en puntos localizados en parcelas adyacentes invadidas y no invadidas por la rana coqui a lo largo de 15 sitios en las islas de Hawái. Usamos modelos de N-mezcla para estimar el efecto de la presencia y la densidad de la rana coqui en la abundancia de las aves tanto nativas como no nativas, mientras controlamos por las posibles diferencias de hábitat entre parcelas con y sin la rana coqui. Encontramos que la rana coqui estuvo asociada con aproximadamente un 35% más de abundancia de aves no nativas en general, y más específicamente con aves generalistas que a veces consumen pequeños vertebrados. Sugerimos que las aves generalistas aumentan con la presencia de la rana coqui principalmente debido a que sirve como un recurso abundante alimenticio. Mientras que cuatro especies de aves nativas convivieron con la rana coqui, la abundancia de las aves nativas (20% de nuestras observaciones totales) no mostró diferencias entre las parcelas con y sin la rana coqui. La rana coqui no parece ser un competidor importante de las aves nativas en Hawái, pero las ranas están asociadas con un aumento de la abundancia de algunas aves no nativas, lo que podría inducir impactos ecosistémicos no deseados.

Palabras clave: anfibios no nativos, aves de Hawái, aves nativas, *Eleutherodactylus coqui,* frentes de invasión, modelos de N-mezcla, presas nuevas

INTRODUCTION

Invasive species, especially vertebrates, can pose significant threats to avian diversity (Courchamp et al. 2003, Clavero et al. 2009). Although predation is the most common way in which nonnative vertebrates affect invaded systems, competition is often cited as another potential driver of community change (Courchamp et al. 2000, Mack et al. 2000, Roemer et al. 2002, Blackburn et al. 2004, Sax and Gaines 2008). Furthermore, native species are often the species of most concern following an invasion, but nonnative species now dominate many invaded systems and can interact with new species in complex ways (Simberloff and Von Holle 1999, Zavaleta et al. 2001, Hobbs et al. 2009, Green et al. 2011). The effects of nonnative mammals, birds, and reptiles on native and nonnative bird communities have been well documented (Fritts and Rodda 1998, Courchamp et al. 2003, Martin-Albarracin et al. 2015), but the effects of nonnative terrestrial amphibians on bird communities are less well known, with the possible exception of cane toads (*Rhinella marina*; Shine 2010, Kraus 2015).

One amphibian invasion that could affect bird communities is that of the Puerto Rican coqui frog (*Eleutherodactylus coqui*), which was accidentally introduced to the Hawaiian Islands in the late 1980s via the nursery trade (Kraus et al. 1999). The Hawaiian Islands have no native terrestrial reptiles or amphibians. After the coqui was introduced, it spread rapidly on the island of Hawaii, USA, where it is now widespread despite control efforts (Kraus and Campbell 2002, Sin and Radford 2007, Olson et al. 2012). The coqui is a terrestrial frog that breeds via direct development (i.e. there is no tadpole phase) in leaf litter (Townsend and Stewart 1994). During the day, coquis use diurnal retreat sites, often on the forest floor, and at night they emerge to forage on invertebrates in the leaf litter and understory and to find mates (Stewart and Woolbright 1996, Wallis et al. 2016). Their invasion is of ecological concern because coquis in Hawaii can reach extremely high densities, up to 91,000 frogs ha^{-1} in some locations (Beard et al. 2008).

The abundance and widespread distribution of coquis makes them of concern for insectivorous birds, or any birds that rely on invertebrates to feed their nestlings, because coquis could reduce food resources (Kraus et al. 1999, Beard and Pitt 2005, Banko and Banko 2009a). Coquis have been found to reduce the total abundance of leaf litter invertebrates in places where they have invaded (Choi and Beard 2012). Kraus et al. (1999) first proposed that coquis could compete with native birds, many of which are insectivorous (Banko and Banko 2009a). However, their interactions might not be straightforward because coquis could also compete with nonnative insectivorous birds, whose distributions overlap extensive-ly with that of the coqui (Scott et al. 1986, Olson et al. 2012). Furthermore, coquis could provide an abundant, year-round food resource for predatory birds, such as the native Hawaiian Hawk (*Buteo solitarius*) and Hawaiian Short-eared Owl (or Pueo, *Asio flammeus sandwichensis*; Beard and Pitt 2005), or for nonnative scavenging birds, such as the Common Myna (*Acridotheres tristis*). Finally, coquis could provide an abundant food resource for nonnative bird predators, such as rats (*Rattus* spp.) and mongooses (*Herpestes javanicus*), and, if coquis bolster populations of bird predators, coquis could reduce birds indirectly through apparent competition (sensu Kraus et al 1999, Beard and Pitt 2006).

Because the Hawaiian bird community has so many rare and endemic species, understanding the effect of the coqui invasion on birds is important for guiding management decisions. For example, on the island of Hawaii, where the coqui is most widespread, 6 of 13 native bird species found in forests are listed as endangered (Banko and Banko 2009b), and could overlap with and be affected by the coqui, currently or in the future (Beard et al. 2009, Bisrat et al. 2012). The overall goal of our study was to determine, at the landscape scale, whether there are measurable differences in bird communities in areas where the coqui has invaded. To address our goal, we sought to answer 3 questions: (1) Are coquis associated with lower insectivorous bird abundances? (2) Are coquis associated with higher abundances of birds that may consume small vertebrates? (3) Are coquis associated with overall differences in native or nonnative bird abundances?

METHODS

Study Design and Site Selection

Our approach was to measure bird communities across the island of Hawaii in areas where the coqui has invaded, and in neighboring areas with similar vegetation where the coqui has not yet invaded, hereafter referred to as invasion fronts (as in Choi and Beard 2012). We took this approach because we wanted any differences that we detected to be attributable to the frog and not to habitat or other environmental differences.

We worked at 15 sites on the island of Hawaii with coqui invasion fronts large enough for our study design (Figures 1 and 2). Ten of these sites had previously been used to investigate invertebrate community change across invasion fronts (Choi and Beard 2012). To find 5 additional sites, we used previously collected data on the presence vs. absence of coqui (Olson et al. 2012) and drove around the island listening for their distinctive 2-note mating call. We believe that we included all sites on the island that met our requirements (see below).

We determined coqui presence or absence on each side of the invasion front by listening for 20 min between 19:00
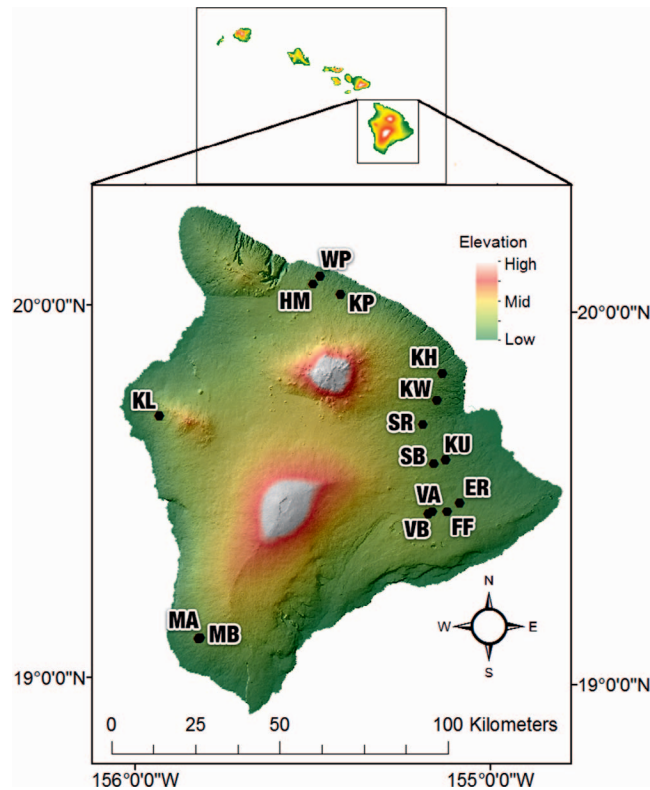
FIGURE 1. Fifteen sites on the island of Hawaii, USA, used to examine the effects of invasive coqui frogs on native and nonnative bird abundances. Site abbreviations are as follows: ER = Eden Roc, FF = Fern Forest, HM = Hamakua Forest Reserve, KH = Kaupukuea Homestead, KL = Kaloko, KP = Kalopa State Park, KU = Kulani, KW = Kaiwiki, MA = Manuka Natural Area Reserve A, MB = Manuka Natural Area Reserve B, SB = Stainback, SR = Saddle Road, VA = Volcano A, VB = Volcano B, and WP = Waipio.

and 02:00, the peak hours of calling (Woolbright 1985), for the loud (70 dB at 0.5 m) 2-note mating call on 3 separate nights over a 3-week period in December 2013 and January 2014. Designations were confirmed during subsequent sampling. Twelve sites were large enough to establish 3 replicate plots with coquis and 3 replicate plots without coquis on each side of the invasion front, while 3 sites (KH, VA, and VB; Figure 1) could only accommodate 2 plots with and without coquis. In total, we had 42 plots with coquis and 42 plots without coquis across the 15 sites.

To minimize duplicate counts in bird observation data among plots within a site, all plots were placed a minimum of 150 m apart (Camp et al. 2009). Plots on the same side of an invasion front had a mean distance between them of 570 m (range: 150–1,634 m), and plots on either side of the invasion front had a mean distance between them of 935 m (range: 294–2,121 m). Although our study design may not have eliminated the possibility of recording duplicate counts among plots on a given day, we felt that it was safe to assume that any duplicate counting occurred at random

and did not affect our ability to address our objectives. Because coqui populations are often near roads (Olson et al. 2012), we placed plots both with and without coquis the same distance (>50 m) from roads, trails, buildings, agricultural fields, and other such habitat edges to avoid biasing bird observations. Because it is challenging to model spatial autocorrelation in the residual variation of the fit of N-mixture models (see below), we limited the chance for it to occur by selecting sites that were on average very distant (55 km) from each other (see also Figure 1), and by measuring and modeling the habitat covariates that we thought would explain any similarity among sites.

Habitat Variables

We measured elevation, percent canopy cover, canopy height, percent native canopy, understory density, understory height, and percent native understory in all plots using methods similar to those of Choi and Beard (2012). We measured these variables to test for habitat differences between plots on either side of coqui invasion fronts and to determine the correlation of these variables with coqui density and bird abundance. These variables have been shown to affect Hawaiian birds at local scales (Scott et al. 1986).

Elevation was collected with a Garmin Etrex 20x handheld GPS unit (Garmin International, Olathe, Kansas, USA), with locational accuracy of ±3.5 m. Percent canopy cover was calculated using a spherical crown densiometer (Convex Model A, Forestry Suppliers, Jackson, Mississippi, USA). We measured canopy cover at the central point of the plot, and at points located 7.5 m and 15 m in each cardinal direction. Canopy height was measured in four 5 m × 5 m subplots, centered 7.5 m from the central point in each cardinal direction. We estimated the height, to the nearest 5 m, of the 2 individual trees closest to the north and south points of each subplot that were >10 cm diameter at breast height (DBH). We identified these 8 individual trees (2 from each of 4 subplots) to species. Percent of native canopy species was calculated by dividing the number of native trees by 8 total species.

Understory density was measured at 4 points within each plot, 7.5 m from the central point, using a Nudds checkerboard (100 squares on a 0.5 m × 2.0 m board; Nudds 1977). From these 4 points, we took 4 photos in each cardinal direction, 1.5 m off the ground, 5 m from each point, for a total of 16 photographs in each plot. Understory density was determined by counting the number of squares in the photographs covered by vegetation, divided by 100. Understory height was measured in four 5 m × 5 m subplots centered 7.5 m from the central point in each cardinal direction. We defined an understory plant as any free-standing stem <10 cm DBH. The height of the 2 understory plants closest to

FIGURE 2. Photos taken from central point count locations in 4 sites showing representative habitat in areas where we studied the effects of invasive coqui frogs on bird abundances on the island of Hawaii, USA. (**A**) Kalopa State Park (KP), (**B**) Eden Roc (ER), (**C**) Manuka Natural Area Reserve A (MA), and (**D**) Stainback (SB; see Figure 1 for locations).

the north and south point of each plot was estimated to the nearest meter for a total of 8 plants per plot. We identified these 8 individuals to species. Percent of native understory species was calculated by dividing the number of native understory plants by 8.

To test whether habitat variables differed between coqui-invaded and uninvaded plots within each site, we conducted a one-way ANOVA for each variable with site as a block, using a significance level of $P < 0.05$.

Coqui Variables

Because changes in bird communities might be greater where coqui densities are higher, coqui density was estimated in each of the invaded plots. Coqui density was measured using line transect distance sampling surveys (Buckland et al. 2001) and methods similar to those used by Choi and Beard (2012). Each 30 m × 30 m line transect plot was centered on the same central point at which bird surveys were conducted on the coqui side of the invasion front.

From June to July of 2014, starting at 19:30, 2 observers with headlamps surveyed frogs in each invaded plot on 1 of 6 adjoining 5-m wide, 30-m long parallel transects, walking slowly and visually searching for frogs by looking at all habitat (vegetation, forest floor, rocks) for 30 min. Because frogs are often sitting on top of vegetation and are usually easily seen, this method works well. When a frog was seen or heard, the perpendicular distance from the observer was recorded. At the end of each transect, researchers moved to the next adjoining transect, until the entire plot and all 6 transects had been surveyed, for a total of 180 observation minutes per plot.

We observed 1,577 frogs during surveys. Coqui densities were estimated using the distance sampling functions in package unmarked (Fiske and Chandler 2011) in R (R Core Team 2016). All distance sampling data were modeled with null models for both detection and density using either half-normal, hazard, or exponential distributions. Akaike model weights for the most-supported detection distributions and P-values for Freeman-Tukey goodness-of-fit tests are provided in Appendix Table 4. To test whether coqui density was linked to habitat variables, we examined collinearity using correlation coefficients and variance inflation factors (VIF), and considered variables signifi-

cantly correlated with coqui density if VIF > 3 (Zuur et al. 2010). Because avian abundance might respond simply to the mere presence of coquis in the local community, as opposed to their magnitude of abundance, we also distilled our count data down to simple presence–absence data to also be used as an explanatory variable in bird abundance modeling (see below).

Bird Abundance Surveys and Estimation

From February to June of 2014, bird surveys were conducted during peak hours of bird activity (between 06:00 and 10:00) in all sites using a variable circular plot design (Camp et al. 2009). An observer stood in the center of a plot and waited for 2 min to allow birds to adjust to observer presence. During this acclimation period, the observer recorded weather conditions, including temperature, precipitation, cloud cover, and wind speed. These variables were recorded for use as covariates when modeling detection probabilities as part of the abundance models (described below). Observations were not made in heavy precipitation or wind above 25 kph, because these conditions affect bird detection probabilities (Scott et al. 1986).

During the next 10 min after the acclimation period, each individual bird seen or heard was identified to species, and distance from the observer was recorded to the nearest 5-m interval (alternately colored flags were placed at 5-m intervals to help the observer estimate distance). Counts were repeated 5 times in each site throughout the study period. We attempted to use these survey methods to estimate bird densities with distance sampling estimators, but almost all bird species exhibited strong patterns of avoidance that violated the most fundamental distance sampling assumption of perfect detection at the center of each point count (Buckland et al. 2001). Given that we repeated our point-count surveys 5 times throughout the study period, we instead took advantage of N-mixture models to estimate bird abundances. Similarly to occupancy models for presence–absence data, N-mixture models utilize data collected on repeated visits to a plot to estimate imperfect detection, but they additionally make use of the observed counts to estimate abundance while accounting for imperfect detection. N-mixture models have been shown to provide robust estimates of bird abundance, and are an attractive alternative to distance sampling when assumptions of the latter are violated. Because 89% of all bird observations were within 30 m of plot centers, and all measurements of frog density and presence as well as measurements of all habitat variables were made within 30 m of the plot center, we truncated observations of birds at 30 m before applying N-mixture models to the bird survey data.

We used N-mixture models to estimate variation in bird abundances (individual species and origin groups: native or nonnative) in relation to coqui presence, coqui density, and habitat variables (see below). Unlike classical distance sampling, which is based on a single survey, N-mixture models use repeated counts at a sampling plot to estimate abundance while accounting for imperfect detection probability (Royle 2004, Kéry et al. 2005). We excluded observations from our first sampling period to control for observer inexperience and to better meet the assumption of population closure across the period of repeated counts (Royle 2004). We limited estimations of abundance to the 13 species that consisted of at least ~1% of total observations and were observed in at least 3 sites (Table 1). Total abundance of native species and nonnative species was also modeled using this framework.

To identify the variables that most influenced avian abundances and detection probabilities, we used a tiered information-theoretic approach to model selection (Franklin et al. 2000). For each of the 13 species and 2 groups of species (native or nonnative), we first evaluated models of detection probability with univariate effects of habitat (canopy cover, canopy height, understory density, and understory height) and weather variables (temperature, precipitation, cloud cover, and wind speed), time of day, and calendar date, while using a null (intercept-only) model for abundance. At this stage, we compared Poisson, zero-inflated Poisson, and negative binomial distributions for latent abundance. For models that had a lower Akaike's information criterion (AIC) value than the null detection model, we next considered additive and 2-way interactive effects of the supported detection covariates when ecologically plausible. The model with the lowest AIC value was then retained for all subsequent analyses of variation in abundance among study plots. Considering a suite of habitat variables (elevation, understory height, understory density, percent native understory, canopy height, canopy cover, and percent native canopy), coqui presence, and coqui density, we then employed the same tiered approach to modeling variation in avian abundances. After completing the last stage of our tiered approach to model selection, we based inference on the model with the lowest AIC value. Collinear covariates were never included in the same model. Coqui density and coqui presence covariates were compared in separate models. We also tested the goodness-of-fit of our models using Freeman-Tukey methods within a bootstrapping framework. All N-mixture analyses were conducted using the unmarked package (Royle 2004, Fiske and Chandler 2011) in R (R Core Team 2016).

RESULTS

We recorded 4,939 individual birds representing 20 species, of which 15 species were nonnative (80% of total observations; Table 1). The Japanese White-eye (*Zerops*

TABLE 1. Total numbers of observations (Obs) of each native and nonnative species in plots where coqui frogs were present (Coqui) vs. absent (No coqui) on the island of Hawaii, USA, and percent of total observations comprised of that species (Percent). Food sources were identified for native species based on Banko and Banko (2009a), and for nonnative species based on del Hoyo et al. (2008a, 2008b).

Species	Obs	Coqui	No coqui	Percent	Food sources
Native					
Apapane (*Himatione sanguinea*)	514	229	285	10.4	Nectar
Hawaii Amakihi (*Chlorodrepanis virens*)	383	175	208	7.7	Insects, Nectar
Hawaii Elepaio (*Chasiempis sandwichensis*)	68	32	36	1.4	Insects
Hawaiian Hawk (*Buteo solitarius*) *	2	1	1	<0.1	Vertebrates
Omao (*Myadestes obscurus*) *	2	0	2	<0.1	Fruits, Seeds
Nonnative					
Japanese White-eye (*Zosterops japonicus*)	2,569	1,209	1,360	52.0	Fruits, Seeds, Insects, Nectar
Northern Cardinal (*Cardinalis cardinalis*)	425	205	220	8.6	Fruits, Seeds
House Finch (*Haemorhous mexicanus*)	269	143	126	5.4	Fruits, Seeds
Red-billed Leiothrix (*Leiothrix lutea*)	197	88	109	4.0	Fruits, Seeds, Insects, Vertebrates
Japanese Bush-Warbler (*Cettia diphone*)	168	78	90	3.4	Insects
Hwamei (*Garrulax canorus*)	125	78	47	2.5	Fruits, Seeds, Insects, Vertebrates
Common Myna (*Acridotheres tristis*)	86	68	18	1.7	Insects, Vertebrates
Spotted Dove (*Streptopelia chinensis*)	41	30	11	0.8	Fruits, Seeds
Yellow-fronted Canary (*Crithagra mozambica*)	32	18	14	0.6	Fruits, Seeds
Zebra Dove (*Geopelia striata*)	26	20	6	0.5	Fruits, Seeds
Scaly-breasted Munia (*Lonchura punctulata*) *	14	6	8	0.3	Fruits, Seeds
Kalij Pheasant (*Lophura leucomelanos*) *	11	2	9	0.2	Fruits, Seeds
Yellow-billed Cardinal (*Paroaria capitata*) *	3	3	0	<0.1	Fruits, Seeds
Rock Pigeon (*Columba livia*) *	2	2	0	<0.1	Fruits, Seeds
Saffron Finch (*Sicalis flaveola*) *	2	1	1	<0.1	Fruits, Seeds, Insects

*Excluded from analysis due to small sample size.

japonicus) was the most abundant nonnative bird, with 2,569 observations across all 15 sites. The Apapane (*Himatione sanguinea*) was the most abundant native bird, with 514 observations in 6 sites. Four of the 5 native species were observed in both coqui-invaded and uninvaded sites. The 2 Omao (*Myadestes obscurus*) that we observed were both in the same coqui-free plot. Thirteen

TABLE 2. One-way ANOVA of environmental differences between study plots with and without invasive coqui frogs (Coqui), with study site (Site) as a block, on the island of Hawaii, USA. An asterisk indicates a significant difference between plots.

Variable	Factor	Sum of squares	df	F-statistic	P-value
Canopy cover	Coqui	4	1	0.03	0.86
	Site	49,133	14	26.13	<0.001 *
Canopy height	Coqui	48	1	1.83	0.18
	Site	4,593	14	12.60	<0.001 *
% native canopy	Coqui	94	1	0.14	0.71
	Site	127,122	14	13.16	<0.001 *
% native understory	Coqui	107	1	0.18	0.67
	Site	61,128	14	7.38	<0.001 *
Understory density	Coqui	0	1	0.75	0.39
	Site	2	14	12.32	<0.001 *
Understory height	Coqui	0	1	0.10	0.75
	Site	60	14	2.87	0.002 *
Elevation	Coqui	7,254	1	6.63	0.01 *
	Site	1,669,924	14	109.00	<0.001 *

of the 15 nonnative species were observed in both coqui-invaded and uninvaded plots. The nonnative Yellow-billed Cardinal (*Paroaria capitata*) and Rock Pigeon (*Columba livia*) were only observed in coqui-invaded plots.

Plot-level Habitat Differences

No habitat variable that we measured, except elevation, differed between coqui-invaded and uninvaded plots (Table 2). Given the nature of the coqui invasion, mean elevation in coqui-invaded plots was lower than that in uninvaded plots (mean difference: 20 m, range: −97 to 160 m; see Appendix Table 5 for elevations across sites), but we do not believe this to be of biological significance for the observed bird species. Additionally, no habitat variable was significantly correlated with coqui density (Appendix Table 6).

Individual Bird Species

For the 13 species with enough observations to develop maximum-likelihood *N*-mixture models, no native species showed a negative or positive response to the coqui (Table 3), whereas the abundances of 3 nonnative species were positively associated with coquis based on the top models. The Common Myna was positively associated with coqui presence at low understory densities, but the interaction indicated that this effect disappeared in locations with a thick understory (Figure 3, Table 3). The Red-billed

TABLE 3. Top *N*-mixture models for spatial variation in abundance and detection probabilities for native and nonnative bird species groups on the island of Hawaii, USA, and for the 13 species with sufficient data to be analyzed separately. Shown are the abundance covariates appearing in the top-ranked models (+ indicates additive effect and * indicates interactive effect), their estimates and corresponding 95% confidence intervals (for Estimates, main effects are shown first, followed by interaction terms if applicable; [†] indicates a significant effect of either coqui frog presence or density), detection covariates appearing in the top-ranked models, the latent abundance distribution (Dist) supported by the data (NB = negative binomial, P = Poisson, ZIP = zero-inflated Poisson), Akaike model weight (w_i), and *P*-values for Freeman-Tukey goodness-of-fit tests (GOF; models were considered to have acceptable fit to modeling assumptions if *P* > 0.10).

Group or species	Abundance covariates	Estimates	Detection covariates	Dist	w_i	GOF
All natives	% native canopy	2.03 (1.21, 2.85)	Cloud cover + Canopy height	NB	0.33	0.88
Apapane	% native canopy	2.11 (1.27, 2.95)	Canopy cover	NB	0.35	0.87
Hawaii Amakihi	Canopy cover	1.55 (0.66, 2.44)	Canopy cover*Understory density	ZIP	0.95	0.49
Hawaii Elepaio	Canopy height*% native canopy	0.97 (0.32, 1.62), 0.56 (−0.14, 1.27), 0.99 (0.32, 1.67)	Wind	ZIP	0.50	0.43
All nonnatives	Coqui density + % native understory	0.08 (0.01, 0.14), † 0.09 (0.03, 0.16)	Date + Wind	NB	0.27	0.44
Japanese White-eye	Elevation*% native understory	0.08 (0.02, 0.14), 0.06 (0.00, 0.12), −0.14 (−0.20, −0.08)	Cloud cover*Time	NB	0.89	0.45
Northern Cardinal	Canopy cover*Elevation	0.11 (−0.04, 0.26), −0.39 (−0.54, −0.24), 0.37 (0.20, 0.55)	Temperature	P	0.49	0.99
House Finch	Coqui density*% native understory	0.49 (0.21, 0.77), † 0.50 (0.23, 0.76), −0.32 (−0.67, 0.04)	Date + Precipitation	NB	0.57	0.66
Red-billed Leiothrix	Coqui density + % canopy cover + Understory density	0.29 (−0.06, 0.64), 0.65 (0.08, 1.23), −0.39 (−0.88, 0.10)	Canopy height + Wind	NB	0.20	0.74
Japanese Bush-Warbler	Canopy height*Understory density	−1.97 (−2.89, −1.05), 2.12 (1.20, 3.04), 1.30 (0.51, 2.09)	Understory density	NB	0.99	0.39
Hwamei	Understory height	−0.47 (−0.79, −0.15)	Canopy height*Understory density	NB	0.46	0.79
Common Myna	Coqui presence*Understory density + Elevation	0.73 (0.21, 1.25), † −0.21 (−0.73, 0.30), −0.52 (−0.95, −0.08), −0.52 (−0.98, −0.07) †	Canopy height + Date*Understory density	NB	0.45	0.47
Spotted Dove	Canopy height + Understory density	−0.77 (−1.64, 0.10), 1.08 (0.29, 1.87)	Cloud cover + Time	NB	0.51	0.70
Yellow-fronted Canary	% native canopy	1.05 (0.34, 1.76)	Date + Temperature	ZIP	0.86	0.39
Zebra Dove	Canopy height + Elevation	−0.46 (−1.06, 0.14), −0.88 (−1.63, −0.14)	Date*Time + Wind	ZIP	0.18	0.42

Leiothrix (*Leiothrix lutea*) was positively associated with coqui density, increasing from an average abundance of ~7 per coqui-free plot to a maximum of ~43 at the highest observed density of coquis, but we note that this relationship was imprecise and statistically indistinguishable from no relationship (Figure 4, Table 3). The House Finch (*Haemorhous mexicanus*) was positively associated with coqui density, but the interaction between coqui density and the percentage of native understory vegetation indicated that this effect was reduced in locations with a high percentage of native understory (Figure 5, Table 3).

Native and Nonnative Birds

As a group, native birds were positively associated with the percentage of canopy cover composed of native plants, but were not associated with coqui density or coqui presence (Table 3), and averaged 3.8 birds per plot (95% CI: 1.55–9.17). In contrast, nonnative bird abundance was much higher and positively associated with coqui density in our top-ranked model (Table 3). The estimated average abundance of nonnative birds was ~57 per coqui-free plot and increased to a maximum of ~90 at the highest observed density of coquis (Figure 6, Table 3). For each
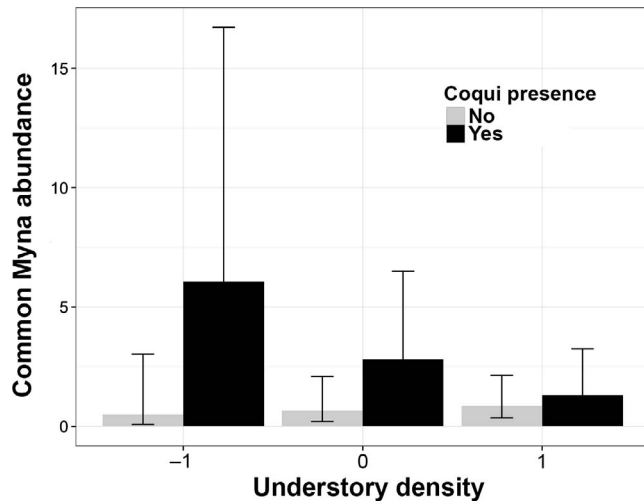
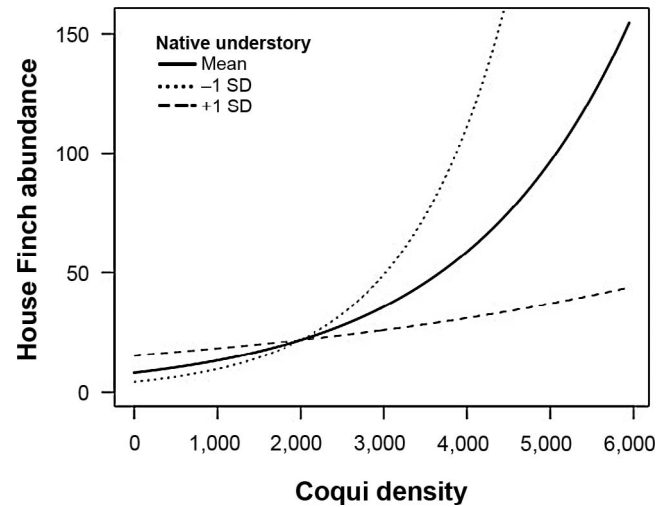**FIGURE 3.** Estimated relationship between Common Myna abundance and coqui frog presence (black bars) vs. absence (light gray bars) in study plots on the island of Hawaii, USA, and the interaction with understory density (0 = mean, ±1 SD), while holding elevation at its mean value. Error bars denote 95% confidence intervals.
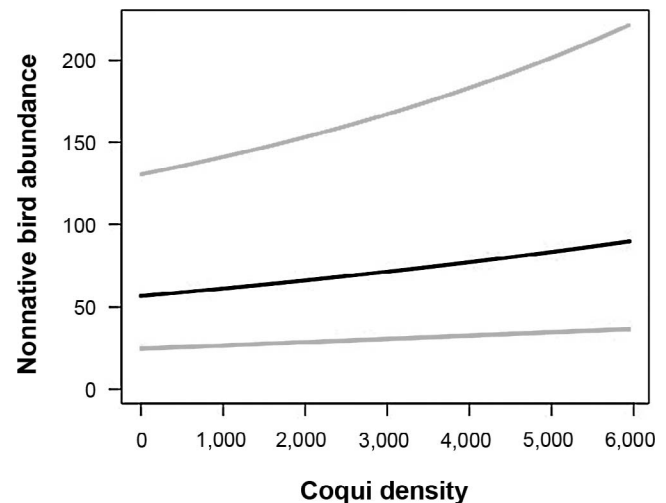

FIGURE 5. Estimated relationship between House Finch abundance and coqui frog density in surveyed plots on the island of Hawaii, USA, while holding percent native understory at its mean value (solid line), −1 SD (dotted line), and +1 SD (dashed line). For clarity, confidence intervals are not shown, but see Table 3 for confidence intervals associated with estimated slopes for the main and interactive effects on the log scale.

analyzed species and group of species, the goodness-of-fit test indicated that our data met the *N*-mixture modeling assumptions (Table 3). In Supplemental Material Table S1, we provide the top 10 candidate models based on AIC values, as well as the top model for detection probability when the parameterization for abundance was held constant (null), and a simple model with constant

parameterizations for both detection probability and abundance.

DISCUSSION

Because coqui frogs are insectivores, it has been hypothesized that coquis could compete for prey with native insectivorous birds (Kraus et al. 1999, Beard and Pitt 2005).

FIGURE 4. Estimated relationship between Red-billed Leiothrix abundance and coqui frog density (thick black line) in surveyed plots on the island of Hawaii, USA, based on the most supported model (Table 3), while holding percent canopy cover and understory density at their mean values. Pale gray lines denote the 95% confidence interval.

FIGURE 6. Estimated relationship between nonnative bird abundance and coqui frog density (thick black line) in surveyed plots on the island of Hawaii, USA, based on the most supported model (Table 3), while holding percent native understory at its mean value. Pale gray lines denote the 95% confidence interval.

Contrary to this hypothesis, no native birds or insectivorous birds showed lower abundances in plots with higher coqui densities or coqui presence (Tables 1 and 3). In fact, coquis were only associated with higher bird abundances, or had no relationship with abundance, and were never associated with lower bird abundances, as would be expected if coquis were significant competitors with birds. Perhaps this result should not be surprising, because coquis in Hawaii mostly forage in the leaf litter (Choi and Beard 2012), whereas most extant Hawaiian birds forage on insects in the canopy and understory (Banko and Banko 2009a, Banko et al. 2015, Smith et al. 2017). Moreover, our results suggest that coquis play a role in the system that favors at least some nonnative birds, because these birds had higher abundances where coquis occurred at higher densities. There are several ways in which higher coqui density may increase nonnative species abundance, including serving as a novel prey item, changing the invertebrate community in ways that benefit nonnatives, and increasing plant growth rates (Beard and Pitt 2005). It could also be that coquis and some nonnative birds are both responding positively to a variable that we did not measure in our study plots, but we addressed this possibility in our study design and do not think that this explains the observed patterns.

We found that coqui presence was positively associated with higher abundance of a nonnative species that we identified a priori as potentially consuming coqui, the Common Myna. The Common Myna is a known predator and scavenger of vertebrates on other islands (Foster 2009, Burns et al. 2013), and can quickly modify its foraging behavior to take advantage of novel prey (Sol et al. 2011). Mynas are likely large enough to consume adult frogs (25–47 mm; Beard 2007) as well as juvenile frogs. Unlike our results for nonnative species generally, coqui presence, and not density, was associated with higher Common Myna abundance. One explanation for this relationship is a feedback loop, such that a higher abundance of mynas keeps coqui densities low. An alternative reason is that mynas have larger home ranges than other forest birds in Hawaii and our plot area was smaller than their average territory size (Scott et al. 1986). Furthermore, the relationship between coquis and mynas was greatest where there was low understory density. While understory density influences detection probability, this was accounted for in our models. This relationship could have resulted because mynas may find coquis more easily where the understory is less dense, or because mynas prefer habitats that are more open (Pell and Tidemann 1997), as well as habitat that has coquis.

As further support for the potential explanation that coquis may increase some nonnative species abundances by serving as a novel food resource, coqui density appeared in the top model for the primarily insectivorous Red-billed Leiothrix, although the relationship was not significant. There are 2 main ways in which higher coqui density may increase the abundance of a nonnative insectivorous species, such as the Red-billed Leiothrix. First, juvenile coquis, which emerge from eggs at ∼7 mm (Woolbright 1985), could provide a novel food for insectivorous birds that feed on large insects and forage in the understory, such as the Red-billed Leiothrix or the Hwamei (*Garrulax canorus*). We have observed both of these species attempting to consume live coquis in Hawaii (S. Hill personal communication, K. Beard personal observation). Second, coquis increase the numbers of certain flying insects, such as Diptera, probably by increasing the amount of decomposing biomass (i.e. frog bodies) and excrement in areas where they invade (Tuttle et al. 2009, Choi and Beard 2012). Increased abundance of Diptera could favor the species, such as the Red-billed Leiothrix, that feed on these insect groups (Male et al. 1998). Thus, coquis may increase the numbers of some nonnative insectivorous birds by changing insect communities in ways that benefit these birds, but also by providing a novel food resource.

Previous studies have not hypothesized that there could be a relationship between coquis and frugivores, granivores, or nectarivores (Kraus et al. 1999, Beard and Pitt 2005). However, we found that House Finches, which are primarily frugivorous and granivorous, had significantly higher abundances with greater coqui densities. This result is more difficult to interpret, but could be explained by the direct effects of coquis on nutrient cycling. Coquis increase nutrient cycling rates and increase nonnative plant growth, in particular that of strawberry guava (*Psidium cattleianum*), a common nonnative plant that bears fruit year-round (Sin et al. 2008). If an increase in nonnative plant growth with greater coqui density leads to greater fruit and seed availability, House Finches, and perhaps other nonnative frugivores and granivores, would be expected to increase with greater coqui density. As further support for this explanation, the positive relationship between coqui density and House Finches was dampened in locations with a high percentage of native understory, where coquis would be less likely to increase plant growth rates and fruit production (Sin et al. 2008). However, because we did not count nonnative fruits and seeds in plots, we cannot determine whether coquis were associated with their increased production.

We found that the overall abundance of native birds showed no difference across coqui invasion fronts. The abundance of the 2 native insectivores investigated, Hawaii Amakihi (*Chlorodrepanis virens*) and Hawaii Elepaio (*Chasiempis sandwichensis*), also did not show any relationship to coquis, which suggests that coquis are not reducing native insectivores along invasion fronts (Kraus et al. 1999, Beard and Pitt 2005). It has been suggested that

native birds could decline if coquis increase predatory nonnative mammals (Kraus et al. 1999, Beard and Pitt 2005). Because we did not find a negative association between coquis and any bird species, our results suggest that apparent competition is not having a significant effect on bird abundances in our sites. The native species that we observed co-occurring with coquis in our mostly lowland sites are those that are the most resistant to avian malaria and poxvirus (Reynolds et al. 2003, Foster et al. 2007). If coquis continue to invade higher-elevation forests, to which many native species are now restricted (Ahumada et al. 2009, Atkinson and LaPointe 2009), they could have impacts on the more location-restricted native birds that we did not observe in our study.

The fact that coquis show up in top models as having positive effects on all nonnative species as a group and some individual nonnative species suggests either that: (1) coquis themselves influence the abundances of bird species, or (2) coquis and birds are responding independently and positively to some other factor(s) in coqui-invaded plots (MacDougall and Turkington 2005, Berglund et al. 2013). To address this second explanation, we purposely chose areas where plots on either side of the invasion front were as similar as possible with regard to habitat so that we could more confidently attribute differences detected across the invasion fronts to coquis and not environmental variables. We also measured habitat variables in our study plots, and no habitat variables that we measured, expect elevation, were different across the invasion fronts. The elevational difference that we found likely occurred because coquis first established in lowlands and tend to move upslope (Bisrat et al. 2012, Olson et al. 2012); however, it should be noted that the difference in elevation between plots with and without coquis was small (mean difference of 20 m) and probably not relevant for the bird species that we studied. We acknowledge that our design cannot completely rule out the possibility that coquis and birds are both responding to a variable that we did not measure. Nevertheless, while it is difficult to determine whether this is occurring without bird abundances prior to the invasion or experimental evidence (Gurevitch and Padilla 2004), we made every attempt to address this possibility during site selection and in our analyses.

Our results suggest that coquis do not affect native bird abundances, but that they are associated with higher abundances of nonnative birds. The fact that a coqui variable was present in the top model for 2 nonnative birds that have the ability to consume them suggests that a main effect of coquis on Hawaii's bird communities is as a novel prey resource (Beard and Pitt 2005). These results support previous studies that have found that nonnative species mainly affect invaded island ecosystems through predatory interactions and not through competition (Mack et al.

2000, Courchamp et al. 2003, Gurevitch and Padilla 2004, Sax and Gaines 2008, Shine 2010). The next step would be to collect data using camera traps, observations, or diet analyses to test whether affected birds consume coquis in numbers that might influence their population sizes. Finally, while controlling coqui populations is not always practical or possible (Tuttle et al. 2008), our results suggest that another reason to prevent future establishment on islands where they do not yet exist (i.e. other Pacific Islands) or from which they have been eradicated (Kauai and Oahu) is to prevent their potential to increase nonnative bird abundances. Nonnative birds are generally undesirable because they transmit disease, prey on native species, and are nuisances (Yap et al. 2002, Blanvillain et al. 2003, Ahumada et al. 2009, Burns et al. 2013, Saavedra et al. 2015). We recommend that managers continue to monitor native and nonnative bird abundance in coqui invasion fronts on the island of Hawaii. Where possible, we recommend measures to reduce the establishment of new coqui populations.

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APPENDIX TABLE 4. Coqui frog density (frogs ha^{-1}) estimated from line transect distance sampling surveys for all sites and plots on the island of Hawaii, USA, using the unmarked package (Fiske and Chandler 2011) in R (R Core Team 2016). We observed 1,577 frogs during surveys. All distance sampling data were modeled with null models for both detection and density using either the half-normal (HN), hazard (HZ), or exponential (E) distribution (Akaike model weights, w_i, are provided for the most supported detection distribution, as are P-values for Freeman-Tukey goodness-of-fit tests [GOF; models were considered to have acceptable fit to modeling assumptions if $P >$ 0.10]). Other abbreviations are as follows: Coq = coqui frogs present, Non = coquis absent. Coqui plots with 0 estimated density were modeled as having 5 frogs because frogs were heard, even though they were not observed, during distance sampling. See Figure 1 for full site names.

Site	Plot	Density	Top model	w_i	GOF
ER	Coq1	590	HN	0.70	0.84
	Coq2	1,122	E	0.52	0.50
	Coq3	511	HN	0.56	0.97
	Non1	0			
	Non2	0			
	Non3	0			
FF	Coq1	631	HN	0.92	0.72
	Coq2	807	HN	0.56	0.75
	Coq3	530	HN	0.52	0.04
	Non1	0			
	Non2	0			
	Non3	0			
HM	Coq1	502	E	0.67	0.93
	Coq2	474	HN	0.53	0.07
	Coq3	401	HN	0.54	0.34
	Non1	0			
	Non2	0			
	Non3	0			
KH	Coq1	691	E	0.78	0.09
	Coq2	290	HN	0.45	0.23
	Non1	0			
	Non2	0			
KL	Coq1	565	HN	0.74	0.39
	Coq2	101	HN	0.46	0.83
	Coq3	0			
	Non1	0			
	Non2	0			
	Non3	0			
KP	Coq1	2,407	E	0.54	0.31
	Coq2	436	E	0.46	0.53
	Coq3	417	HZ	0.51	0.24
	Non1	0			
	Non2	0			
	Non3	0			
KU	Coq1	419	HN	0.42	0.69
	Coq2	389	HN	0.42	0.88
	Coq3	469	E	0.38	0.07
	Non1	0			
	Non2	0			
	Non3	0			
KW	Coq1	121	HN	0.43	0.25
	Coq2	200	HN	0.42	0.32
	Coq3	123	HN	0.42	0.39
	Non1	0			
	Non2	0			
	Non3	0			

APPENDIX TABLE 4. Continued.

Site	Plot	Density	Top model	w_i	GOF
MA	Coq1	2,170	E	0.60	0.58
	Coq2	2,872	E	0.94	0.74
	Coq3	5,948	E	0.95	0.67
	Non1	0			
	Non2	0			
	Non3	0			
MB	Coq1	2,730	E	0.96	0.03
	Coq2	2,998	E	0.97	0.77
	Coq3	4,328	E	0.86	0.14
	Non1	0			
	Non2	0			
	Non3	0			
SR	Coq1	968	HN	0.68	0.38
	Coq2	79	E	0.47	0.42
	Coq3	463	E	0.41	0.87
	Non1	0			
	Non2	0			
	Non3	0			
SB	Coq1	607	HN	0.84	0.02
	Coq2	769	HN	1.00	0.96
	Coq3	293	HN	0.46	0.60
	Non1	0			
	Non2	0			
	Non3	0			
VA	Coq1	78	HN	0.53	0.56
	Coq2	50	E	0.44	0.73
	Non1	0			
	Non2	0			
VB	Coq1	0			
	Coq2	211	HN	0.56	0.65
	Non1	0			
	Non2	0			
WP	Coq1	227	HN	0.68	0.10
	Coq2	0			
	Coq3	390	HN	0.53	0.33
	Non1	0			
	Non2	0			
	Non3	0			

APPENDIX TABLE 5. Mean values of plot-level environmental covariates, coqui density, and coqui presence or absence for each of the 15 study sites on the island of Hawaii, USA. Covariates were included in models that were used to determine the variables that most explained bird abundance. Coq = coqui frogs present, Non = coquis absent. Full site names are in Figure 1.

Site	Annual rainfall (mm) [§]	Annual temperature (°C) [†]	Plot type	Coqui density (frogs ha^{-1})	Canopy cover (%)	Canopy height (m)	Native canopy (%)	Understory density (%)	Understory height (m)	Native understory (%)	Elevation (m asl)
ER	4,702	18.9	Coq	741	37	5.2	33	71	2.2	29	537
			Non	0	40	4.5	67	87	2.4	25	507
FF	4,915	18.1	Coq	656	35	7.9	100	67	1.4	75	685
			Non	0	27	8.1	100	58	1.8	75	636
HM	2,432	18.9	Coq	459	85	22.1	5	51	3.0	8	666
			Non	0	90	18.6	17	36	3.2	4	654
KH	4,250	19.0	Coq	491	88	28.8	0	56	2.1	0	466
			Non	0	84	23.9	0	56	2.9	0	466
KL	1,251	17.7	Coq	333	89	15.3	100	49	2.9	88	878
			Non	0	84	19.0	100	62	2.4	78	902
KP	2,640	19.1	Coq	1,087	90	9.7	90	30	1.8	92	650
			Non	0	93	15.7	68	34	2.5	42	685
KU	5,248	18.9	Coq	426	89	13.0	56	78	5.6	8	509
			Non	0	92	25.7	0	70	2.1	4	516
KW	4,373	18.2	Coq	148	72	10.6	67	84	1.9	38	565
			Non	0	82	10.2	40	81	3.3	29	648
MA	838	19.7	Coq	3,663	68	19.0	69	42	1.2	18	572
			Non	0	73	18.8	100	46	2.5	95	599
MB	838	19.8	Coq	3,352	79	21.6	72	55	2.3	58	604
			Non	0	63	20.9	85	45	1.2	75	652
SB	5,759	17.8	Coq	556	86	20.9	8	65	2.4	58	689
			Non	0	91	24.3	0	62	2.4	17	694
SR	4,815	17.3	Coq	503	20	5.3	100	45	1.0	54	739
			Non	0	6	1.9	100	37	1.1	42	844
VA	5,483	17.2	Coq	64	82	3.7	100	81	3.7	13	823
			Non	0	86	8.4	90	81	5.5	31	810
VB	4,075	17.0	Coq	211	68	10.0	100	74	2.6	25	969
			Non	0	74	6.4	100	72	2.3	92	929
WP	2,264	20.9	Coq	309	90	21.3	0	45	1.4	0	372
			Non	0	88	27.9	0	36	1.8	9	420

[§] Data from Giambelluca et al. (2013).
[†] Data from Giambelluca et al. (2014).

APPENDIX TABLE 6. Variance inflation factors (VIF) and univariate correlation coefficients (*r*) between coqui frog density and 7 habitat variables across 15 sites on the island of Hawaii, USA. A conservative estimate of collinearity is based on a threshold of VIF > 3 (Zuur et al. 2010).

	Canopy cover	Canopy height	% native canopy	Understory density	Understory height	% native understory	Elevation
VIF	1.98	1.90	2.18	1.36	1.97	1.90	1.45
r	0.03	0.30	0.09	0.32	0.21	0.09	0.14