

Bottom-up processes influence the demography and life-cycle phenology of Hawaiian bird communities

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Abstract. Changes in climate can indirectly regulate populations at higher trophic levels by influencing the availability of food resources in the lower reaches of the food web. As such, species that rely on fruit and nectar food resources may be particularly sensitive to these bottom-up perturbations due to the strength of their trophic linkages with climatically-influenced plants. To measure the influence of climatically-mediated, bottom-up processes, we used climate, bird capture, bird count, and plant phenology data from the Big Island of Hawaii to construct a series of structural equation and abundance models. Our results suggest that fruit and nectar-eating birds arrange life cycle events around climatically-influenced food resources, while some of these same food resources also influence seasonal patterns of abundance. This trend was particularly strong for two native nectarivores, ‘Iiwi and ‘Apapane, where we found that the dissimilar timing of molting and breeding activity was associated with peak abundance of the two most common flowers at our study site which, in turn, were each driven by dissimilar climatic cues. Given the rapidly changing Hawaiian climate, we suggest that determining behavioral plasticity, or evolutionary capacity of birds to mitigate changes in climatically-influenced food resources, should be recognized as a future research priority.

Key words: bottom-up; climate; community ecology; food web; Hawaiian birds; plant phenology; structural equation models.

INTRODUCTION

Community dynamics are often dependent on whether individual species are more strongly influenced by bottom-up processes, such as food availability, or by top-down and density-dependent processes, such as predation, disease, or competition (e.g., Hunter and Price 1992, Pascual and Dunne 2006, Bascompte 2010). Measuring bottom-up processes is particularly important because the strength and number of trophic linkages in the lower reaches of the food web can determine the resilience of species to environmental and climatic change at higher trophic levels (e.g., Grant et al. 2000, Visser et al. 2006, Both et al. 2009). To date, many empirical studies that evaluate the influence of abiotic factors, such as climate change, on biological communities via bottom-up processes are from aquatic systems (Flinkman et al. 1998, Menge 2000, Whalen et al. 2013). While insights from aquatic systems have informed how bottom-up-processes influence community structure, inferences may not be generalizable to terrestrial systems. We believe that many land bird assemblages represent model systems to evaluate the effects of climate on food webs via bottom-up processes in terrestrial systems because land birds are ubiquitous and represent

a diversity of measureable dietary guilds and trophic linkages. Land bird communities also exhibit distinct life cycle phases, such as breeding and molting that are sensitive to the availability of food (e.g., Studds and Marra 2011, Plummer et al. 2013, Danner et al. 2014). Thus, determining the influence of climate on food resources that land birds use during discrete life cycle events can help reveal community dynamics and identify mechanisms that regulate terrestrial populations.

Only a few studies have simultaneously measured the multitude of trophic and climatic linkages necessary to disentangle bottom-up processes that influence land bird communities. One such study found heavy rains increased food availability, which lead to longer nesting periods, more broods, increased clutch size, and larger egg-size in two species of Darwin’s finches, *Geospiza fortis* and *G. scandens* (Grant et al. 2000). Interestingly, the correlation between rain, food resources, and avian productivity was broken during a particularly wet year when density dependent interactions with other finches limited breeding success (Grant et al. 2000). Thus, bottom-up and density-dependent processes may dynamically interact over time to regulate some bird communities. Similarly, increased precipitation in semiarid grasslands in Chile produced more seeds, leading to small rodent eruptions, followed by delayed increases in hawk and owl abundance, suggesting that a lag effect may exist at higher trophic levels (Meserve et al. 1995, 1999, Jaksic et al. 1997, Lima and Jaksic 1999).

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Identifying directionality of trophic interactions between food resources and avian lifecycle events is often complicated by migratory behaviors and predictable seasonal weather patterns. For example, climatic cues have been associated with flower and fruit phenology as well as avian migration (Rathcke and Lacey 1985), while flower and fruit phenology have also been linked to the migratory timing of avian pollinators and seed dispersers (dispersal facilitation hypothesis described by Burns 2002). These relationships create circularity where migratory movements of pollinators and seed-dispersers obscure cause and effect: are migratory behaviors a cause (top-down) or effect (bottom-up) of seasonal flower and fruit availability (Rathcke and Lacey 1985)? Or, alternatively, there is no effect, where birds and plants simply use similar climatic cues resulting in synchronous timing of migration and flower-and-fruit activity (Wolfe et al. 2014). Clearly, trophic interactions between birds and their fruit and flower food resources are less complex and more easily measured in the absence of migratory behaviors.

The archipelago of Hawaii provides a tractable system to better understand how community dynamics are influenced through bottom-up processes because Hawaii hosts communities of largely non-migratory nectar and fruit-eating birds. Thus, those seasonal migrations of pollinators and seed dispersers that may have evolutionarily shaped plant phenology in mainland systems are largely absent in Hawaii. Given the relative absence of migratory nectar and fruit-eating birds in Hawaii, we believe that Hawaiian plant phenology was primarily shaped by bottom-up effects, namely climatic influences. If this is true, then we predict that Hawaiian birds will structure energetically-taxing life cycle events – such as breeding and molt – around climatically-mediated flower and fruit abundance.

Hawaii's biological communities have undergone a notable diversification process that resulted in coevolution between native birds and plants; these processes established mutualisms and distinct trophic linkages in forested landscapes throughout the archipelago (Scott et al. 2001). The subsequent introduction of disease and invasive species disrupted many plant-animal mutualisms, and aided in the extinction of various endemic Hawaiian birds (Pratt et al. 2009). Currently, the remaining native plant-bird mutualisms are largely restricted to high elevation refugia where they coexist with numerous non-native species (Foster and Robinson 2007). Given broad interest in the conservation and management of endangered Hawaiian birds, a team of biologists collected comprehensive life history information on both plant and bird populations near Hawai'i Volcanoes National Park between 1976 and 1982. The resulting database is an unparalleled collection of climate, plants, and bird observations. These data serve as historic benchmarks from which contemporary studies can be compared to identify changes in community structure. A more recent long-term monitoring project near Volcanoes National Park demonstrated that sustained drought

lead to precipitous declines and local extinctions of native bird species (Banko et al. 2013). The dramatic response of Hawaiian land birds to drought suggests a climate-mediated reduction or shift in food supply which influenced avian demographics and the subsequent structure of biological communities (Badeck et al. 2004, Banko et al. 2013).

To test our prediction that climate influences biological communities through bottom-up processes, we used the 1976–1982 Hawaiian dataset in two ways. First, we examined how climatic variation influenced the timing of fruit and flower food resources and how such influences resonated at higher trophic levels through the timing of avian life cycle events. Second, we measured the seasonal abundance of birds relative to food availability, abundance of potential native and non-native competitors, and time trends to ascertain how climatically-influenced food resources and competition may affect avian populations. Native Hawaiian birds used in this study include: a largely frugivorous species, the 'Oma'o (Hawaiian Thrush) (*Myadestes obscurus*); two nectarivorous honeycreepers, 'Apapane (*Himatione sanguinea*) and 'I'iwi (*Vestiaria coccinea*); and one honeycreeper generalist, Hawai'i 'Amakihi (*Hemignathus virens*). Non-native species used in the study were one frugivore, the Red-billed Leiothrix (*Leiothrix lutea*), and two generalists, the Northern Cardinal (*Cardinalis cardinalis*) and Japanese White-eye (*Zosterops japonicus*). Here, we define generalists as species that regularly feed on nectar (Hawai'i 'Amakihi and Japanese White-eye), as well as fruits and insects. The inclusion of non-native species helped determine if detected patterns occur across dietary guilds irrespective of evolutionary history. To our knowledge, this study represents the first attempt to directly measure climate and interacting trophic linkages to determine their direct and indirect influence on Hawaiian bird behavior and abundance.

METHODS

Study area and data collection

Data used in our study was collected from a 16-ha study plot, gridded with 81 points, located at Keauhou Ranch, 1650 m elevation, 8 km ENE of the headquarters of Hawai'i Volcanoes National Park (Fig. 1). The study area was comprised of wet forest with a long history of logging and grazing, and was being grazed during the collection of data at the study site. Former logging roads and other open areas were a substantial (ca. 10–20%) fraction of the site, making a discontinuous canopy. These openings were covered in grass with extensive regeneration of native trees and shrubs, dominated by naio (*Myoporum sandwicense*) which often makes dense thickets 5–9 m high. Despite its open character, the study site had a substantial amount of mature koa (*Acacia koa*) and 'ohi'a lehua (*Metrosideros polymorpha*) as well. During the study, trees in a nearby stand were harvested and it is possible that the scale of

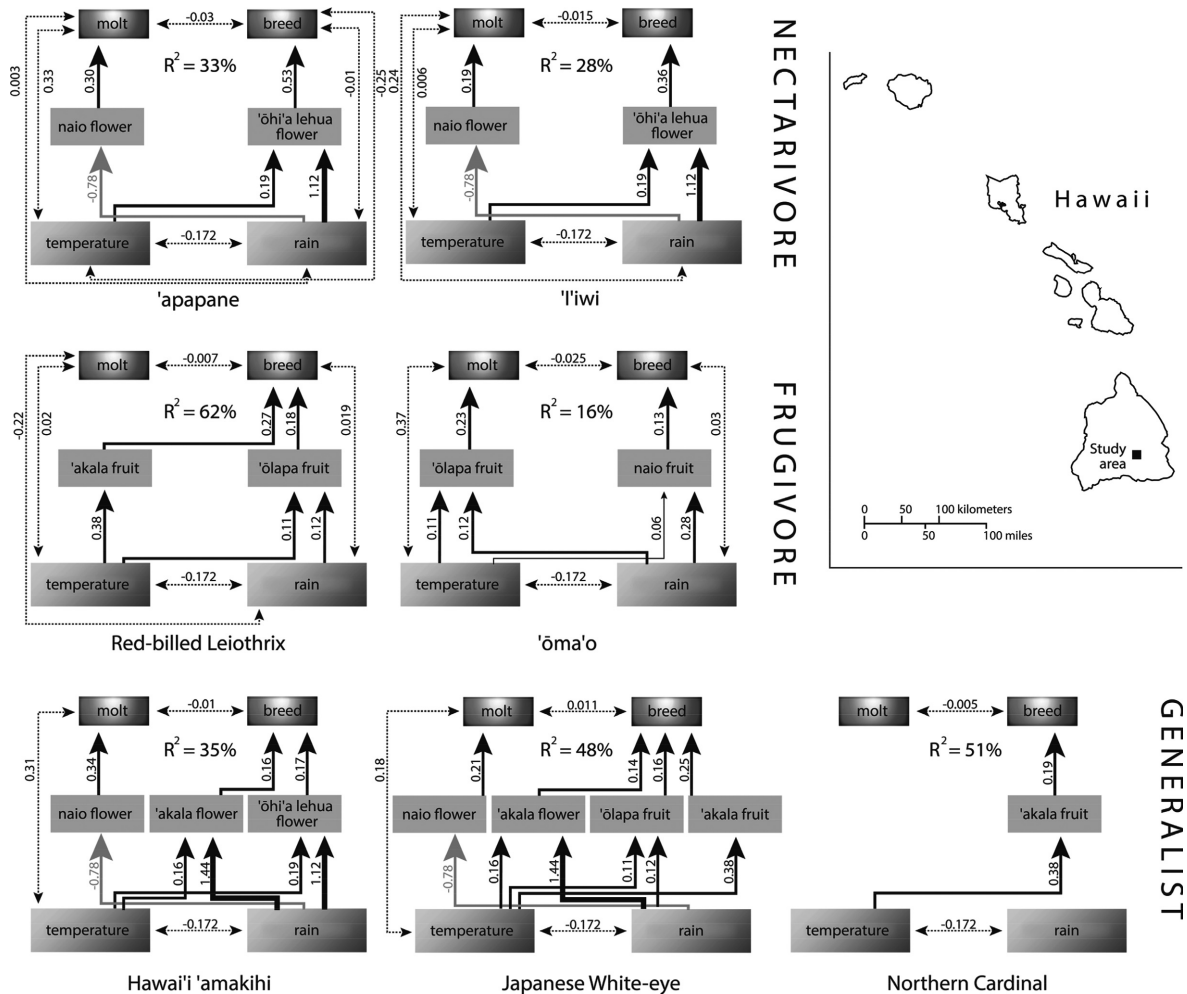


FIG. 1. The study was conducted at the Keauhou Ranch, near Hawai'i Volcanoes National Park, on the Big Island ($19^{\circ}31'37.72''$ N $155^{\circ}18'59.20''$ W) from 1976 through 1982. Known variable structural equation models for seven study species included the following exogenous variables: monthly rain and temperature with a 4-month time lag; endogenous food variables included: monthly abundance of fruit and flower resources; endogenous avian life cycle variables included: monthly percentages of birds in symmetrical flight-feather molt and breeding condition. Black arrows indicate positive correlations, gray arrows negative correlations and their thickness represents the size of the beta estimate; dotted two-headed arrows are co-variances with an associated estimate.

forest clearing could have affected bird abundance and behavior to some unknown extent. Climatic data used in the study were based on daily weather observations taken by National Park personnel between January 1977 and April 1982 at the nearby headquarters of Hawai'i Volcanoes National Park.

Bird data were collected, in general, following the various protocols of Ralph et al. (1993). We conducted eight-minute point counts at each of the 81 points within the 16-ha study plot every month, weather permitting. Birds were detected visually, as well as by song and call. The number of point counts conducted each month varied between 25 to 12, depending upon available personnel. In addition, we captured birds using mist nets operated throughout the study site at weekly intervals at 16 permanent net locations, and at ten additional

locations that were rotated around the four corners of the 16-ha study plot on a 1–3 month basis. Each net was 2.5 m high and 12 m long with 36 mm stretched mesh size. Eight of the permanent nets were double, one atop another. We opened nets at dawn, or the night before, and closed in mid-afternoon. Each bird was color banded with a unique combination of three plastic bands and one aluminum band. Various measurements were taken during capture following Ralph et al. (1993), including an assessment of body and flight feather molt, sex and breeding condition by brood patches and enlargement of the male cloacal protuberance. Age was determined primarily through the extent of skull ossification. In addition, we took approximately 35 observations of each species each month recording activity budgets that included: substrates used for foraging and

foods being consumed (e.g., species of flower or fruit). Phenology and abundance of flowers and fruits used by the various species was quantified each month throughout the study site. Specifically, we recorded the number and species of fruits or flowers of trees and shrubs within a 10-m line between the individual 81 grid points.

Analysis of climate, food and timing of nesting and molting

To measure the influence of climate on food resources, and the effects of food resources on timing of avian breeding and nesting, we employed Structural Equation Models (SEMs) with known variables, using package Lavaan (Rosseel 2012) in program R (R Core Team 2014). SEMs are particularly well suited to model multiple associations within a community because they combine likelihood estimation, regression and multivariate techniques to determine the influences of interacting endogenous and exogenous variables on phenomena of interest. We used four datasets in the analysis: (1) mean estimates of monthly precipitation and temperature (see Appendix S1: Fig. S1); (2) monthly percent of captured adult birds undergoing symmetrical flight feather molt or exhibiting breeding condition – defined by smooth, wrinkled or vascularized brood patch, or medium or large cloacal protuberance; (3) log-transformed abundance of species-specific flower and fruit resources by month (see Appendix S1: Fig. S1); (4) activity budgets to determine what flowers and fruits each particular species was using. For each species, we constructed models that included paths between two climate variables, average monthly rainfall and temperature values, to food resources known to be used by each study species. Next, paths were created between food variables to life cycle events: the percent of adult birds captured in molt and breeding condition. Because we used percent as a response variable, potential differences in capture rates between species was considered negligible. We varied each species' model by a 1-, 2-, 3-, or 4-month time lags associated with climatic covariates (e.g., the cumulative climate from the past 4 months associated with the current month's food resources would be a 4-month lag). Each of these four time-lag models, for each species, was ranked using AIC. We used a chi-square test, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) as measures of model fit for each of the top models, according to the following criteria (Grace 2006, Sandom et al. 2013): (1) *P*-values of chi-square tests >0.05; (2) lower 90% confidence intervals of RMSEA close to 0; and (3) CFIs ≥0.9. Missing paths were identified and non-informative linkages were pruned based on the above measures of model fit, residuals, and modification indices. Missing paths were subsequently accounted for by adding error covariances between pairs of variables (Grace 2006). Significance was assessed by examining standard errors and *P*-values associated with each SEM path.

Effects of fruit and flowers on bird abundance

To assess the effects of food resources and potential competitors on the abundance of study species we used a three-stage hierarchical modeling approach. Specifically, our models examined associations between monthly estimates of bird abundance and: (1) time-trends across the entire study period; (2) food resources (logged monthly-estimates of flowers and fruit abundance); and (3) monthly-abundance estimates of ecologically similar species using multiple-linear regression in program R (R Core Team 2014). The top model from each stage was selected using AICc and included in subsequent stages as an additive effect; models from preceding stages without any additional covariates were included as null models in each subsequent stage. We also examined predicted vs. residual plots for each study species to ensure homoscedasticity following suggestions by Zuur (2009).

The first stage allowed monthly-abundance estimates of birds to vary by either a linear-month effect (each month indexed between 1 and 12). Additionally, we allowed monthly-abundance estimates of each species to vary as a linear, quadratic or pseudo-threshold (natural log) time trend in monthly increments across the entire study period; we also examined interactions between month and time-trends. Null models were included within the first modeling stage as well. In the second model stage we allowed monthly-abundance estimates of species to vary by commonly-used fruit and flower food resources. We used the log-transformed monthly abundance of selected fruit and flowers as covariates. In addition to single fruit and flower covariates in stage two models, we also created models with additive effects that included the two most frequently used plant resources for each bird species, as well as an additive model that included all food resources known to be commonly used by each species. In the third and final model stage, we allowed monthly-abundance estimates of each individual bird species to vary by the abundance of other ecologically-similar species in the same month. Within the third model stage, we suggest that positive associations between species' abundances may reflect two possibilities: (1) different species selecting similar resources; and/or (2) density dependent mechanisms where birds select habitats based on the presence of individuals of another species. Further, we interpreted negative relationships between species abundance as: (1) potential evidence of competition between species within similar ecological guilds; and/or (2) other explanations, such as synchronous timing of different preferred food resources of different species. In addition to single species, we created global models that included additive effects of the entire suite of ecologically similar species on study species' abundance. To ascertain positive and negative associations between the abundance of each species and abundance of ecologically-similar species, we first ignored models with negative associations and only reported results from models with positive associations within four AICc values of the

top model. This allowed us to examine putative positive density-dependent associations between the abundance of one species on another. Next, we ignored positive associations of species responding similarly to the same resource, and, instead, examined those models with species exhibiting negative associations (i.e., putative competitors) within four AICc values of the top model. Finally, overall top models (with covariates from each of the three model stages) were used to produce predicted values and standard errors for each species. We examined covariate beta estimates and their associated *P*-values to further explore relationships between each species' abundance, time trends, food and ecologically similar birds.

RESULTS

Nesting and molting

The two most common and widely used flowers among nectarivorous birds were 'ohi'a lehua and naio. Abundance of each species responded to different climatic cues. Specifically, naio flowers were associated with dry climatic conditions (4-month lag negative correlation with precipitation; $\beta = 0.78$, $SE = 0.37$, $P = 0.03$), while 'ohi'a lehua was associated with wet conditions (4-month lag positive correlation with precipitation; $\beta = 1.12$, $SE = 0.26$, $P < 0.001$; Fig. 2). Fruits commonly used by birds were generally found to vary positively with warm and wet conditions. For example, although not statistically significant, both 'olapa fruit ($\beta = 0.11$, $SE = 0.13$, $P = 0.36$) and naio fruit ($\beta = 0.28$, $SE = 0.36$, $P = 0.43$) abundance were in the top model and were positively associated with a 4-month precipitation time-lag. Additionally, 'olapa fruit ($\beta = 0.11$, $SE = 0.02$, $P < 0.001$), naio fruit ($\beta = 0.06$,

$SE = 0.05$, $P = 0.17$) and 'akala fruit ($\beta = 0.38$, $SE = 0.03$, $P < 0.001$) abundance were all positively associated with a 4-month temperature time-lag. After measuring correlations between climatic cues and the abundance of flowers and fruits, we used these same structural equation models to examine relationships between flower and fruit resources and the timing of bird breeding and molt activity (Fig. 1).

For native and non-native birds that commonly fed on nectar, we found that each species exhibited correlations between the timing of molt and naio flower abundance: 'Apapane ($\beta = 0.30$, $SE = 0.04$, $P < 0.001$), 'I'iwi ($\beta = 0.19$, $SE = 0.03$, $P < 0.001$), Hawai'i 'Amakihi ($\beta = 0.34$, $SE = 0.04$, $P < 0.001$), and Japanese White-eye ($\beta = 0.21$, $SE = 0.04$, $P < 0.001$) (Fig. 2). Similar to detected relationships between molting activity and a single species of flower, we detected associations between breeding activity of the three-native species that commonly fed on nectar and 'ohi'a lehua flower abundance: 'Apapane ($\beta = 0.530$, $SE = 0.07$, $P < 0.001$), 'I'iwi ($\beta = 0.36$, $SE = 0.06$, $P < 0.001$) and Hawai'i 'Amakihi, a native generalist ($\beta = 0.17$, $SE = 0.06$, $P = 0.006$). We also found that both native and non-native generalists that commonly fed on nectar exhibited breeding activity associated with 'akala flower abundance: Hawai'i 'Amakihi ($\beta = 0.16$, $SE = 0.04$, $P < 0.001$) and Japanese White-eye ($\beta = 0.14$, $SE = 0.03$, $P < 0.001$).

Unlike relationships between abundance of a single species of flower and the molting and breeding activity in the nectarivorous species (e.g., naio associated with molt and 'ohi'a lehua with breeding), we found a diversity of relationships between fruit resources and breeding activity of frugivorous birds. For example, 'olapa fruit abundance was positively associated with breeding

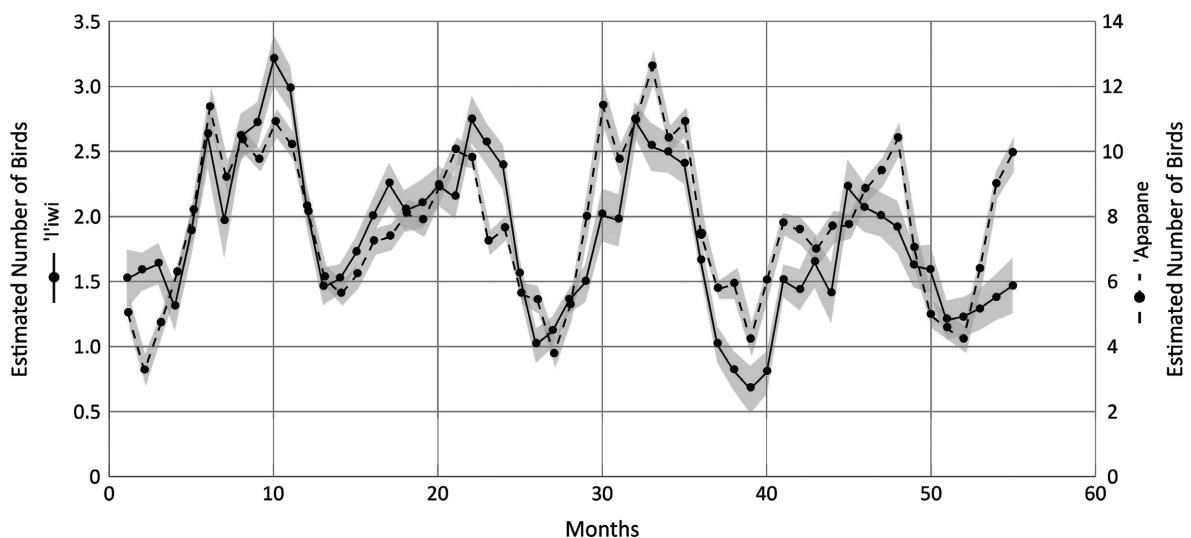


FIG. 2. Predicted abundance estimates of native nectarivores, 'Apapane and 'I'iwi, per point count station with standard errors based on the averaged top model from the hierarchical model selection routine; estimates were derived from point count data collected near Hawai'i Volcanoes National Park from 1976 through 1982.

activity of non-native species: Red-billed Leiothrix ($\beta = 0.18$, $SE = 0.08$, $P = 0.036$) and Japanese White-eye ($\beta = 0.16$, $SE = 0.09$, $P = 0.074$), while 'akala fruit was positively associated with breeding activity of several non-native species: Red-billed Leiothrix ($\beta = 0.27$, $SE = 0.03$, $P < 0.001$), Japanese White-eye ($\beta = 0.25$, $SE = 0.03$, $P < 0.001$) and Northern Cardinal ($\beta = 0.19$, $SE = 0.03$, $P < 0.001$). Naio fruit abundance was only associated with breeding activity of a single species, the 'Oma'o, a native frugivore ($\beta = 0.13$, $SE = 0.05$, $P = 0.017$). Unlike multiple correlations between flowers and bird molt, we only found a single correlation between the abundance of fruit and the timing of bird molt, where 'olapa fruit was associated with molting activity of 'Oma'o ($\beta = 0.23$, $SE = 0.16$, $P = 0.094$). We found R^2 values associated with each structural equation model were similar among native species that commonly fed on nectar: 'Apapane ($R^2 = 33\%$) and 'I'iwi ($R^2 = 28\%$). However, among native and non-native generalists and frugivores, we found dissimilar values, where R^2 values ranged from a low of 16% for 'Oma'o to 62% for Red-billed Leiothrix (Fig. 2).

Abundance

The first stage of the model selection routine found that five of the seven study species exhibited abundances that varied by month (Table 1, see Appendix S2: Tables S1–S7). Based on an examination of predicted abundance estimates from top models, the two native nectarivores, 'Apapane and 'I'iwi, exhibited the highest predicted abundances from December through May

and lowest from July through September (Fig. 2). Conversely, the non-native generalist that commonly fed on fruit and nectar, Japanese White-eye, and the native frugivore, 'Oma'o, both exhibited the highest predicted abundances from August through December and lowest abundance during January and February (Figs. 3, 4). The native generalist, Hawai'i 'Amakihi, exhibited a quadratic time trend where abundance was highest during the beginning the study (Fig. 4). Two additional non-native species, the Northern Cardinal and Red-billed Leiothrix, both yielded predicted abundances that were highest between the months of June and September and lowest from November through January (Figs. 3, 4).

In the second hierarchical stage of the analysis, we examined associations between flower and fruit food resources and study species' abundances. We found that abundances of the two native nectarivores, 'Apapane and 'I'iwi, were positively associated with 'ohi'a lehua flowers and negatively associated with naio flowers (Table 1). With regards to fruit, two non-native fruit-eating birds, the Red-billed Leiothrix and Northern Cardinal, and the native 'Oma'o exhibited a positive association with 'olapa fruit (Table 1). 'Oma'o and Red-billed Leiothrix also exhibited associations with naio and akala fruits: naio fruit was positively and negatively associated with Red-billed Leiothrix and 'Oma'o abundance, respectively, and akala fruit was positively and negatively associated with 'Oma'o and Red-billed Leiothrix abundance, respectively. We detected no relationship between flowers and fruits and the abundance of Japanese White-eye, or Hawai'i 'Amakihi.

TABLE 1. Beta estimates and standard errors (in parentheses) from the three stages of the hierarchical abundance modeling analysis. Bolded covariates indicate statistical significance ($P < 0.05$). Models were formulated for seven study species that were measured using point counts on the Island of Hawaii from 1977–1982. During the first model stage, we used "month" to denote an effect of month (seasonality), T to denote linear, TT for quadratic and "ln[T]" for log-linear (pseudo threshold) time trends.

Species	Stage 1 - time trends	Stage 2 - flowers and fruits	Stage 3 - density dependence	Stage 3 - competition
'Apapane	Month 0.22 (0.10)	ohi'a lehua + naio flowers 0.26 (0.21), 1.63 (0.21)	'I'iwi 1.80 (0.37)	Null
Hawai'i 'Amakihi	TT 0.01 (0.04)	Null	Null	Null
'I'iwi	Month + T + (month $\times$ T) 0.082(0.07), 1.15 (0.16) 0.002 (0.02)	ohi'a lehua + akala + naio flowers 0.18 (0.07) , 0.11 (0.10), 0.22 (0.08)	'Apapane 0.15 (0.04)	Hawai'i 'Amakihi, Japanese White-eye 0.004 (0.152), 0.186 (0.161)
Japanese White-eye	Month 0.22 (0.10)	Null	Null	'I'iwi 0.14 (0.08)
Northern Cardinal	Month 0.03 (0.02)	'olapa fruit 0.20 (0.064)	Red-billed Leiothrix 0.15 (0.04)	Japanese White-eye 0.16 (0.12)
'Oma'o	Month + TT + (month $\times$ TT) 0.11 (0.05), 0.15 (0.05), 0.006 (0.003)	Akala + 'olapa fruit + naio fruits 0.14 (0.07), 0.07 (0.21), 0.02 (0.07)	Null	Null
Red-billed Leiothrix	ln[T] 0.83 (0.34)	'olapa + akala + naio fruits 0.006 (0.242), 0.54 (0.13), 0.33 (0.11)	Northern Cardinal + Japanese White-eye 0.91 (0.38), 0.98 (0.30)	Null

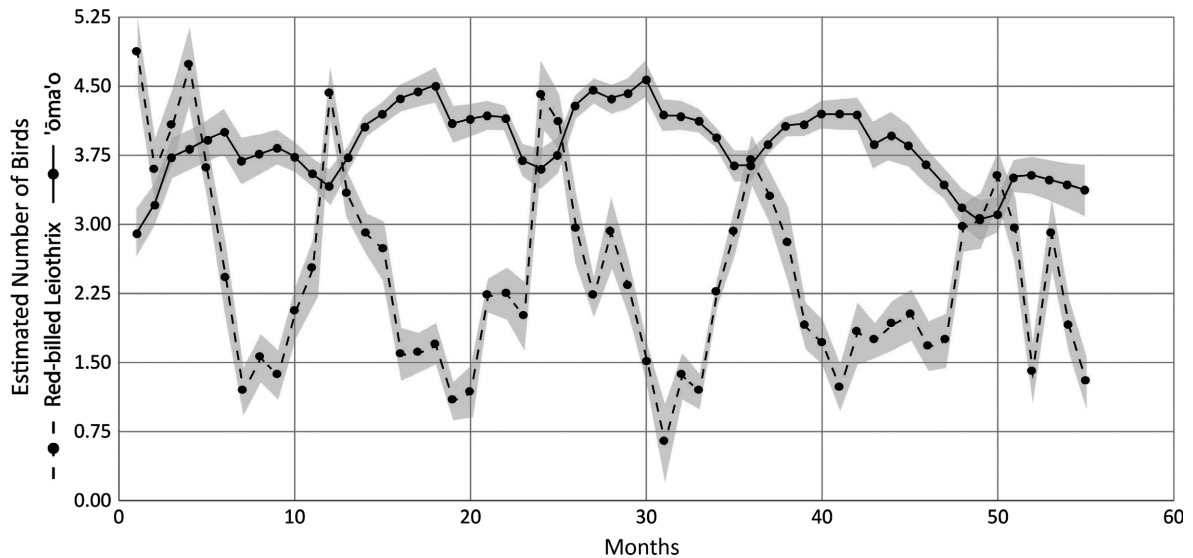


FIG. 3. Predicted abundance estimates of native and non-native frugivores, 'Oma'o and Red-billed Leiothrix, per point count station with standard errors based on the averaged top model from the hierarchical model selection routine; estimates were derived from point count data collected near Hawai'i Volcanoes National Park from 1976 through 1982.

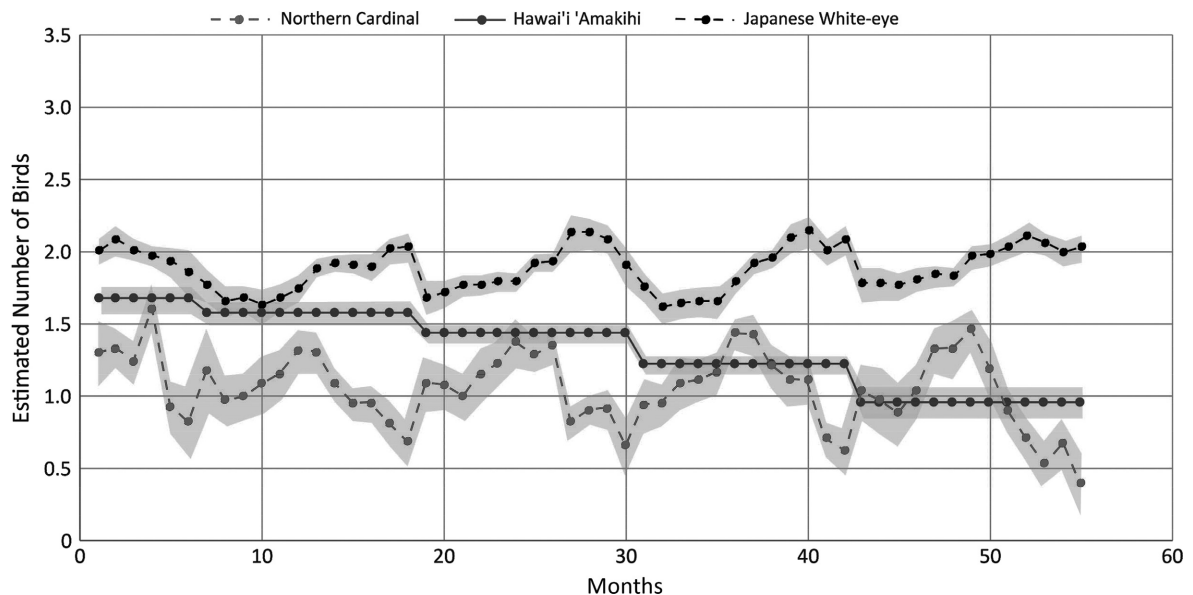


FIG. 4. Predicted abundance estimates of native and non-native generalists, Hawai'i 'Amakihi, Northern Cardinal and Japanese White-eye, per point count station with standard errors based on the averaged top model from the hierarchical model selection routine; estimates were derived from point count data collected near Hawai'i Volcanoes National Park from 1976 through 1982.

In the third stage we evaluated potential competition and density dependence of other species within each study species' respective foraging guild (either frugivore or nectarivore). With regards to positive associations, we found that the two native nectarivores, 'Apapane and 'I'iwi, did exhibit abundances that were positively associated with each other (Table 1). Similarly, the two non-native study species that commonly eat fruit, Northern Cardinal and Red-billed Leiothrix, exhibited abundances

that were also positively associated with each other (Table 1). Two non-native species were also found to have positive associations between their respective abundances: Red-billed Leiothrix and Japanese White-eye (Table 1). Finally, we examined negative relationships between study species' abundances to investigate potential evidence of competition. We found the abundance of the non-native Japanese White-eye and the native Hawai'i 'Amakihi – species that regularly feed on nectar

– were negatively associated with the abundance of ‘Iiwi (Table 1). Further, the non-native Northern Cardinal – a non-native generalist – was negatively associated with Japanese White-eye abundance (Table 1).

DISCUSSION

Despite recognition that climate-mediated bottom-up effects often structure terrestrial systems, it remains difficult to document the response of primary producers to climatic changes, and how such responses affect organisms at higher trophic levels (but see Gruner 2004). In this study, we used community-wide data from Hawaii, and move beyond merely documenting seasonality, to assessing the effects of climate and food resources on the abundance and life cycle phenology of fruit and nectar eating birds (Ralph and Fancy 1994). Our results demonstrate that birds do arrange life cycle events around climatically-influenced food resources, while some of these same food resources influence seasonal patterns of abundance. This pattern was particularly strong for two obligate nectarivores, ‘Apapane and ‘Iiwi, that exhibited peak breeding and molting activity when ‘ohi’a lehua and naio flowers were most abundant, respectively. Given that naio has small and white flowers it is unclear how much nectar they produce, and if ‘Apapane and ‘Iiwi were actually feeding on nectar, insects in the flowers, or a mixture of both. Considering that obligate insectivores were rarely documented feeding on naio flowers (Ralph and Noon 1986), and we regularly documented nectarivores visiting naio flowers at our study site, we presume that our nectarivorous study species were actually feeding on naio flower nectar. We failed to find a strong relationship between ‘ohi’a lehua flower abundance and breeding phenology of the non-native Japanese White-eye – a species that regularly consumes nectar – which may reflect a lack of co-evolution between the white-eye and native Hawaiian flowers, a more diverse diet, or a combination of diet and lack of co-evolution. Interestingly, the two common and important plant resources for native nectarivores, ‘ohi’a lehua and naio, appeared to have used different climatic cues to initiate flower events: we found that naio had peak flower abundance during dry weather, and ‘ohi’a lehua had peaks during wet weather. However, the effect size of rain and naio (-0.78) was smaller than the effect size of rain and ‘ohi’a lehua (1.12). Further, decreases in naio flowers appeared to be heavily influenced by a two large rain events in February 1979 and March 1980 (see Appendix S1: Fig. S1). These relationships may suggest a threshold, whereby infrequent and sustained heavy rains may damage naio flowers. Asymmetry in climate-mediated flowering activity between two prolific plant species at our study site may also suggest character displacement in phenological timing where, to minimize competition for pollinators, each plant adapted different reproductive strategies. Presumably, nectarivorous birds responded in kind by timing some of their most

energetically demanding behaviors in synchrony with abundant food resources. Thus, bottom-up processes initiated by climatic variation may have leveraged strong influence on the evolution of avian life cycle events at our study site.

Only one obligate frugivorous species, the native ‘Oma‘o, exhibited patterns similar to its nectarivorous counterparts, where peak breeding and molt activities were associated with different fruit resources. More specifically, ‘Oma‘o was found to have a positive correlation between naio and ‘olapa fruit during the breeding and molting seasons, respectively (Fig. 1). Although each frugivorous bird did have specific fruits associated with breeding seasonality, no correlation between fruit and molt was documented for any frugivore except ‘Oma‘o (Fig. 1). The relationship between ‘Oma‘o molt and ‘olapa fruit is biologically significant because the ‘Oma‘o adult prebasic molt typically occurs immediately after the breeding season when most fledglings are beginning to forage for themselves (Freed and Cann 2012). Thus, the ‘Oma‘o life cycle may be structured to maximize the abundance of important food resources during the post-fledging and molting periods. The absence of correlation between molt and fruit abundance in other fruit-eating species may be explained in three ways: (1) birds may structure molting events around arthropod food availability; (2) no one single fruit species was important enough to drive molting activity; or (3) we simply failed to accurately measure timing of molting events. Given the diversity of food resources the non-native Red-billed Leiothrix and Northern Cardinal consume, we suspect that these species may rely more strongly on insects during the post-breeding molt.

In addition to timing of life cycle events, climate-mediated fruit and flower resources also influenced patterns of bird abundance. For example, our hierarchical abundance modeling regime suggested that high abundances of both ‘Apapane and ‘Iiwi were associated with increased numbers of ‘ohi’a lehua flowers (Table 1); ‘ohi’a lehua flowers were positively correlated with breeding activities in both nectarivores as well (Fig. 2). The association between ‘ohi’a lehua flowers and nectarivore breeding and abundance suggests that these flowers represent a critical food resource for Hawaiian honeycreepers. The identification of such relationships highlights the importance of conserving ‘ohi’a lehua as a dominant feature of Hawaii’s forested ecosystem; this is particularly timely given the ongoing decline and deaths of ‘ohi’a lehua due to infection by *Ceratocystis fimbriata* (e.g., Mortenson et al. 2016). In fact, Mortenson et al. (2016) found that an average of 39% of the ‘ohi’a lehua found on their study plots near the southern reaches of the Island of Hawai’i have perished; such die-offs within the historic range of native honeycreepers present managers with pressing conservation challenges across multiple trophic scales. In addition to associations with flower and fruit resources, we found numerous positive and negative intraspecific associations between the abundance of

study species themselves (Table 1). Positive associations between the abundance of one species on another, such as 'Apapane and 'I'iwi, are perhaps difficult to interpret and may simply reflect similar patterns of habitat selection at our study site or mutual dependence on a common resource. Conversely, negative interspecific associations may reflect actual patterns of competitive exclusion. For example, we found that 'I'iwi exhibited negative associations with the presence of Japanese White-eye; similar findings have been described on O'ahu Island (Ralph 1991), and on Hawai'i Island as it pertains to the deleterious effects of competition from Japanese White-eye on native species, including the 'I'iwi (Mountainspring and Scott 1985) and other species (Ralph and Noon 1986). Freed and Cann (2009) found increases in the number of Japanese White-eyes was correlated with lower mass and shorter bills and tarsi in juveniles – which subsequently affected survival – of multiple native bird species, including several of our study species ('Oma'o, 'Apapane, 'I'iwi and Hawai'i 'Amakihi). Relative to Freed and Cann's (2009) study, our study site at 1650 m had more Japanese White-eyes (0.0124 per net hour) than their comparable 1650 m site (0.004 birds per net hour), but far fewer than their 1900–1770 m sites (0.022 birds per net hour). Thus, our results are concordant with several additional lines of evidence that white-eyes negatively affect nectarivores.

Because our abundance estimates could not separate floaters and migratory individuals from residents, it remains difficult to draw inference regarding population trends based on apparent abundance estimates (*sensu* Ralph and Fancy 1995). Additionally, forest clearing adjacent to our study area may have displaced territorial individuals, thereby affecting patterns of abundance in unforeseen ways. Nonetheless, we believe that climatically-induced food shortages do decrease fitness as supported by research (Banko et al. 2013) conducted near our study site which linked drought and habitat degradation to population declines in both the 'Apapane and 'I'iwi. Given our findings, we believe that contemporary droughts documented by Banko et al. (2013) probably depressed 'ohi'a lehua flower production, an important resource during the breeding season, which may have lowered survival and reproduction among obligate nectarivores. Furthermore, we found that Hawai'i 'Amakihi, a dietary generalist, was the only native nectar-feeding study species without a food resource covariate in its top abundance model; Hawai'i 'Amakihi was also the only species found to have a stable population by Banko et al. (2013). Thus, reliance on multiple food resources may have buffered the species from climatic perturbations.

The susceptibility of many Hawaiian birds to climatically-induced changes in their food web is alarming when considering that the archipelago has been subject to an increasingly drier climate over the past 30 yr (Frazier et al. 2011, Giambelluca et al. 2013), an increasing number of non-native avian competitors (Mountainspring and Scott

1985, Freed and Cann 2009), and a decrease in native food resources due to disease (Mortenson et al. 2016). Our results in association with the more recent field study of Banko et al. (2013) suggests that the increasingly dry climate may change the timing of plant phenology and availability of food resources to birds. The future of native Hawaiian birds may depend on their behavioral plasticity to mitigate changes in food resources and to successfully compete with co-occurring non-native bird species.

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