SEED DISPERSAL & GERMINATION BY NATIVE VS. EXOTIC AVIAN FRUGIVORES
OF HAWAIʻI ISLAND

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ABSTRACT

On islands worldwide, mass avian extinctions related to anthropogenic activity have enabled exotic generalists to fill empty niches left by larger native specialists. In Hawaiʻi, this trend is prevalent; therefore, ensuring the survival Hawaiʻi's last few native frugivores, the ʻalalā (*Corvus hawaiiensis*) and ʻōmaʻo (*Myadestes obscurus*), is integral in preserving proper seed dispersal function. Recently proposed management actions include reintroducing native frugivores into former ranges on leeward Hawaiʻi Island. This study sought to determine which native fruiting plants would benefit from native frugivore reintroductions and how exotic frugivores compare to natives in seed dispersal efficacy. I measured and compared the diet composition of two non-native, warbling white-eye (*Zosterops japonicus)* and red-billed leiothrix (*Leiothrix lutea*), and two native (ʻōmaʻo and ʻalalā) bird species. I also compared germination success of nine native fruiting plants consumed by these species. To examine diet composition and germination, I collected seeds from avian fecal samples and planted them in growth media to detect differences in gut-passage effects on germination percent and rate among avian species. I also collected avian seed rain using aerial seed traps hung above the fruiting understory to determine if avian diet and seed rain were similar in composition. ʻŌmaʻo had significantly higher diet diversity than other frugivores. Leiothrix and ʻalalā had similar but lower diversity, and warbling white-eye had the lowest diet diversity and were the least frugivorous. For germination success, the key influence was pulp-removal, by bird or hand, as there were no conclusive differences between avian gut-passage in birds and control seeds without pulp. Results showed a proportional representation of different fruits in bird diet matched that in seed rain. These results support ʻōmaʻo and ʻalalā reintroductions as a strategy to

promote dispersal of native plants and provide insight into potential changes in the native plant

community composition should native frugivores go extinct and be supplanted by exotics.

TABLE OF CONTENTS

List of Tables

List of Figures

INTRODUCTION

Seed dispersal has long been recognized as an important service provided by birds to plants (Clark *et al.* 1999, Chimera & Drake 2010). Two ways the avian community may benefit fruiting plant reproduction is by increasing germination rates and recruitment success of seeds through gut-passage, and dispersal away from conspecific individuals and populations; this reduces chances of infection from host-specific pathogens and competition with others that have similar trait and resource use patterns (Schupp 1993, Traveset 1998). These benefits are essential for promoting forest health and the spread of fruiting plant species across the natural landscape into habitats they otherwise may not get to (Gorrensen *et al.* 2009, Wandrag *et al.* 2017).

Two important factors to consider in an animal's seed dispersal ability is gut-passage and diet diversity. Fruits that are consumed and passed through the gut of a frugivore promote germination through the removal of the pericarp and inducing seed scarification (Traveset 1998). Pericarp removal improves germination probability by minimizing fungal growth, removing chemical inhibitors found in pulp and promoting scarification through chemical and mechanical procedures (Traveset 1998). These factors promote seed coat degradation that increases water permeability and imbition by the embryo that initiates germination (Toole *et al.* 1956, Traveset & Wilson 1997, Paulino-Neto *et al.* 2016). Additionally, an animal's capacity for consuming a range of different fruit influences its diet diversity and determines the fruiting plant species that are dispersed and comprise the plant community structure in the landscape (Foster & Robinson 2007). In the tropics, the fact that the majority of woody plants are fruit bearing and can be eaten and dispersed by animals, suggests that the mutualistic relationships between plants and animals are important (Howe & Smallwood 1982).

In Hawaiʻi, this relationship between fruiting plants and native frugivores is evident, as dispersal of the majority of Hawaiʻi's fruiting plant species was exclusively via native birds due to the lack of terrestrial mammals (Carlquist 1974). However, since the arrival of humans over half of Hawaiʻi's endemic avifauna have gone extinct (Banko *et al.* 2001). As a result, ecological processes such as seed dispersal have been disrupted due to the wide-scale extinctions of bird species (Culliney *et al.* 2012, Pejchar 2015). This mutual relationship now only exists in remnant upland forests where native avian seed dispersers and Hawaiian fruiting plants have yet to succumb to impacts caused by invasive species, habitat loss and diseases brought by humans like their counterparts in lowland areas (Banko *et al.* 2001, Culliney *et al.* 2012).

Currently, there are only four passerine bird species that exist in Hawaiʻi Island forests that are frugivorous enough to serve as seed dispersers of native fruiting plants (Pejchar *et al.* 2015). These include the exotic warbling white-eye (*Zosterops japonicus*; WAWE) and red-billed leiothrix (*Leiothrix lutea*; RBLE), and the native ʻōmaʻo (*Myadestes obscurus*) and ʻalalā crow (*Corvus hawaiiensis*). Similar to other Hawaiian forest birds, the populations of the two aforementioned native species have undergone dramatic declines due anthropogenic effects such as spread of invasive species and avian diseases and habitat loss (Culliney *et al.* 2012; Pejchar 2015). For example, the historic range of the ʻōmaʻo, Hawaiʻi's last functionally extant avian frugivore*,* is limited to 25-30% of its historic range that formerly spanned the majority of Hawaiʻi Island (Wakelee & Fancy 1999, Van Riper & Scott 2001, Fancy *et. al* 2001, Wu *et al.* 2014). Today, ʻōmaʻo are confined to the upper montane forests and sub-alpine shrubland of the windward side of Hawaiʻi Island (Wakelee & Fancy 1999, Judge *et al.* 2012).

Similarly, the ʻalalā or Hawaiian crow has been extirpated from the wild following over a century of anthropogenic impacts including introduced predators, habitat destruction by feral

ungulates and avian diseases (Culliney *et al.* 2012). However, since 2016 wildlife managers have begun efforts to release approximately 30 captive-bred ʻalalā into the wild (Bryce Masuda/ personal communication, 2020). These actions serve as the initial steps in restoring seed dispersal function in Hawaiian forests where ʻalalā have been declared extinct since 2002 (Faike 2006). The windward montane forests of Hawaiʻi Island are now one of the final refugia where the relationship between native Hawaiian plants and birds can be observed—a relationship both parties have developed over thousands of years in co-evolution (Wakelee & Fancy 1999, Van Riper & Scott 2001). This strong inter-dependent relationship between woody-stemmed fruiting plants and Hawaiian birds is further exemplified by the correlation between fruiting phenology and important annual behaviors such as breeding and molting (Wolfe *et al.* 2017).

In a few cases, the exotic warbling white-eye, and red-billed leiothrix, have filled the role of seed disperser for a few native fruiting plants (Pejchar 2015). However, due to size limitations, these introduced birds are confined to consuming smaller seeded species (<2mm) (Wu *et al.* 2014). This physical limitation excludes many larger-seeded plants from being dispersed and does not facilitate a diverse and even distribution of native fruiting plants species in the landscape (Wu *et al.* 2014). Additionally, introduced birds are generalists and often disperse the seeds of invasive plants, thus furthering the invasion and degradation of Hawaiian forests (Foster & Robinson 2007). In contrast, the native ʻōmaʻo and ʻalalā were found to prefer native fruits due to their larger gape size, and consumed a wider variety of native fruiting, plants including those with bigger seeds (Culliney *et al.* 2012, Wu *et al.* 2014, Pejchar 2015). Furthermore, native and exotic birds forage in and occupy different habitat types in the forest thus, leading to disparities in dispersal locations of seeds carried by both groups (Paxton *et al.* 2017).

Knowledge gaps in these diet studies are created by limited sampling periods that did not account for seasonal disparities in fruiting phenology, fluctuations in alternative food availability and changes in behavior during breeding and molting times (Foster & Robinson 2007). Additionally, the consistent monitoring of newly released ʻalalā allowed us to analyze their diets and bridge the knowledge gap on their ability to fulfill seed dispersal function like their ancestors. Lastly, while previous studies have looked at gut-passage effects of ʻalalā on seed germination they did not compare the gut-passage effects of multiple avian frugivore species on various Hawaiian fruiting plant species.

Overall, gut-passage effects and fruiting plant diet diversity are two important factors considered in measuring seed dispersal efficacy. With these two parameters, the aim of this study was to further assess the efficacy at which introduced birds, such as the warbling white-eye and red-billed leiothrix, affect the dispersal and recruitment of native fruiting plant seeds in relation to Hawaiʻi Island's last remaining frugivores, ʻōmaʻo and ʻalalā, in native-dominanted forests. To determine the role of native and exotic frugivores as seed dispersers in Hawaiʻi Island's forest, this study addressed the following questions. (1) Is the diet diversity and abundance of fruiting plant seeds found in fecal samples of native avian frugivores different from exotic frugivores? (2) Are there differences between the germination rates and percentages of seeds passed through the guts of native and exotic birds? I hypothesized that the larger gape size of ʻalalā and ʻōmaʻo would allow the consumption of a greater size range and abundance of fruiting plants; therefore, the diversity and abundance of seeds in native frugivore feces will be higher than in smaller exotic frugivore feces. I also hypothesized that the evolutionarily-adapted digestive tract of the native frugivores will scarify seeds and remove pulp more effectively, and

yield higher germination success relative to corresponding controls (seeds with no gut-passage) and seeds passed through exotic frugivores.

As Hawaiian bird populations continue to decline in Hawaiian forests, managers must examine how exotic avian seed dispersers fulfill the ecological niches left vacant by native frugivores. It is important to determine whether novel ecosystems will maintain important ecological functions and services. If not, an alternative action consists of reintroducing frugivores birds, such as ʻōmaʻo and ʻalalā, into historic ranges and mitigating their threats with the hope of exstablising a new popualtion. In order to guide these actions towards success, assessing the current relationship between native and exotic frugivores, especially in locations that are becoming overrun by introduced species, is crucial in guiding future management decisions and strategies.

METHODS

Species of Interest

The ʻōmaʻo is endemic to Hawaiʻi Island and exists in stable populations on the windward side but has been absent from the leeward side for over 100 years (Van Riper & Scott 1979, Judge *et al.* 2012). The extirpation of ʻōmaʻo from the leeward side of Hawaiʻi Island is believed to have been caused by the spread of avian diseases in the late 1800s (Fancy *et al.* 2001) (Fig.1). Members of the thrush family (*Turdidae*) were previously found throughout the main Hawaiian islands, but all except one other, the critically endangered puaiohi (*Myadestes palmeri*) of Kauaʻi, have since gone extinct (Wakelee & Fancy 1999). The ʻōmaʻo plays an important role in Hawaiian ecosystems as the primary extant seed disperser for a variety of native fruiting plants (Wu *et al.* 2014, Pejchar 2015). In the study by Wu *et al.* (2014), ʻōmaʻo in the kīpuka

system fed almost exclusively on fruit as it made up 99.7% of its diet in that study. However, this preference for fruits may be seasonal and vary between populations as other studies by Wakelee (1996) and Banko *et al.* (2015), found that ʻōmaʻo fecal samples contained invertebrate matter. A study by Wolfe *et al.* (2017), found a positive correlation between high breeding and molting activity and the peak fruiting of *naio* (*Myoporum sandwicense)* and *ʻōlapa* (*Cheirodendron trigynum*), respectively. These data suggest these particular native fruiting plants species influence ʻōmaʻo behavior and are an important resource for their survival (Wolfe *et al.* 2017).

The ʻalalā crow is an endemic corvid native to Hawaiʻi Island which was found commonly in the Kona and Kaʻū districts. However, due to a number of factors, including habitat loss and invasive species, the ʻalalā population of Hawaiʻi Island dwindled to extinction with the last confirmed sighting of wild ʻalalā occurring in 2002 in South Kona (Faike 2006). The ʻalalā crow was officially listed as extinct in the wild in 2004 (IUCN 2020). However, a captive population of 125+ individuals have kept the ʻalalā crow from extinction. There are roughly 89 individuals at the Keauhou Bird Conservation Center (KBCC) on Hawaiʻi Island and a smaller captive population 35+ individuals at the Maui Bird Conservation Center (MBCC). In the fall of 2017, 2018 and 2019 three cohorts totaling roughly 30 crows (7-12 crows per cohort) were released a year apart at the Puʻu Makaʻala Natural Area Reserve (NAR) on the east slope of Mauna Loa where they currently exist. Historically, this bird played an important role in seed dispersal function as it was capable of consuming wide variety of native fruiting plants due to its larger gape size (Culliney *et al.* 2012). For example, the ʻalalā was also found to have an obligate relationship with the hōʻawa plant (*Pittosporum* spp.) as this plant requires ʻalalā ingestion to facilitate germination (Culliney *et al.* 2012). The ʻalalā is known as an omnivorous generalist and consumes a wide variety of fruits, bird nestlings, bird eggs, insects and carrion (Faike 2006).

The WAWE is deemed the most common bird in Hawaiʻi and exists in habitats from sea level to high elevation montane forests (Guest 1973). This small passerine bird was first introduced on Hawaiʻi Island in 1937 with the intent of insect control for agriculture operations. Since then, the warbling white-eye has established itself on all the major Hawaiian islands (Guest 1973). This species is considered an opportunistic generalist and consumes a variety of fruits, insects and nectar (Guest 1973). Fruit comprised roughly 30% of the warbling white-eye diet in kīpuka system populations (Wu *et al.* 2014). Relative to ʻōmaʻo in the kīpuka system, warbling white-eyes were found to be less frugivorous with fruit pulp comprising only 30% of their diet and the other 70% being insect matter (Wu *et al.* 2014). However, a study on the neighboring island of Maui showed that warbling white-eye diets seemed to vary among populations as fruit was found to make up roughly half of the warbling white-eye diet in this East Maui population (Foster & Robinson 2007). warbling white-eye are known to breed throughout the year but have peak breeding periods from March till June (Guest 1973, Van Riper 2000). warbling white-eye have two estimated gut-passage times of 30 ± 6 and 60 ± 10 minutes (Wu *et al.* 2014).

The red-billed leiothrix was first brought to Hawaiʻi in 1911 with more consistent subsequent releases starting in 1918 on Kauaʻi. The leiothrix spread throughout the archipelago and now exist on Hawaii, Maui, Molokaʻi and Oahu. This species originates from Southern Asia (Ralph *et al.* 1998). The leiothrix are larger than warbling white-eye with a mean weight of 20-23g and culmen length of 10-12mm (Pejchar 2015). The leiothrix is found in a range of habitats from sea level to upper montane forests and can be found in both native and exotic Hawaiian forest. The red-billed leiothrix is considered a generalist and spends the majority of its time in the forest understory foraging on fruits and invertebrates, which comprised 60% and 40% of

their diet respectively (Ralph *et al.* 1998). The red-billed leiothrix's diet of arthropods and fleshy-fruited plants and resilience to avian diseases, such as avian malaria and pox, allows it to thrive in a variety of different habitat types (Ralph *et al.* 1998). A survey done near Hawaiʻi Volcanoes National Park, forest similar to the study sites, determined that the density of leiothrix was approximately 23-380/km^2 (Male *et al.* 1998). The red-billed leiothrix is ubiquitous throughout the Hawaiian landscape and has successfully established in wet and dry forest across an elevational gradient.

Site Descriptions

The kīpuka system provides habitat for a variety native and introduced bird species and understory fruiting plants (Table 1). A kīpuka is defined as a forest fragment of older growth forests and substrate isolated fragmented by a more recent surrounding lava flow. To examine differences in seed germination, bird diet and seed rain among native and non-native frugivores, the kīpuka system in the saddle between Mauna Kea and Mauna Loa was chosen (Fig. 1 & 2). The specific kīpuka for this study are located off Powerline road between mile markers 18 and 21 perpendicular to the Daniel K. Inouye Highway at around 19°40'N, 155°21'W. This site consists of upper montane Hawaiian forests dominated by ʻōhiʻa (*Metrosideros polymorpha)* canopy with sporadic koa (*Acacia koa)* dispersed throughout (Flaspohler *et al.* 2010). In the fragmented kīpuka system, the kīpuka range in size from 2.5-12 ha. The matrix substrate between the kīpuka was created by either one of two Mauna Loa lava flows in 1855 or 1880 (Aplet *et al.* 1998, Flaspohler *et al.* 2010). The substrate age for the kīpuka range between 3000-5000 years old (Flaspohler *et al.* 2010). The Powerline Road kīpuka site falls within an area with a mean annual rainfall range of 205-10,300 mm and at an elevation of 1480-1740 m above sea

level (Giambelluca *et al.* 2013). The average temperature in the kīpuka system is approximately 14.4 ° C with temperature range of 4-24 °C (Aplet & Vitousek 1994, NOAA 2019).

The Puʻu Makaʻala NAR was established in 1981 and consists of 7,570 ha of old growth native continuous forest at approximately 1220 m elevation (Vitousek *et al.* 1995). The NAR systems are parcels of land designated by the State of Hawaiʻi as the best remaining examples of Hawaiian ecosystems that are designated for the highest level of protection and restoration. Therefore, activities such as excluding invasive ungulates through fences, invasive species removal, predator trapping and heavy monitoring of endangered species are conducted to maintain the pristine state of this native forest (Hawaiʻi DLNR 2013). The Puʻu Makaʻala NAR falls within an area with a mean annual rainfall of 4000 mm and the substrate age is estimated at approximately 6000 years old (Vitousek *et al.* 1995). This site exist in upper montane forest with the same fruiting plant species and Hawaiian forest birds found in the kīpuka system off of Powerline Road (Table 1) in addition to a number of endangered outplanted lobeliads. The average temperature in the Puʻu Makaʻala NAR is approximately 13.1° C with a temperature range of 4-24°C.

Starting in 2016, ʻalalā bred at the San Diego Zoo Global's conservation breeding centers were released in the Puʻu Makaʻala NAR. The released ʻalalā are closely monitored and tracked everyday using VHF transmitters and telemetry equipment. Each ʻalalā is observed for behaviors and interactions with their surroundings and other ʻalalā. They are also provided daily supplemental food that is similar to the food they were fed at the breeding centers. The supplemental feeder stands are stationed around their soft-release aviaries with the goal of anchoring them to the particular release site.

Seed Rain

To measure the seed rain in the kīpuka, 1m diameter mesh baskets were hung from the non-fleshy fruited dominant canopy species of koa and 'ōhi'a (Rose *et al.* 2017). These seed rain traps were hung above the fruiting plant understory to allow us to deduce that any seeds from fruiting plant species found in the traps were transported there via fecal of an avian frugivore. There were 48 total seed rain traps throughout the study site with equal number of seed rain traps in each location category. Every seed rain trap was lined with silkscreen to ensure that plant species with seeds < 1mm were not filtered through the basket and missed in the final counts.

The silkscreen in all seed rain traps was changed out every 4-6 weeks and brought back into the lab for analysis. The silkscreens were dried in an oven at approximately 32° C and then examined using a microscope to tease out and identify seeds of fruiting plants using a seed reference library provided by the Drake lab at the University of Hawai'i at Mānoa. This reference library consist of photos and real samples of depulped seeds of every species identified in the baskets. Seed rain was only collected during the summer (May- August) and winter (November-February) seasons to sample both annual peak fruiting times during the year (Kovach 2012).

'Alalā Fecal Collection

To measure wild 'alalā diet diversity and seed abundance, fecal samples and casts were collected from feeding platforms by the San Diego Zoo Global 'alalā field tracking team. Fecal sample and casts were only collected if it was obvious that the sample came from a single defecation or regurgitation event. This procedure was to ensure that seed abundance and diversity are measured for an individual fecal sample. Each sample was collected in a clean

container and stored in a refrigerator until it was taken to the lab for seed sorting and identification.

Typically, less than one cast and about two fecal samples in total are observed on the feeding platforms each week. Fecal samples and casts were collected incidentally from the feeding platforms at the end of each day when the field tracking team was changing out supplemental food. Although I was not be able to identify the exact bird each fecal came from, I was able to identify the source cohort on collection dates prior to the mixing of the 2017 and 2018 cohorts. It is important to note that no native fruits were provided at the hoppers during the sampling period as this would bias the data.

Additionally, to supplement seeds in the germination trials, captive 'alalā held at KBCC were fed ripe fruit from fruiting plants around the facility. Approximately 30 of the 89 'alalā at KBCC are known to commonly consume fruit. All 30 'alalā were sampled but only 5 were allowed to be fed per week. Fruits were collected based on phenology and availability and only fruit at peak ripeness were used in the feeding trials. There were 5 native fruiting plants found around the KBCC facility in high enough abundances to use in the feeding trials. These fruiting plant species include 'ōlapa (*Cheirodendron trygynum*) , pilo (*Coprosma spp.*) , shrub 'ōhelo (*Vaccinium spp.*) , pūkiawe (*Leptecophylla tameiameia*) and kōlea (*Myrsine lessertiana*). Fecal samples from birds were collected on wooden platforms placed below favored perches and feeders of each 'alalā enclosure. The following day fecal were scraped off and collected from each wooden platform and brought back to the lab for sorting and identification.

'Ōma'o, Warbling White-eye, Red-billed Leiothrix and Fecal Collection

To collect fecal material from ʻōmaʻo, WAWE and RBLE, I captured them in mist nets. Banding, research and access to the Upper Waiākea Forest Reserve kīpuka site were covered under USGS Bird Banding Laboratory Permit #23064, State of Hawaiʻi Protected Wildlife Permits: WL-18-11 and WL 19-20 and a State of Hawaiʻi DLNR Access and Forest Reserve Special Use Permit. Net lanes were placed perpendicular to the Puʻu ʻŌʻo trail and in clearing caused by tree falls at the Kīpuka site. At the Puʻu Makaʻala NAR, nets were placed along the fenceline, road and tree clearings. Nets were set in the early morning after sunrise and left up until the early afternoon depending on the weather. Captured birds were extracted from mist nets and placed in cloth bags until they were ready for processing. If the bird did not defecate by the time it was ready to be processed I placed them in an opaque holding box for a maximum of 20 mins or until they defecated on the wax paper below their perch. The holding box had opaque padded walls and a dark interior to ensure the comfort and safety of the birds. Once the birds defecated, their fecal samples were stored in vials labeled with the appropriate descriptions and were refrigerated until sowing time. Samples were usually processed within a month of the collection date. The collection period for fecal collection spanned over two years from Fall 2017 to Fall 2019. The highest collection effort went from Fall 2017 to Fall 2018 with the incidental collections thereafter depending on banding opportunities for other projects.

Seed Germination

To measure the germination rates (total germinated/ days since sowing) and percentages (total germinated/total planted) of seeds that had undergone avian gut-passage, fecal samples were first collected from wild birds. The seeds were extracted and sorted from the fecal matter with distilled water and a 1 mm sieve. Seeds were then identified to the species level using a

dissecting microscope and a seed catalog (Wu *et al.* 2014, Pejchar 2015). *Vaccinium* &

Coprosma seeds were indistinguishable among species within the genus so were labeled more

generally as *Vaccinium* spp. & *Coprosma* spp. However, *C. ernodioides*, which is in the genus

Coprosma, was distinguishable from *Coprosma* spp. in fecal samples and labeled separately as

C. ernodioides. The abundance and species richness of seeds per fecal sample were recorded.

Seeds were soaked in 10% sodium-hypochlorite (NaOCl) for 5 mins to mitigate fungal infection

and determine viability (Khah & Passam 1992, Traveset *et al.* 2001), then sowed into pots of 3:1

sand to vermiculite media. The seeds that floated in the solution signified an aborted embryo and

were removed and discarded (Traveset *et al.* 2001). The remaining seeds were then washed

multiple times with distilled water to clean off residual NaOCl and placed in pots with other

seeds of the same species originating from the same fecal sample (Navarro & Guitian 2003). The

seeds were monitored every 7-10 days to check for fungal infection and germination. Seeds that

did not germinate were removed after 7-months of being sowed and all seeds were given

between 7 months and 1.5 years to germinate.

Seeds and fruits that had not undergone avian gut passage were used as a control. The

seeds of all plant species found in fecal samples were collected from fruiting plants in the field

when fruits were fully mature. Control seeds and fruits were tested for germination in two groups

delineated by seeds with the pericarp still attached (whole fruit) and bare seeds with the pericarp

manually removed by hand. Control seeds were processed and cleaned following the same

protocol as the regular germination trials. Each plant species had one control group with the

pericarp attached and another control group with no pericarp attached (Paulino-Neto *et al.* 2016).

An approximately even number of seeds from each fruiting plant species found in avian fecal

samples were represented in controls with and without the pericarp attached (Table 3). For

controls with the pericarp still attached, the number of fruit used in the control depended on the mean number of seeds commonly found in an individual fruit of that species. Accordingly, plant species with small seeds and large quantities of seeds per fruit had fewer fruits per control while fruits with large and fewer seeds had more individual fruits per control. For controls without the pericarp, seeds from each individual fruit were planted in their own separate pot and seeds were spaced at least one seed length away from adjacent seeds of the same species. For species with a high number of seeds per fruit (i.e., *Vaccinium* spp.), a minimum of 10 fruits were planted for controls with the pericarp still attached.

The greenhouse where germination trials were held was located at KBCC in the Volcano area of Hawaiʻi Island. The temperature regime and photoperiod are roughly similar to that of the kīpuka system off powerline road and the Puʻu Makaʻala (NOAA 2019). All treatment types were watered at the same rate, with timed irrigation system to ensure that growth media remains damp at all times. All plant species found in the bird fecal samples were represented in all treatment types. These germination trials were run for a period of 5-9 months and were monitored weekly. The germinated seedlings from wild and captive ʻalalā were grown until they were large enough to outplant around the KBCC facility. Outplanted seedlings derived from ʻalalā fecal were designated to be used for outreach activities for school groups visiting the KBCC facility.

Data Analysis

The program R (version 3.4.1) was used to analyze seed abundance, diversity and species richness in addition to gut-passage effect on germination success. A Kruskal-Wallis test was used to compare the overall median germination rate and percentage for all seed species passed

through the guts of the native and exotic birds relative to their corresponding controls. The two control categories for germination comparisons were seeds with pulp and seeds with no pulp attached.

A Sørensen index was used to quantify the number of overlapping fruiting plant species found in the fecal matter of the native and exotic birds. A Kruskal-Wallis test was used to compare seed abundance (total number of seeds), species richness (total number of species) and seed diversity between fruiting plant species found in the fecal of all native and exotic birds. Seed diversity was calculated using the Shannon Diversity Index formula: $H = -\sum[(pi) \times \ln(pi)]$ where p_i is the proportion (n/N) of individuals of one species found (n) divided by the total number of individuals found (N).

Generalized linear models (GLMs) were also used to determine if bird species and collection sites significantly influence the presence and diversity of plant seeds in avian fecal. Because 'alalā are only found at the Puʻu Makaʻala collection site it was excluded from the presence/absence of seeds in this GLM.

RESULTS

Seed Rain

A total of 145 seeds from eight plant species were collected over summer and winter sampling seasons from the seed rain traps. Seed rain traps were left out to collect seeds for approximately four months (~120 days) in the summer and winter seasons for a total of approximately 240 days. *Vaccinium* spp. made up the majority of the seeds in the seed rain traps (Fig. 3). The similarity comparison between the avian seed rain traps and fecal samples showed an 89% similarity between plant species present in both sampling methods. The only species

missing from the seed rain traps that was found locally and in avian fecal samples was *M. lessertiana*.

Fecal

A total of 271 fecal samples were collected from the four bird species in this study. Ninety-six fecal samples were collected from 'alalā, 81 from warbling white-eye, 65 from 'ōma'o and 29 from red-billed leiothrix. These samples contained a total of 2,174 seeds from seven plant species and two broader genera.

The three plant species that were most likely to be dispersed by avian frugivores were *Vaccinium* spp.*, C. trygynum* and *C. ernodeoides* which made up 72%, 10%, 5% of all fecal samples respectively. The plant species that 'ōma'o, 'alalā and WAWE were most likely to disperse was *Vaccinium* spp. while, the most commonly dispersed seed by RBLE was *R. hawaiiense* (Fig. 5).

When comparing the frequency of plant species in the total fecal samples collected, the 'ōma'o and 'alalā had a greater relative frequency of fruiting plant seeds in their fecal than exotic WAWE and RBLE (Fig. 6) . Of all the avian frugivores, 'ōma'o was the most frugivorous with 96% of it's fecal samples containing seeds. For 'ōma'o, *Vaccinium* spp. was the most commonly found fruiting plant species with a relative frequency of 34% (Fig. 6). Alalā had a more evenly distributed relative frequency of *L. tameiameia* (18%) and *C. ernodeoides* (21%)*, C. trygynum* (22%) and No seeds (18%) in its diet (Fig. 6). In contrast, RBLE (38%) and WAWE (74%) were found to be less frugivorous and both had None (no seeds found in fecal), as the highest relative frequency in their fecal (Fig. 6).

Overall seed abundance, species richness and diversity varied greatly among the four avian frugivore species. 'Ōma'o lead in all three categories with the highest seed abundance (X^2 = 82.641, df = 3, p <0.001), species richness (X^2 = 47.716, df = 3, p <0.001) and Shannon Diversity (X^2 = 47.716, df = 3, p <0.001) (Fig. 4). Additionally, 'alalā and red-billed leiothrix did not differ signicantly in seed abundance, species richness, and diversity found in the fecal. The warbling white-eye was significantly lower in all comparisons except in Shannon Diversity where it did not differ significantly in seed abundance and species richness with the red-billed leiothrix (Fig. 4).

I found strong support for the influence of 'ōma'o (b = 1.9216, z = 8.219, p < 0.001) and RBLE (b = 0.9105, z = 2.811, p < 0.001) on the presence/absence of seeds in the fecal samples (Table 4). According to the odds ratio, the chances of seeds being present in fecal samples increased by a factor of 683% (95% CI 4.4 to 11.03) for 'ōma'o when compared to warbling white-eye. Additionally, the chances of seeds being present in the fecal of RBLE increased by a factor of 248% (95% CI 1.3 to 4.7) when compared to the WAWE.

Germination

Overall, germination rate data show that plant seeds without pulp, which includes seeds that underwent gut-passage and control seeds with pulp manually removed, generally germinated faster than the controls with pulp still attached (Fig. 7). For the majority of the plant species, passing through the gut of an avian frugivore expedited germination relative to both controls types (pulp & no pulp) where seeds had not undergone gut-passage. The exception to this is *M. lessertiana*, which had faster and overall germination than the seeds that had passed through the guts of their corresponding avian frugivore (Fig. 7). Interestingly, *C. ernodioides* had a slower

germination rate for both control treatments but had a higher overall germination of both control treatments over 'ōma'o. 'Alalā still had a slightly higher overall germination percentage than the other treatments for *C. ernodioides* (Fig. 7). Ultimately, there was no consistent trend across the fruiting plant species to suggest that gut-passage through one particular frugivore species enhanced germination rate over another frugivore. Additionally, I was also unable to produce at output to show the a siginificant trend of gut-passage effect on germination rate. Furthermore, the sample sizes are between treatments are dispropotionate leading some treatments to carry higher power than others.

When comparing the percentage of plant seeds that germinated under the various gut-passage treatments, all species except *M. lessertiana* showed significant differences of germination proportion (Fig.8). The gut-passage treatments for *Vaccinium* spp. ($X^2 = 11.56$, df = 3, p = 0.009), *Coprosma* spp. ($X^2 = 10.441$, df = 3, p = 0.033), *C. ernoidioides* ($X^2 = 9.1923$, df = 3, p = 0.02684) and *C. trigynum* ($X^2 = 15.718$, df = 3, p = 0.001) all showed a significant difference between the percentage of seeds that germinated in different treatments (Fig. 8). For *Coprosma* spp., *C. trygynum, Vaccinium* spp. and *C. ernodioides* going through the gut of a bird increased germination percentage while gut-passage effects on *M. lessertiana* seeds had little effect and may have inhibited germination (Fig. 8). For *C. ernodioides,* going through a bird had a slight effect on germination percentage relative to controls with no pulp and the germination rate was similar if not better than controls with and without pulp. The results also suggest that some plant species germinate better after passing through certain bird species. For example, *Vaccinium* spp. seeds passed through 'alalā germinated faster and at higher proportions than all the other treatments (Fig. 7 & 8). *C. trygynum* germinated most efficiently passing through 'ōma'o and *C. ernodioides* germinated the fastest passing through 'alalā. The germination trends

suggest that smaller seeded plants, like *Vaccinium* spp., had higher germination success when passed through an avian gut when compared to the larger seeded plants like *M. lessertiana* and *C. ernodioides*. These final five plant species were included in the final analysis because they were the only species with enough samples to compare between the various gut-passage treatments (Fig.8).

Lastly, when combining the percentage of the seeds that germinated and the percentage of the seeds that comprised the total number of seeds found in avian fecal samples I was able to determine the percentage likelyhood that a seed would be dispersed and germinate (Table 5). The results show that all five species had similar odds of being dispersed and germinating although, the percent germinated and percentage of the total number of seeds found in the avian fecal were very different. For example, while *Vaccinium* spp. comprised 72% of the seeds found in all the avian fecals only 2% of the seeds sowed for this species actually germinated; the two factors combined gave *Vaccinium* spp. a 1.44% chance of being dispersed and germinating (Table 5). Similarly, *Coprosma* spp. also had a 1.44% chance of being dispersed and germinating but the percent of seeds germinated and percent of seeds found in fecal for this species were very different than *Vaccinium* spp. at 48% and 3% respectively.

DISCUSSION

The decline and extinction of Hawaiian forest birds may have far-reaching consequences to the resilience, regeneration and overall vigor of this threatened ecosystem. However, the presence of exotic frugivores may prove to be useful as they proceed to fill empty niches left open by the extinction of larger native frugivores. The primary findings of this study were that native and exotic birds consumed similar fruiting plants but at different proportions, seed rain

and avian frugivore diet had similar species richness, scarification of seeds through gut-passage was less important for germination success than pulp removal, and fruit preference by avian frugivores is dependent on the plant species. Overall, the exotic WAWE and RBLE are incomplete replacements for native frugivores in the upper montane forests of Hawaiʻi Island.

Avian Diet

The results support my hypothesis on avian diet that the larger gape size of native frugivores allows them to consume a wider variety of fruit resulting in higher diversity and abundance of fruiting plants when compared to exotics. Both native and exotic frugivores generally overlapped in the plant species they consumed but, there were notable disparities with exotic birds showing significantly lower diversity and relative frequency of seeds in their diet. Generally, small-seeded fruiting plants (e.g., *Vaccinium*) made up a decent proportion of diets in all four avian frugivores but exotic frugivores were more limited to these species. This trend is consistent with previous studies that found plants with high nutrient-rich pulp-to-seed ratios were consumed more than fruits with larger seeds and less pulp due to higher foraging profitability for the frugivore (Howe 1983).

Overall, WAWE only dispersed three small-seeded plant species, *Vaccinium* spp., *R. hawaiensis* and *I. anomala,* all of which were within 0.5-2.5 mm in length. This is likely due to the smaller gape size of the WAWE which limits its diet to these smaller seeds (Wu *et al.* 2014). In particular, *Vaccinium* spp. comprised the vast majority of the total seeds found in WAWE fecal at 75%. However, this was still a small proportion of the total WAWE diet with 74% of the 81 WAWE fecal samples having no fruiting plant seeds at all; fecal samples were otherwise comprised of insect parts. The trend of WAWE having a lower proportion of fecal samples

without fruiting plant seeds is generally consistent with previous studies (Foster & Robinson 2007, Wu *et al.* 2014). In contrast, RBLE consumed seven of the nine total plant species found in the diet samples of this study. While *R. hawaiensis* and *Vaccinium* spp. still made up the majority of seed abundance in RBLE fecal (Fig. 5) the seed size range of plant species consumed, 0.5- 6 mm, was higher than WAWE's. Additionally, the RBLE had a higher proportion of native plant species than anticipated with almost two-thirds (62%) of their fecal samples containing fruit seeds and a more evenly distributed relative frequency of fruiting plant species. The higher level of frugivory in RBLE is also conveyed in their diet diversity, seed abundance and species richness not being significantly different to the native 'alalā (Fig. 4), with the caveat that sample size of RBLE fecal samples were lower.

For the native frugivores, 'alalā had a relatively high abundance and even proportion of fruiting plant species in its diet, but as mentioned it was not significantly different in seed abundance and species richness to the exotic RBLE. Nonetheless, fruiting plant seeds were still present in more than 75% of 'alalā fecal samples even when these birds were provided with a sufficient amount of daily supplemental food. This result is a good indication that innate foraging skills still exist in this captive flock of 'alalā, which may facilitate an easier transition to the wild. The diet of released 'alalā also demonstrates there is a reliable and diverse resource of fruits at the release site for 'alalā to consume post-weaning from supplemental feeders. Additionally, this finding suggest that gut-passage effects by 'alalā may promote the recruitment success of these fruiting plant species thus, producing healthier forest dynamics and ecosystem function at the 'alalā release sites.

To no surprise, the 'ōma'o was the most frugivorous of the four avian species and had significantly higher seed abundance, species richness and Shannon diversity than the other

frugivores (Fig. 4). Similar to the Wu *et al.* (2014) study, the ʻōmaʻo diet had every fruiting plant

considered in this study and had fruiting plant seeds present in 96% of the fecal samples

collected. The greater sampling period (1.5 years) for ʻōmaʻo relative to previous diet studies

(Wu *et al.* 2014, Pejchar 2015) align with the general consensus that ʻōmaʻo diet is comprised

mainly of fruit. The remaining 4% of fecal samples without fruiting plant seeds were comprised

of arthropods. The ʻōmaʻo surpassed all the other frugivores in diet diversity including the ʻalalā

which has a gape roughly double its size (Culliney *et al.* 2012, Pejchar 2015). However, the

current released flock of ʻalalā are not a fair comparison since they are not fully wild as they still

dependent on supplemental feeders and require intense monitoring by a tracking team.

Alternatively, the ʻōmaʻo is wild, well adapted and completely dependent on native fruiting

plants for sustenance and survival. The ʻōmaʻo's larger gape size is more suited to consuming a

wider variety of native fruiting plants and coevolution with these native plants has caused ʻōmaʻo

to be dependent to the point where its molting and breeding cycle coincide with Hawaiian

fruiting plant phenology (Wolfe *et al.* 2017).

Contrary to native frugivores, the relative frequency (fecal samples with seeds

present/total fecal samples) of fruit seeds in exotic frugivore fecal was lower – especially in

WAWE (Fig. 6). The smaller body, gape size and limited fruiting plant diet of the WAWE

suggest they serve as only a partial replacement for native frugivores as they disperse a few

native plants. The WAWE's proficiency as a native seed disperser is mainly based on their

capacity to disperse large amount of small seeds due to their high abundance (14.8 birds/ha) in

these montane forests (Kovach 2012). Similarly, the RBLE may be a partial replacement for

native frugivores in forests that are primarily native dominated. Like WAWE, the RBLE is

found at an elevational gradient from sea level to sub-alpine zone; their role as important seed

dispersers for native ecosystems may vary depending on what ecosystem they inhabit (Guest 1973, Ralph *et al.* 1998). For example, Foster & Robinson (2007) found that in forests where all native frugivores had been extirpated exotic frugivores, such as Hwamei, RBLE and WAWE, ate the fruits that were readily available to them and the understory plant composition reflected the fruiting plant species commonly found in fecal; these common plant species include *C. trigynum* and *R. hawaiensis,* which align with the results in this study. At the same time, multiple studies also determined that common, generalist, exotic frugivores, are effective dispersers of highly invasive weeds such as Sawtooth Blackberry (*Rubus argutus*), Thimbleberry (*Rubus rosifolius*), Kahili Ginger (*Hedychium gardnerianum*) and *Lantana camara* (Foster & Robinson 2007, Chimera & Drake 2010, Pejchar 2015, Ramaswami *et al.* 2016). However, in this study only native seeds were found in the fecal of both native and exotic frugivores. At both of my study sites there is a small number of exotic fruiting plants including thimble berry (*Rubus rosifolius*) but none were identified in any of the samples. This may be partly due to relatively low exotic plant abundance and the alignment of banding effort to seasonal fruiting availability. Nonetheless, these data support the idea that exotic frugivores in a predominantly native forest habitat provide seed dispersal services to native plants therefore, benefitting native ecosystems (Foster & Robsinson 2007, Wu *et al.* 2014).

Given their flocking behavior and relatively high abundance in native-dominated montane forest, exotic frugivores could benefit a number of common fruiting plant species. Previous studies suggest that RBLE are more common in forest where native frugivores have been extirpated, suggesting they are already filling these empty niches (Pejchar 2015). Moreover, the synchronized breeding and fruiting cycles of RBLE and WAWE with multiple native fruiting plants suggest these birds are already reliant and adapted to spreading their seeds (Wolfe *et al.*

2017). Previous studies are consistent with my results in that smaller-seeded plants dominate the diets of exotic frugivores such as WAWE (Foster & Robinson 2007, Wu *et al.* 2014, Pejchar *et al.* 2015). However, for RBLE my results also counter those same studies by showing RBLE diet is more diverse with native species and overlaps with native frugivores more than previously thought. Again, this may be the product of higher native fruit availability at the Hawai'i Island sites compared to the sites of previous studies that had a higher prevalence of invasive fruiting plants (Wu *et al.* 2014, Pejchar 2015). Ultimately, the data suggest effective exotic frugivores such as the RBLE will utilize and disperse the food source that is readily available to them. In the case of the kīpuka system and the Pu'u Maka'ala NAR, which are semi-pristine-native dominated forest, these exotic birds are influential in dispersing seeds and likely benefit recruitment success in these native dominated forests. Future studies should determine the influence of movement patterns and forest column occupancy of RBLE vs. 'ōma'o relative to the likelihood of seeds being dispersed into favorable substrates and mircoclimates for germination and survival.

Seed Rain

Seed dispersal by avian frugivores can be an important determinant of plant community composition and forest succession, recovery and resilience (Cole *et al.* 2010, Rose *et al.* 2017). Seed rain sampling was done to determine if the fruiting plant species composition in the avian fecal samples were a good index of avian seed rain. The results showed the fecal and seed rain had an 89% overlap. Similar to the fecal samples, *Vaccinium* spp. comprised over half of the total seeds found in all the seed rain traps. This finding is consistent with previous studies that suggest smaller seeded plants are dispersed more — especially in the presence of generalist

exotic frugivores. The three avian frugivores found in the kīpuka system (excluding ʻalalā) where the seed rain traps were set up all consumed *Vaccinium* spp.; while, the larger seeded plant species were not as common in certain avian species (Wunderle 1997). The proportion for total abundance of seeds found in the seed rain (Fig. 3) and the proportion of seeds found in the fecal samples (Fig. 5) had the same three most abundant seeds in both fecal samples and seed rain. Therefore, these data do suggest the diet composition of avian fecal samples are a good index of of the corresponding seed rain composition. For future research, using seed rain to quantify avian diet on a landscape level could be a cost-effective alternative to banding birds.

As previously noted, seed rain composition is driven by avian frugivore presence and fruit preference, seasonal fruit availability and the limitations of gape size on the birds ability to consume seeds (Loiselle & Blake 1999, Pejchar 2015). The small seeded *Vaccinium* spp. made up the majority of the seed rain likely due to its higher abundance of seeds per fruit. For example, all it takes is one fruit to be consumed and defecated in a basket for roughly 285 seeds (mean number of seeds in *Vaccinium* spp. fruit) to be represented in seed rain. After *Vaccinium* spp., the next most prevalent seed species were *C. trigynum* and *C. ernodioides* – both species in the larger seed size class. From this we can infer forests with larger birds, such as ʻōmaʻo, may see a higher prevalence of larger seeds in the avian seed rain, therefore, we can expect higher seed dispersal diversity in forests where larger avian frugivores exist (Wunderle 1997, Pejchar 2015). Unfortunately, this study did not examine the seed rain at a site where ʻōmaʻo were absent to obtain a clear comparison in seed rain. However, the species composition in our seed rain is consistent with Pejchar (2015), who found species richness and seed abundance in seed rain was significantly higher in areas where the ʻōmaʻo were present than where they were absent. While the influence of season was not a component of this study, seasonal variation in fruit availability

had a big influence on what was dispersed into seed rain baskets; for this reason, sampling seed rain during both biannual fruiting peaks gave us sufficient representation of annual seed rain at the kīpuka site (Kovach 2012, Wolfe *et al.* 2017).

Germination

Overall, the goals of the germination trials were to compare gut-passage effects of native versus exotic avian frugivores on seed germination rate and percentage. Prior to this study, no published literature in Hawaiʻi compared gut-passage effects on seed germination among frugivore species. More specifically, this study hypothesized that the morphology of the native frugivores, through gut-passage, was more favorable than exotics for promoting germination success due to co-evolution; however, there were not enough consistent trends across the board to infer this among the frugivore species. Instead, the results show clearer differences in gut-passage effects on germination amongst fruiting plant species. For example, plant species like *Myrsine lessertiana,* did not show a definitive difference in germination success among treatments while others, such as *Vaccinium* spp., did to a certain degree.

There were a lot of issues with the germination monitoring, which resulted in difficulty interpreting and analyzing the data. One issue included limitations on regularly viewing germination progress due to logistical issues. This resulted in inconsistent temporal results that made unsuitable data for General Linearized Models to run. However, the figures still show there were some notable differences between germination treatments. According to the results, pulp removal facilitated earlier germination, but then germination slowed down and the curve flattened as time went on. Additionally, the germination percentage of the total seeds planted varied on the gut-passage treatment. Overall, seeds with the pulp removed, including controls

with pulp manually removed and no gut-passage, had higher germination success than seeds with pulp still attached (Figs. 7 & 8). These results align with previous studies where ingested seeds and seeds with pulp manually removed were similar and had significantly higher germination success than controls with the pulp still attached (Reid & Armesto 2011). These studies suggest pulp removal rids the seed of chemical inhibitors that stymie germination (Traveset 1998, Traveset *et al.* 2007). Moreover, a study in New Zealand found that effects of seed deinhibition through pulp removal had significantly higher effects on seed germination compared to scarification effect by avian gut-passage; this study suggests pulp removal is a generally more influential factor in germination success than scarification through avian gut-passage (Robertson *et al.* 2006). In general, these results suggest that pulp removal and not scarification has a greater influence on expediting the germination rate of fruiting plant seeds.

Additionally, the seed size within and among fruiting plant species also plays a major role in the dispersal distance and germination success of a plant species (Wunderle 1997). In general, seed size is positively related to number of days until first germination and negatively related to the viability and proportion of seeds that germinate (Murali 1997). In this study, this is supported by smaller-seeded plants, like *Vaccinium* spp., having a faster relative germination rate to controls with pulp compared to other species (Fig. 7); although, only 2% of the total seeds sowed for this species germinated at all (Table 5). The higher number of seeds per fruit and smaller surface area of the seed, the less dependent the seed is on scarification by gut-passage in its dispersal strategy, and therefore, deinhibition by pulp removal is a more important factor. This trend may be due to the lower likelihood that smaller seeds are abraided by other objects in digestive tract to properly scarify seeds to expedite germination. In contrast, larger seeds like *C. trigynum* or *Coprosma* spp. have delayed germination and require the step of avian consumption,

gut-passage and possibly scarification to expedite germination (Murali 1997). Interestingly, in both this study and Culliney *et al.* (2012) ʻalalā seemed to have little to no effect on germination of these larger seeds like *C. trigynum*, Coprosma spp., and *M. lessertiana*. This trend may be attributed to the different dispersal strategies of fruiting plant species relative to their seed sizes. For example, the smallest seed species in this study, *Vaccinium* spp., had only 2% of the total seeds sowed germinate but comprised 72% of the all seeds collected from fecal (Table 5). In contrast, the largest seed, *M. lessertiana*, had 80% of its total sowed seeds germinate but only made up less than 1% of the total seeds extracted from fecal. These data suggest the *Vaccinium* spp. would be classified an early successional strategist that produces many less viable seeds increasing the likelihood of recruitment while *M. lessertiana* is a late-succesional strategist that produces more viable seeds but in lesser abundance. This trend in seed size and germination proportion is consistent with previous studies where larger seeds germinate slower but at higher proportions while smaller seeds germinate quickly at lower proportions (Traveset *et al.* 2001). Anecdotally, this trend is also evident in the fragmented kīpuka landscape where *Vaccinium* spp. and *Metrosideros polymorpha*, another small seeded wind dispersed plant, are common in the early successional substrates of the new lava flows. The only way for *Vaccinium* to be dispersed into the open lava fields is by birds given the restriction on their large sized fruit to be carried by wind. The dispersal strategies of native plants may reflect their behavior and life history as well as their co-evolved primary disperser. Fruit selection was found to favor small-seeded plants, like *Vaccinium* spp., when frugivores are common and larger seeded plants with highly competitive seedlings, such as *M. lessertiana* when fruit-eating animals are absent (Howe 1983). Fruits that are not consumed and dispersed away from parent-plant have higher competition with conspecifics, limited light availability and higher risk of predation (Howe *et al.* 1985, Schupp

1995). The crucial step of dispersal away from conspecifics lowers intraspecific competition and ideally moves seeds into more suitable habitats to germinate and colonize (Traveset 1998).

When applying this concept to restoration, removing pulp manually to expedite germination could serve as an important management tool. Anecdotally, native plants generally germinate slower than invasive and exotic plants therefore, removing pulp and giving native seeds a competitive advantage at colonizing a restoration site may serve as an important step to initiating forest regenation. It is important to note that float tests were only done to seeds removed from pulp, via manual removal or avian-passage. I was not able to test the viability of seeds with pulp still attached. This could have also been a factor in the lower germination success of seeds with the pulp attached since there is a higher chance for inviable seeds to be included in the germination trial. Nonetheless, many of the control seeds with pulp did germinate close in time suggesting the influence of pulp had a similar effect on a large proportion of the total sample.

The results also suggest that overall recruitment success may not be primarily influenced by the gut-passage effects but by foraging behavior, movement patterns and general morphology avian frugivores deposition (Herrera *et al.* 1994, Loiselle & Blake 1999). For example, large birds, such as ʻōmaʻo and ʻalalā, are able to consume and carry more seeds than the smaller warbling white-eye away from conspecific fruiting plants (Howe *et al.* 1985, Traveset 2007). Already, this morphological advantage makes larger frugivores more adept seed dispersers than smaller exotic frugivores. Body size delineates frugivores into feeding guilds where larger frugivores usually swallow fruit and smaller frugivores are limited to biting and mashing fruit (Schupp 1993). When biting or mashing larger fruit, smaller frugivores may only consume fruit pulp and not the seed itself; even when there are small seeds that can be consumed the relative

quantity dispersed is much smaller. Larger frugivores, like the 'alalā, also have a gizzard that holds more seeds for longer periods; moreover, seeds that are consumed may be stored with more abrasive objects such as rocks or bone fragments that may induce higher scarification and expedite the germination process (Traveset 2002, Culliney *et al.* 2012). Many of the seeds extracted from 'alalā casts were still intact and passed the float test suggesting the 'alalā gizzard does not commonly destroy seeds. Lastly, as a result of thousands of year of coevolution with native Hawaiian fruiting plants, native frugivores are naturally cueing in to native plants during their foraging bouts because their innate foraging strategy requires them to do so for survival (Howe & Smallwood 1982). Because exotic frugivores are less adapted generalists, if there is an abundance of insects that requires less energy expenditure than fruiting plants they will likely forage for fruits less reducing contributions to avian seed dispersal.

Study Limitations

Limitations in this study were mainly with seed rain, germination and fecal collection specifically for 'alalā. There were complicated logistics in monitoring seed rain traps and a hurricane knocked down many of the aerial seed rain traps hanging from trees. These events changed my original goal of comparing seed rain composition at varying distances in and around kīpuka to just looking at seed rain composition relative to frugivore diet. For germination trials, there were limitations due to the amount of time it took for seeds to germination (2-10 months) and the logistics of monitoring the germination trays consistently enough to get a narrowed down time frame of when seeds germinated. Ultimately, this high variation in seed germination rate data made it unfeasible to run the Generalized Linear Models as originally planned.

With fecal collection, there were seasonal limitations on sampling due to fruiting phenology at the study sites. Data on avian diet composition may be influenced by the time of year the the majority of banding effort was conducted relative to fruit availability in the landscape. However, it is important to note the majority of banding effort was conducted in the mid Fall to early Summer which encompasses the two known fruiting peaks at the kīpuka site (Kovach 2012). The only species that may not have been well sampled is *R. hawaiensis* which fruits early Summer to early Fall and was only partially covered by banding effort in this study.

It's also important to note sampling limtations for 'alalā fecal collection in this study. First, the fecal samples were collected incidentally from the feeding stations likely limiting fruit consumption to plant species in the vicinity of the feeders. The fecal samples were also only collected from the feeders and incidentally from the forest floor. This sampling restriction limited the number of fecal samples that could be collected. Additionally, all the 'alalā were captive-born juveniles from two cohorts released approximately one to two years prior to the fecal collection period. Each cohort varied in the time they were in the wild and familiarity with their landscape and knowledge of available fruit resources. Age and release cohort were not separated and all fecal samples were lumped into the same sample pool. Many of these 'alalā were previously exposed to some but not all the native fruit species found at the release site and the fruits they were exposed to in captivity were presented in food dishes not off natural tree branches (Bryce Masuda/ personal communication, 2019). The most commonly found fruit in 'alalā diet was *C. trygynum*, *C. ernodeoides* and *L. tameiameia*. This is interesting because at the conservation breeding centers the 'alalā were never exposed to *C. ernodeoides*. Alternatively, the 'alalā did consume a lot of *C. trygynum* and *L. tameiameia* — two fruits that were regularly fed to the 'alalā prior to their release. More robust research is needed to examine the effects of

species specific gut-passage of avian gut-passage on native plant seeds to determine the functional role of avian frugivores on the regeneration and vigor of native Hawaiian forests. Future studies should also consider comparing the seed dispersal effects of less common exotic frugivores such as Hwamei and Northern Cardinals (*Cardinalis cardinalis*) and game birds such as Kalij pheasants in native-dominated montane forests. These larger birds have bigger gape sizes potentially allowing them to disperse larger seeds at higher quantities than WAWE and RBLE.

Implications

Today, many understory fruiting plant species are dispersal limited due to lack of avian seed dispersers (Inman-Narahari *et al.* 2013). Translocating native frugivores to other islands where they once existed could be a useful management tool to restore seed dispersal function in forests where native frugivores are extinct. Many endangered plants exist solely due to conservation efforts of humans. By reintroduing ʻalalā and ʻōmaʻo into restoration areas, conservationists could mitigate operational cost and effort by restoring natural seed dispersal function while simultaneously increasing the range of these avian species (Paxton *et al.* 2017). Frugivore reintroductions may promote the regeneration of native understory fruiting plants known for slow natural recruitment and overall forest health (Yelenik 2016).

Additionally, resource managers may also consider removing invasive fruiting plants thereby, limiting exotic frugivores to disperse natives seeds only which in theory would enhance native seed dispersal and regeneration. However, if that is unsuccessful, the inevitable spread of RBLE and WAWE across the Hawaiian islands could serve as a partial substitute for promoting native plant dispersal. This niche replacement by exotic frugivores may only benefit native

forests if invasive fruiting plants are virtually absent thus, reducing opportunities for exotic frugivores to facilitate their spread. However, the caveat is the quantity of seeds dispersed by exotic frugivores does not equate to efficacy of dispersal as many seeds could be dispersed into unfavorable habitats or be rendered unviable during gut-passage (Schupp 1993, Loiselle & Blake 1999). While is has not been determined that RBLE have a negative association with native birds through resource competition, WAWE are negatively associated with native birds such as the ʻōmaʻo and threatened and endangered species like the Hawaiʻi ʻākepa and ʻiʻiwi (Freed & Cann 2009). Regardless, ʻōmaʻo, ʻākepa and ʻiʻiwi are still colonizing restoration areas populated by WAWE just at a slower rate than other forest birds (Paxton *et al.* 2017). This finding should be integrated with managament plans to maintain a broader ecosystem function in the context of conserving the well being of Hawaiʻi's avifauna community. The results of this study also suggest that resource managers may want to time releases with the peak fruiting to ensure sufficient food resources are available at the time of release and/or translocation. The preferred plants in frugivore diet may also be used as an index to scope out future release sites for ʻalalā and ʻōmaʻo. Similarly, these preferred plant species may also be used in outplanting and restoration efforts to prepare the release sites for future releases of native frugivores.

Ultimately, grasping the extent to which exotic frugivores overlap with the niches of ʻōmaʻo and ʻalalā will give us insight on how the plant community will change if Hawaiʻi's frugivorous avifauna are extirpated. Based on current available literature, if native frugivores were to go extinct, the plant community composition would shift to benefit fruiting plant species with small seeds such as *Vaccinium* spp. and *R. hawaiensis*. The result would be smaller- seeded plant species having a wider distribution in the landscape while large-seeded plants who lack animal dispersers exist in more aggregated assemblages resulting in lower within-site diversity

(Wandrag *et al.* 2017). However, seed dispersal effects of common galliformes such as Kalij pheasants still need to be considered to make this determination to the fullest extent. As noted in the Foster and Robinson (2007) study, these are the plants that make up the majority of the forest understory in Hawaiian forest where native frugivores have been lost to extinction. Fruiting plant species with their primary disperser present have an ecological advantage at colonizing disturbed landscapes and persisting in the landscape overall (Howe & Miriti 2000). Because ʻōmaʻo are the only functionally extant native frugivore remaining in Hawaiʻi, my study sites reflect some of the mosts pristine native forest in Hawaiʻi. Since ʻalalā are currently functionally extinct, we should consider the ʻalalā in this study as an initial step at determining the potential but not the full function of seed dispersal by avian reintroductions. If managers want to maintain this baseline level of forest health and ecosystem functions that have existed for millenia, we must ensure the existence of ʻōmaʻo and ʻalalā for future generations.

Looking forward, there is good news on the Southern end of leeward Hawaiʻi Island where The Nature Conservancy (TNC) purchased the Kona Hema Preserve parcel where the last ʻalalā went extinct in 2002 (Culliney *et al.* 2012). Recent plans of reintroducing captive ʻalalā at this second release site are underway. Additionally, a small population of ʻōmaʻo have been discovered encroaching from the windward side of Hawaiʻi into the leeward facing Kona Hema Preserve (Griffin 2017). ʻŌmaʻo have not been seen on this side of the island for roughly 40 years (Pejchar 2015). These circumstances provide optimal conditions to determine the effects that reintroductions of native frugivores have on Hawaiian forests vigor and plant community composition. Researchers should take this opportunity to measure seed rain and seed recruitment before and after the ʻalalā and ʻōmaʻo become established in Kona Hema in order to get a better understanding of their functional role in shaping the plant community structure in native

Hawaiian forest. Managers may also use this and other studies to solicit recommendations for supplementing forest with the appropriate fruiting plant species to enhance habitat for encroaching ʻōmaʻo and released ʻalalā to thrive.

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Tables

Table 1. List of the fruiting plants and birds known in the *kīpuka* system off mile markers 18-21 off Saddle Road. *Known frugivorous bird species (Wu *et al.* 2014*)*.

Native Understory Fruiting Plant Species	Native Bird Species	Introduced Bird Species
Pilo (*Coprosma* spp.)	*ʻŌmaʻo (*Myadestes obscurus)*	*warbling White-eye (*Zosterops japonicus)*
Kōlea (*Myrsine lessertiana*)	ʻIʻiwi (*Drepanis coccinea)*	*Red-billed Leiothrix (*Leiothrix lutea)*
ʻŌhelo (*Vaccinium calycinum*)	*Hawaii ʻAmakihi (*Chlorodrepanis virens)*	House Finch (*Carpodacus mexicanus)*
ʻŌlapa (*Cheirodendron trigynum*)	ʻApapane (*Himatione sanguinea)*	*Kalij pheasant (*Lophura leucomelanos)*
Pūkiawe (*Styphelia tameiameiae*)	ʻElepaio (*Chasiempis sandwichensis*)	Yellow-fronted canary (*Serinus mozambicus*)
Kawaʻu (*Ilex anomala*)	ʻAkiapolaʻau (*Hemignathus wilsoni*)	*Hwamei (*Garrulax canorus)*
Naio (*Myoporum sandwicense*)	ʻĀkepa (*Loxops coccinea*)	*Northern Cardinal (*Cardinalis cardinalis)*
ʻĀkala (*Rubus hawaiensis*)		
Kūkaenene (*Coprosma ernodeoides*)		

Table 2. General background information of fruiting plant species used in this study. From Culliney **et al.** 2012, Wu *et al.* 2014 & Pejchar 2015.

Latin Name	Hawaiian Name	Family	Mean Fruit Size (mm)	MeanSeed Size – length (mm)	Mean # of seed per fruit
Cheirodendron trigynum	ʻŌlapa	Araliaceae	7.5	4-5	3
Coprosma ernodeoides	Kūkaenēnē	Rubiaceae	11	6	2
Coprosma spp: *C. pubens, C. ochracea, C. rhynchocarpa*	Pilo	Rubiaceae	10	3.5-4, 7	2
Ilex anomala	Kawaʻu	Aquifoliaceae	9	3	11
Myoporum sandwicense	Naio	Scrophulariaceae	6	4.5	1
Myrsine lessertiana	Kōlea	Primulaceae	9	6	1
Leptecophylla tameiameiae	Pūkiawe	Epacridaceae	5	3.5	1
Rubus hawaiensis	ʻĀkala	Rosaceae	35	1.5	38
Vaccinium spp	ʻŌhelo	Ericaceae	12	0.5	285

Table 3. Displaying the number of control seeds for each treatment type (gut-passage through an avian frugivore) in the germination trials for each plant species. *Because its not possible to count number of seeds in control fruits with pulp still attached, I used the mean number of seeds per fruit commonly found for that fruit species.

Plant Species	Control w/ Pulp	Control w/o Pulp	Seeds in Alala	Seeds in Omao	Seeds in WAWE	Seeds in RBLE
Cheirodendron trigynum	135	40	615	20	0	4
Coprosma ernodeoides	150	119	177	4	0	0
Coprosma spp.	36	100	58	18	0	4
Myrsine lessertiana	88	120	7	16	0	15
Vaccinium spp.	2850	270	1132	1275	57	6

Table 4. Displaying the top competing models derived from the Akaike's information criterion adjusted for models with small sample sizes (AICc). These models show the factors that influence presence/absence of seeds in fecal samples based on the competing explanatory variables of bird species (Bird) and the site (GenSite) the fecals were collected from. Additionally, the w_i (Akaike weights) for all of the top competing models are shown. logLik: the measure of model fit. Df = degrees of freedom.

Model Description	df	logLik	Δ AICc*	W_i
Bird	3	-458.882	0.00	0.727
Bird, GenSite	4	-458.858	1.96	0.273
GenSite	2	-504.228	88.68	0.00

Table 5. Displaying the relative likelihood of each fruiting plant species to be dispersed by an avian frugivore and germinate. The mean number of fruit is included to suggest how each species compensates for low germination or dispersal likelihood in their dispersal strategy.

Fruiting Plant Species	% Germinated	% of total Fecal	% of seeds likely to be dispersed and germinate	Mean number of seeds per fruit
Vaccinium spp.	2%	72%	1.44%	285
Cheirodendron tryginum	20%	10%	2%	3
Coprosma spp.	48%	3%	1.44%	2
Coprosma ernodioides	32%	5%	1.6%	2
Myrsine lessertiana	80%	1%	0.8%	1

Figures
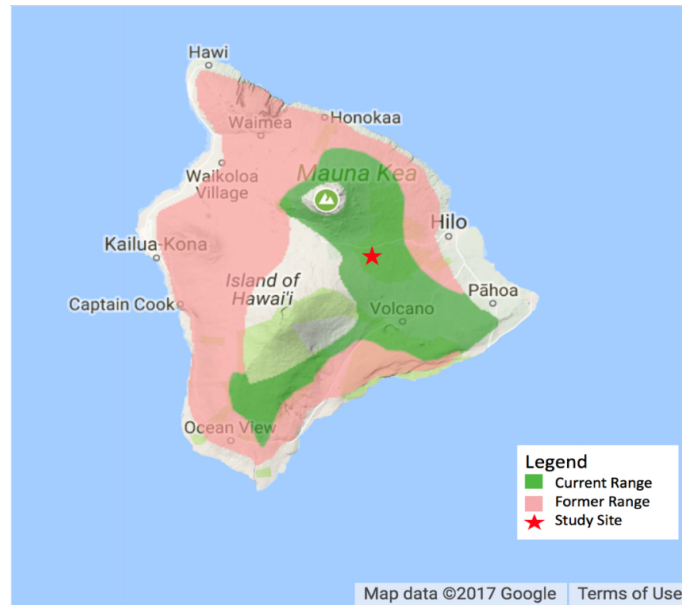
Figure 1. The former and current range of ʻōmaʻo on Hawaiʻi Island (BirdLife International 2017) and the study site.
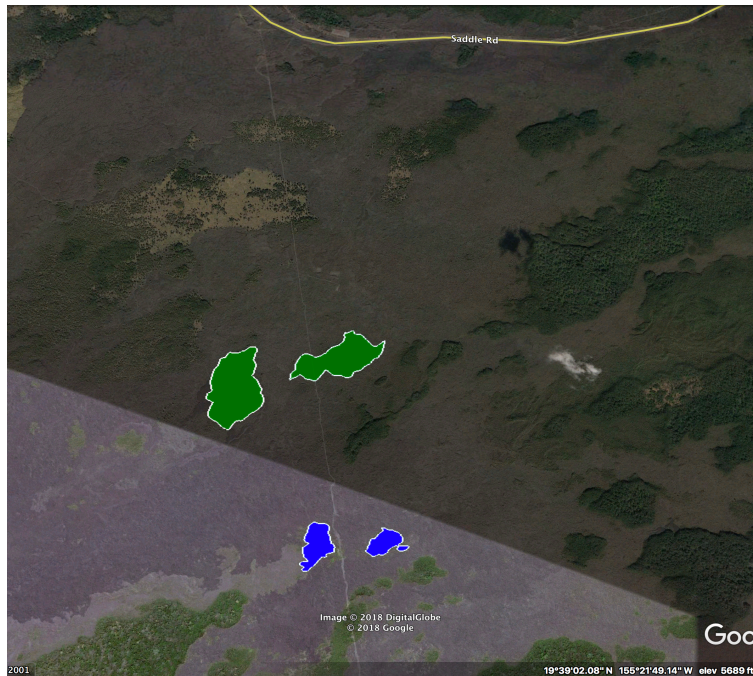
Figure 2. The four kīpuka sites highlighted by blue and green. The green kīpuka signify the larger kīpuka of ~11 ha and the blue kīpuka show the small kīpuka of ~3 ha. The yellow line at the top of the figure marks the Daniel K. Inouye highway. The perpendicular white line marks Powerline road. The site is at approximately 19°38'50.09" N 155°22'33.12" W.
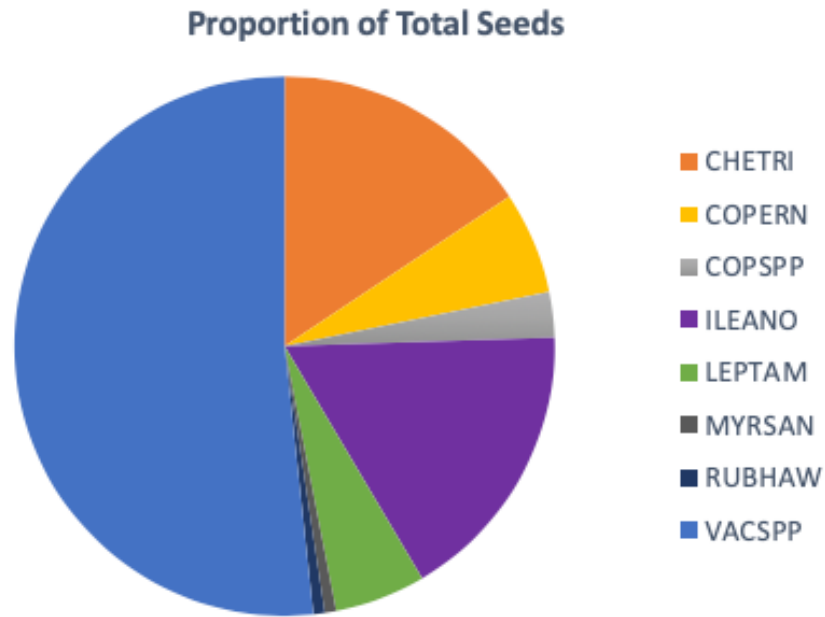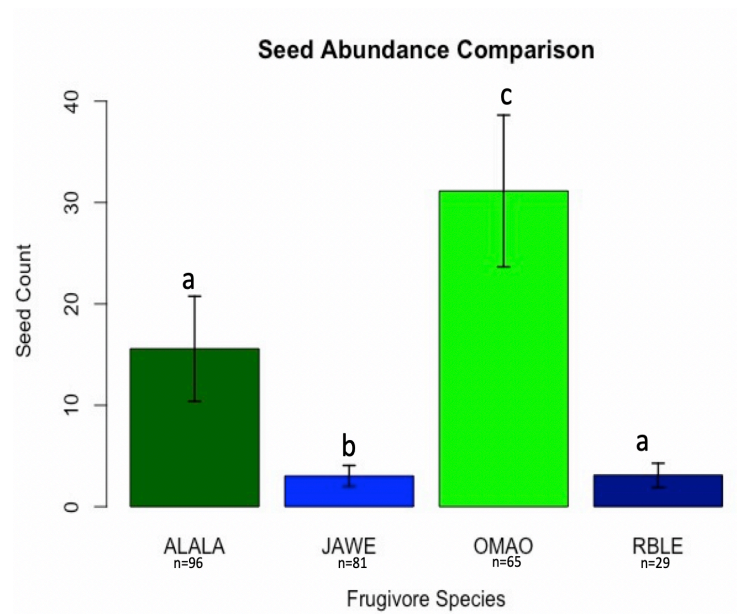
Proportion of Total Seeds

Legend:
- CHETRI
- COPERN
- COPSPP
- ILEANO
- LEPTAM
- MYRSAN
- RUBHAW
- VACSPP

Figure 3. Pie charts depicting the proportion of seed and fruit of each plant species found in all the seed rain traps. The number of fruit of each species was calculated using the total number of seeds found per species/ mean number of seeds found in fruit of each species. *M. lessertiana* was not found in the seed rain. (n= 145 seeds, ~240 sampling days)
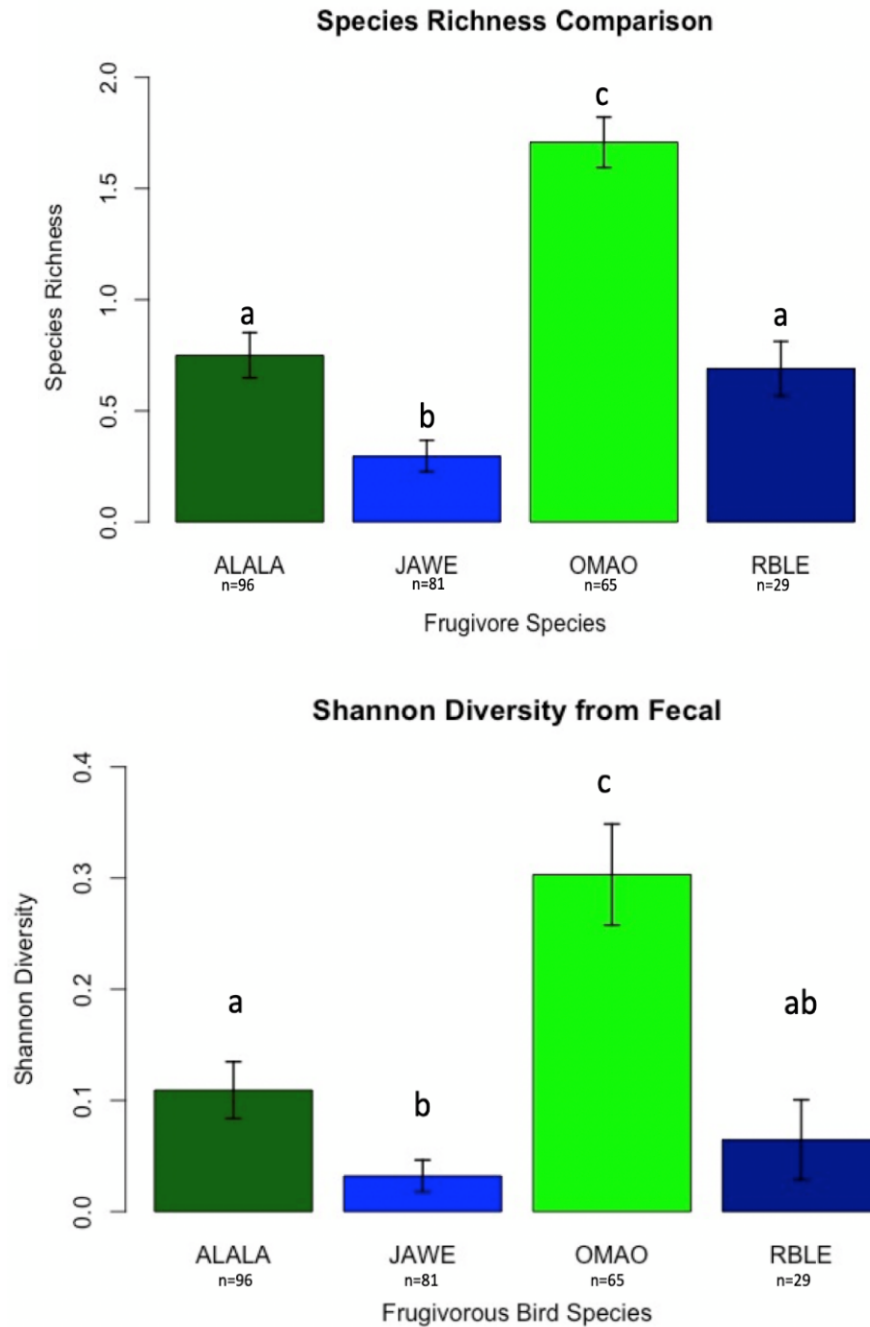

Seed Abundance Comparison. Seed Count versus Frugivore Species (ALALA n=96, JAWE n=81, OMAO n=65, RBLE n=29).

Species Richness Comparison

Shannon Diversity from Fecal

Figure 4. Barplot comparing means and standard errors for seed abundance per fecal sample ($X^2 = 77.374$, df = 3, p<0.001), plant species richness (number of species per fecal samples) ($X^2 = 82.641$, df = 3, p<0.001) and Shannon diversity ($X^2 = 47.716$, df = 3, p<0.001) in fecal samples collected from the four avian frugivore species in this study ('alalā, warbling white-eye, 'ōma'o and red-billed leiothrix). The letters above each bar signify significantly different means. Fecal sample sizes are listed below each species abbreviation.
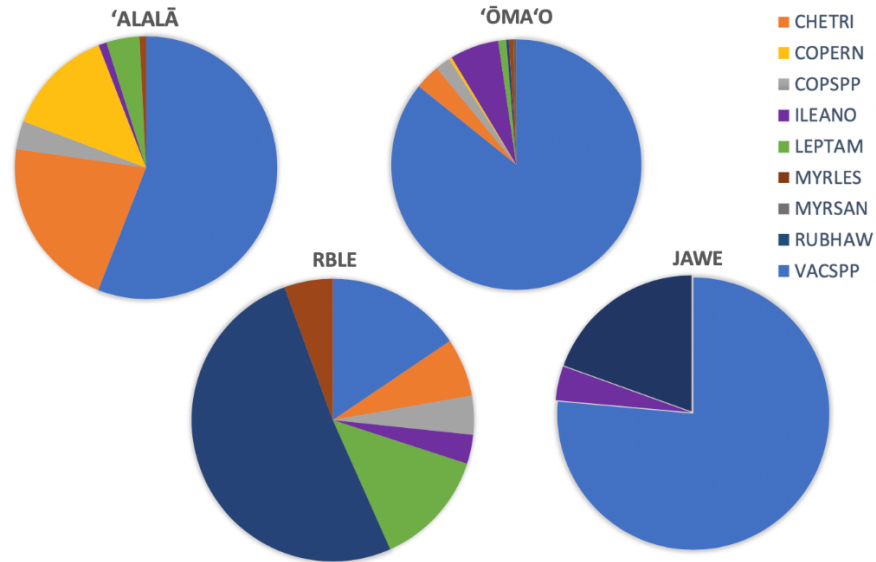
Figure 5. Pie charts showing the relative abundance of fruiting plant seeds in the fecal samples of four avian species. Relative abundance is calculated as the total number of seed from each plant species/ the total number of fruit collected from the fecal of each avian frugivore species.
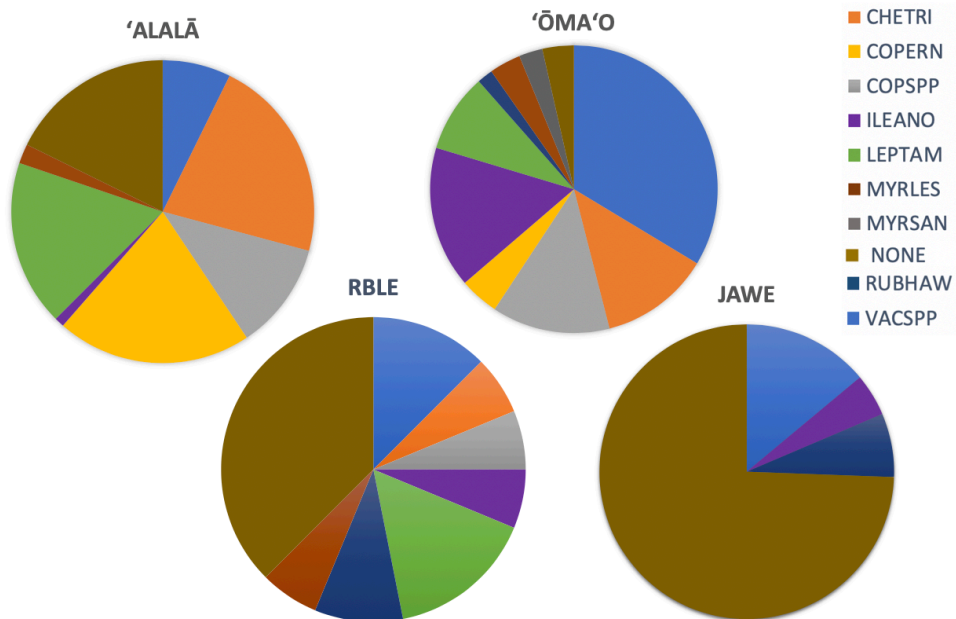

Figure 6. Pie charts showing the relative frequency of fruiting plant seeds in the four avian species. Th pie charts indicate the relative proportion of fruiting plant seeds that comprised the overall diet of each avian frugivore species. Relative frequency is calculated as # fecal samples containing an individual plant species / total number of fecal samples collected from each avian frugivore species.
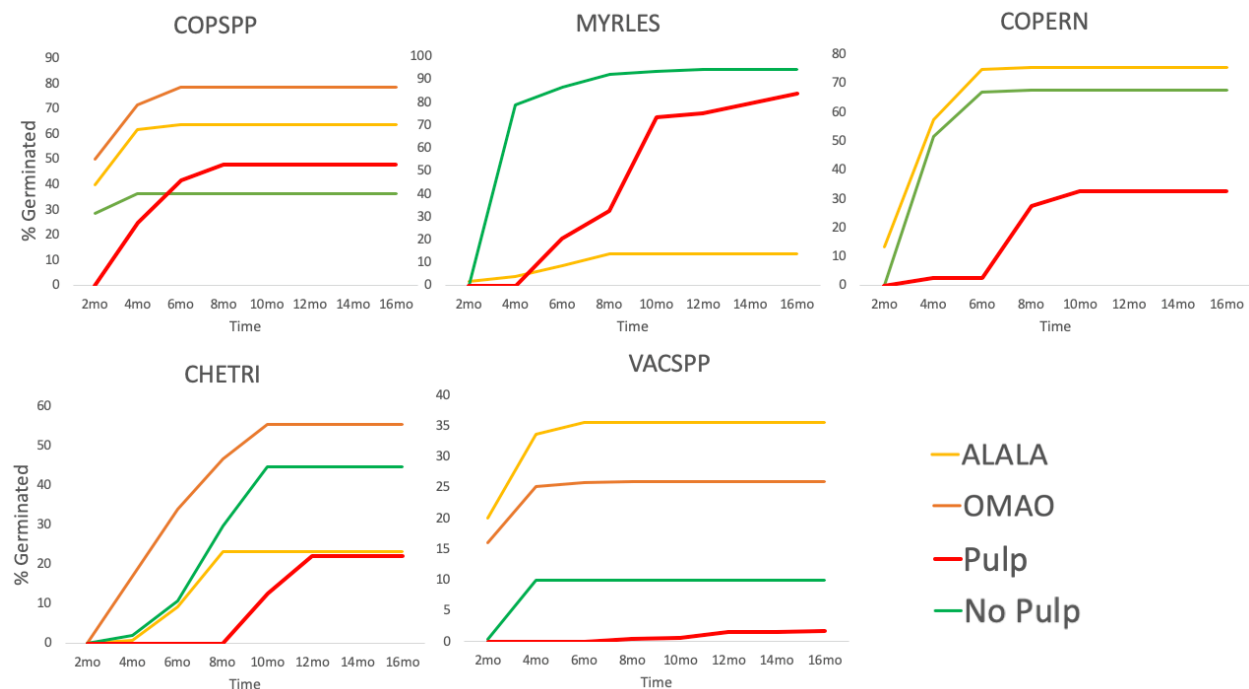
Figure 7. Line plots showing germination percent (%) of five native fruiting plant species over time. The colored lines represent a different control or a gut-passage treatment through an avian frugivore. The notable red line represents the control with the pulp still attached (C_w_P) as the baseline comparison of gut-passage effects on germination rate. (Pulp: control with pulp, No Pulp: control without pulp).
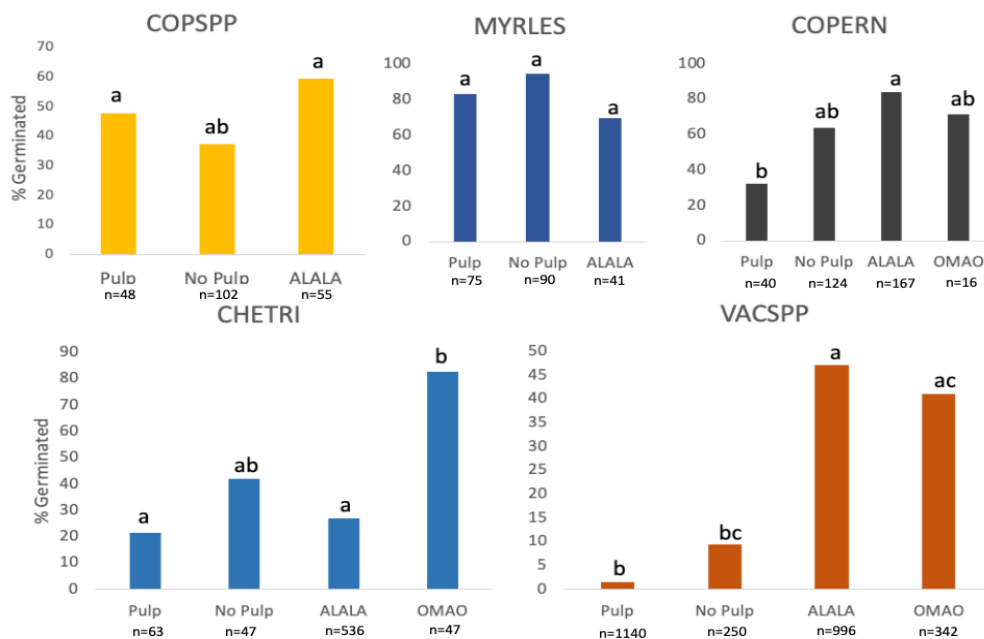

Figure 8. Barplots showing differences of overall germination proportions for five plant species under various gut-passage treatments. *Myrsine lessertiana* ($X^2 = 3.1122$, df = 4, p = 0.5393) did not have any signifcant differences between the the proportion of seeds that germinated. Sample size was determined by individual seed of a particular species planted under each gut-passage treatment. Letters above bars show significant differences among germination percentages for each treatment type.