NON-NATIVE TREES PROVIDE HABITAT FOR NATIVE HAWAIIAN FOREST BIRDS

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ABSTRACT

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On the Hawaiian island of Maui, native forest birds occupy an area dominated by non-native plants that offers refuge from climate-limited diseases that threaten the birds' persistence. This study documented the status of the bird populations and their ecology in this novel habitat. Using point-transect distance sampling, I surveyed for birds over five periods in 2013-2014 at 123 stations across the 20 km² Kula Forest Reserve (KFR). I documented abundance and densities for four native bird species: Maui ʻalauahio (*Paroreomyza montana*), ʻiʻiwi (*Drepanis coccinea*), ʻapapane (*Himatione sanguinea*), and Hawaiʻi ʻamakihi, (*Chlorodrepanis virens)*, and three introduced bird species: Japanese white-eye (*Zosterops japonicas*), red-billed leiothrix (*Leiothrix lutea*), and house finch (*Haemorhous mexicanus*). I found that 1) native forest birds were as abundant as non-natives, 2) densities of native forest birds in the KFR were similar to those found in native forests, 3) native forest birds showed varying dependence on the structure of the habitats, with ʻiʻiwi and ʻalauahio densities 20 and 30 times greater in forest than in scrub, 4) Maui ʻalauahio foraged most often in non-native cape wattle, eucalyptus, and tropical ash, and nested most often in non-native Monterey cypress, Monterey pine, and eucalyptus. Overall, native forest birds appeared to select habitat based on structure rather than composition. Thus, the diversity and structural heterogeneity of this non-native forest may be important in allowing native birds to achieve relatively high densities. This study documents the use of a novel habitat by native species, and also contributes to a better understanding of the ecology, distribution, and conservation of the native Hawaiian forest birds.

Acknowledgements

I am grateful for the many people that have influenced my success in completing this thesis. The scope of their influence spans from directly contributing to data collection to deep emotional inspiration and support, and includes everything in between. There is also much overlap as many people offered help in a wide variety of ways. For this reason, I found it futile to categorize and describe each individual and their influences into a reasonable acknowledgements section; therefore I offer a simple list of those I am grateful for. Exceptions include special thanks to Hanna Mounce, my field technicians, and my committee.

I first volunteered for the Maui Forest Bird Recovery Project in 2009, and it was then that Hanna Mounce first shared the idea of studying the native forest birds in the Kula Forest Reserve. My time working with MFBRP gave me a strong foundation to pursue this research and Hanna facilitated my undertaking of these questions as a master's thesis. Once work began, my field technicians, Erick Lundgren, Aaron Spidal, and Jie Kim dealt with some very challenging situations, and I appreciate their patience, their conscientious data collection, and all their efforts in the field. My graduate committee, Jeff Foster, Tad Theimer, and Carol Chambers, provided guidance, support, and patience that were invaluable to my growth and advancement as a student, a scientist, an educator, and a person.

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Dedication

I dedicate this research to all who have worked to conserve things natural, wild, and free.

This thesis is composed of three chapters with different styles and structures. Chapter one is an overview of the study species and the site to thoroughly introduce the reader to the fundamental theme of the thesis. In its current state, it serves only as an introductory thesis chapter, and is not formatted for journal submission. Chapter two is the manuscript chapter that is formatted for the journal, Biological Conservation. Upon submission of this thesis to Northern Arizona University, this chapter will be edited by additional co-authors and prepared for the peer-reviewed journal. Chapter three is a list of future research that would better inform conservation management efforts in Hawai'i and elsewhere. There is some redundancy across chapters, as in titles and abstracts, because Chapter two is meant to stand alone.

Non-native species, novel ecosystems, and their value.

"For the first time in the history of the human species, two things are now impending. One is the exhaustion of wilderness in the more habitable portions of the globe. The other is the world-wide hybridization of cultures through modern transport and industrialization. Neither can be prevented, and perhaps should not be, but the question arises whether by some slight amelioration of the impending changes, certain values can be preserved that would otherwise be lost." – Aldo Leopold (1949)

Since the time of Leopold, transportation systems and globalization have advanced rapidly, and as a result, ecosystems worldwide are being increasingly impacted by non-native species (Gaston 2000; Hobbs et al. 2006; Kier et al. 2009). Many of these impacts have had negative consequences for native species, especially on oceanic islands (Vitousek 1988; Vitousek et al. 1997; Myers et al. 2000; Richardson & Rejmánek 2004; Sugiura 2016). Yet the potential value of non-native species is a complicated issue because they vary in form and function, and although some have become invasive and negative in our view, some also provide valuable ecosystem services. (Pejchar & Mooney 2009; Shackelford et al. 2013; Dickie et al. 2014; Murcia et al. 2014).

Recently, the novel ecosystem concept has offered a paradigm shift by acknowledging the beneficial roles that non-native species can potentially play in an environment (Hobbs et al. 2006; Hobbs et al. 2009), and managers today are increasingly considering these ecological roles instead of making decisions solely based on the biogeographical origins of the organisms (Shackelford et al. 2013; Buckley & Catford 2016). This alternative perspective was in part inspired by the enormous costs required to effectively control non-native species, namely those with established populations (Restani & Marzluff 2002; Leonard 2008; Hobbs et al. 2009; Luther et al. 2016). Despite the ever-growing collection of literature on non-native species facilitating

native species (Rodriguez 2006; Foster & Robinson 2007; Aslan & Rejmánek 2010; Schlaepfer et al. 2011), this novel ecosystem theory has been critiqued by those who question the term "novel ecosystem" due to ambiguous thresholds of what defines novel (Murcia et al. 2014). These authors and others recognize the high variability across novel habitat conditions, and recommend that scientific efforts be increased in order to properly identify which ecological roles are important at a local scale (Lindenmayer et al. 2003b; Kuebbing et al. 2013; Dickie et al. 2014; Murcia et al. 2014).

In this study, I researched the ecological roles of native and non-native plants in a forest reserve on the Hawaiian island of Maui, where populations of threatened native birds are known to persist, but are poorly understood (Scott et al. 1986; Mounce et al. 2007; Warren et al. 2015). This habitat lies above 1500 meters in elevation, and therefore offers refuge to the birds from avian malaria, the climate-limited disease that threatens their existence (Atkinson et al. 2014; Fortini et al. 2015). Considering the negative impacts that non-native species have incurred on the native Hawaiian fauna and flora, the non-native origins of the plants seem to contradict the value of this disease-free habitat.

Non-native species and forestry in Hawaiʻi

Along with habitat loss, non-native species introduced to Hawaiʻi by humans are responsible for the extirpation and extinction of numerous endemic organisms (Warner 1968; Olson & James 1982; Scott et al. 1986; Pratt & Jacobi 2009), and today these non-native species remain a threat that must be mitigated against in order to conserve extant species (United States Fish and Wildlife Service 2006; VanderWerf 2012). Perhaps the most conspicuous of threatened Hawaiian taxa is a group of endemic forest birds called the Hawaiian honeycreepers. Over 50 of these endemic bird species radiated from a common ancestral finch species (James & Olson

1991; Lerner et al. 2011), yet only 15 of those remain with certainty today (Fortini et al. 2015). Six million years of evolution in the absence of mammalian predators and mosquito-borne disease rendered the honeycreepers naïve to many of these threats, leaving them vulnerable (Banko & Banko 2009b).

Introduced rats, mongoose, and feral cats depredate nestlings and adult birds (VanderWerf & Smith 2002; Hammond et al. 2015), and introduced avian diseases have directly contributed to extinctions with the help of their introduced arthropod vectors (Warner 1968; Scott et al. 1986; van Riper III et al. 1986). The mosquito-borne disease, avian malaria, is also currently responsible for limiting the range of the remaining honeycreepers (Atkinson et al. 2014). Other threats include introduced plants such as firetree (*Morella faya*), banana poka (*Passiflora mollissima*), and kahili ginger (*Hedychium gardnerianum*) that outcompete native plants and alter bird habitat (Vitousek & Walker 1989; Vitousek 1992; LaRosa 1992; Pratt & Jacobi 2009). Introduced birds disperse the seeds of non-native plants, contribute to avian disease dynamics, and may be competing with native birds for food resources (Foster 2005; Foster & Robinson 2007; Freed & Cann 2009; Foster 2009). Introduced ungulates such as pigs, goats, sheep, and cows browse native vegetation, disturb soils, and disperse non-native plants (Banko & Banko 2009b; Banko et al. 2013) . Also, for a variety of reasons, much of the native forest has been cleared (Judd 1931; Woodcock 2003).

Early Hawaiian forests were cleared to harvest timber resources and to make way for ranching and agriculture (Woodcock 2003). By the late 1800s, the kings of Hawai'i and the Hawai'i Sugar Planters Association (HSPA) noted concern for the water resources that were being impacted by this land conversion (State of Hawaii Department of Agriculture 2013). Shortly after claiming the Hawaiian Islands as a territory, the United States government, with

support from the HSPA, founded the Board of Agriculture and Forestry and initiated the Forest Reserve System. Between 1934 and 1941, the Civilian Conservation Corps planted over two million trees per year in 1.2 million acres of forest reserves across the state (State of Hawaii Department of Agriculture 2013).

Harold Lyon, a botanist for the HSPA declared that native Hawaiian trees are inferior to non-native trees for restoration, and therefore records of forest reserve plantings include over 1000 non-native species (Lyon 1919; Lyon 1929; Woodcock 2003). These plantings spanned multiple plants families that included Pinaceae, Myrtaceae, Fabaceae, Rosaceae, and Oleaceae. Not coincidentally, these families represent the most widely planted trees and shrubs in the world, and researchers have raised concern over their invasive properties (Richardson & Rejmánek 2011; Richardson et al. 2011).

Among the tree species planted in the Hawaiian forest reserves, eucalyptus (Myrtaceae), acacia (Fabacae) and pine (Pinaceae) are featured in global lists of the most important genera of invasive trees that provide ecosystem services (Dickie et al. 2014). In regards to the biodiversity these trees support, research worldwide has shown that native birds will use these non-native trees, but habitat quality is increased by a developed understory, higher plant diversity, and/or native plants nearby (Estades & Temple 1999; Lindenmayer et al. 2003a; Lindenmayer & Hobbs 2004; Barlow et al. 2007; Traill 2016).

Non-native tree plantations including eucalyptus and pine are still managed on both private and state lands in Hawai‘i (Scheffel 1990; Phillips et al. 1995; Pejchar & Press 2006). In 2004, a University of Hawai‘i report identified non-native plantation tree species to be a major driver of growth for the local Hawaiian timber industry (Yanagida et al. 2004), and noncommercial plantations with similar plant compositions occur in Hawai‘i as well (Mascaro et

al. 2008). Little is known about native birds that may use these non-native tree because many occur at low elevations, where the birds are restricted by avian malaria (Mascaro et al. 2008; Fortini et al. 2015)

Conservation of the Hawaiian forest birds

Today, only 15 Hawaiian honeycreeper species persist in the wild with certainty, and future projections for many species are bleak (Fortini et al. 2015). Avian disease and climate change are compounded by limited habitat, mammalian predators, low population sizes, and low genetic diversity in contributing to the decline of the endemic Hawaiian forest birds (Scott et al. 1986). Monitoring programs are in effect, and although insufficient funding and resources limit their extent and ability to infer trends, the evidence supporting a high level of extinction risk is clear (United States Fish and Wildlife Service 2006; Camp et al. 2009; Atkinson et al. 2014; Fortini et al. 2015).

Conservation management is currently focused on mitigation against the advancing threat of avian disease, which has been modeled to increase its elevational range due to a warming climate (Benning et al. 2002; Atkinson et al. 2014). Mitigation efforts include fencing and feral ungulate removal, predator reduction, and habitat restoration (VanderWerf & Smith 2002; Kilpatrick 2006; VanderWerf 2012; Banko et al. 2013; Warren et al. 2015). Research regarding the needs of these birds has been compelling, yet funding and resources are still far less than what are needed to accomplish conservation goals (Leonard 2008; Leonard 2009). The cost to recover Hawai'i's birds and their habitats is estimated to be nearly one billion dollars over the next 10 years, which is nearly five times less than the cost of similar restoration efforts on the mainland that are currently underway (Leonard 2008). Furthermore, the Hawaiian birds, which account for over one-third of the birds listed under the Endangered Species Act, receive about 15

times less funding than mainland species, and only 4% of the total funding provided for all listed species (Leonard 2009).

Considering these hindrances to obtaining sufficient resources, conservation management decisions must be cost-effective and open to alternative opportunities (Hobbs et al. 2006). Habitats provided by non-native species can be valuable to native species of concern (Schlaepfer et al. 2011), and management decisions should be based more on the resources and services that organisms can provide to the ecosystem, rather than whether they are native or non-native species (Shackelford et al. 2013; Buckley & Catford 2016).

Research objectives and general methods

The state-managed Kula Forest Reserve (hereafter KFR) contains forest dominated by non-native trees, and is an area of conservation concern for the native Hawaiian forest birds because it offers habitat above the range of avian malaria (United States Fish and Wildlife Service 2006; Mounce et al. 2007; VanderWerf 2012; Warren et al. 2015). My research addresses the following four questions: 1) what is the status of bird populations in the KFR, 2) how do densities of native birds compare in the KFR versus other sites across Hawaiʻi, 3) are the birds selecting for different habitat structures and plant compositions within the reserve, and if so, 4) which variables correlate with higher or lower bird densities?

To obtain estimates of abundance and density for birds, my field team conducted distance sampling surveys at 123 points across the KFR in 2013-2014. To maximize the number of detections for the calculation of detection functions (Buckland et al. 2001), I surveyed each point 5 times, and pooled detections across all survey periods. Density was calculated at multiple scales, and these estimates were used as the dependent variables when comparing across different habitat structures and plant compositions. Habitat structures were identified and defined

a priori using descriptions from the original Hawaiian Forest Bird Survey (Scott et al. 1986). Plant compositions were determined by vegetation surveys at each of the 123 points surveyed for birds. I used various methods to compare and observe patterns including stratifying abundance and density estimates for habitat types and single survey points, mapping the distributions of seven birds and 22 plants across the KFR, indicator species analyses, NMDS ordination, generalized linear regression, and comparing used habitat to what was available.

My underlying goal with this research is to contribute to the conservation of the Hawaiian forest birds, and offer insights into the highly variable phenomena that occur when native and non-native organisms interact. The factors threatening the continued existence of the Hawaiian forest birds are clear (VanderWerf 2012), and management strategies to mitigate against them are underway (Warren et al. 2015), but time is running out (Fortini et al. 2015), and conservation resources are limited (Leonard 2008). I pursued a better understanding of the ecological resources that a neglected novel habitat may offer to the conservation of Hawai'i's threatened birds. In 1949, Aldo Leopold observed the impending destruction and homogenization of our wild places, and then he asked us to consider ways of finding value in the remains. This study represents my search for that value.

CHAPTER 2. NON-NATIVE TREES PROVIDE HABITAT FOR NATIVE HAWAIIAN FOREST

BIRDS

ABSTRACT

On the Hawaiian island of Maui, native forest birds occupy an area dominated by non-native plants that offers refuge from climate-limited diseases that threaten the birds' persistence. This study documented the status of the bird populations and their ecology in this novel habitat. Using point-transect distance sampling, I surveyed for birds over five periods in 2013-2014 at 123 stations across the 20 km² Kula Forest Reserve (KFR). I documented abundance and densities for four native bird species: Maui ʻalauahio (*Paroreomyza montana*), ʻiʻiwi (*Drepanis coccinea*), ʻapapane (*Himatione sanguinea*), and Hawaiʻi ʻamakihi, (*Chlorodrepanis virens)*, and three introduced bird species: Japanese white-eye (*Zosterops japonicas*), red-billed leiothrix (*Leiothrix lutea*), and house finch (*Haemorhous mexicanus*). I found that 1) native forest birds were as abundant as non-natives, 2) densities of native forest birds in the KFR were similar to those found in native forests, 3) native forest birds showed varying dependence on the structure of the habitats, with ʻiʻiwi and ʻalauahio densities 20 and 30 times greater in forest than in scrub, 4) Maui ʻalauahio foraged most often in non-native cape wattle, eucalyptus, and tropical ash and nested most often in non-native Monterey cypress, Monterey pine, and eucalyptus. Overall, native forest birds appeared to select habitat based on structure rather than composition. Thus, the diversity and structural heterogeneity of this non-native forest may be important in allowing native birds to achieve relatively high densities. This study documents the use of a novel habitat by native species, and also contributes to a better understanding of the ecology, distribution, and conservation of the native Hawaiian forest birds.

1. Introduction

Non-native species introductions and habitat loss have both contributed to biodiversity loss and the endangerment of species and populations worldwide (Scott et al. 1986; Vitousek et al. 1997; Myers et al. 2000). Yet non-native species sometimes can buffer native species from the impacts of habitat loss by providing the structure and function to which the native organisms are adapted (Rodriguez 2006), and this facilitation can be valuable in the conservation of threatened species (Hobbs et al. 2006; Schlaepfer et al. 2011).

Few communities in the world have suffered more from the impacts of non-native species and habitat loss than the native biota of the Hawaiian Islands (Vitousek 1992; Banko & Banko 2009b). Millions of years of isolation and vacant niche opportunities lead to an extensive evolution of endemic organisms (Banko & Banko 2009b). Recent changes imposed by human beings and the organisms they have introduced have resulted in the loss of over 90% of undisturbed native forest, and the extinction of countless native species (Gagné 1988; Pratt & Jacobi 2009). Among the native taxa that have suffered great losses are the forest birds; more than half the endemic species have been driven to extinction by humans (Olson & James 1982). Many of the factors responsible for these extinctions still persist today (VanderWerf 2012).

Avian malaria, a mosquito-borne disease, has directly contributed to the extinction of forest bird species, and today restricts many of the remaining species to elevations above 1500m (Warner 1968; Atkinson et al. 2014; Fortini et al. 2015). Cold temperatures at high elevations restrict both the mosquito vector and the malarial pathogen (Warner 1968), yet as global climate change results in warmer temperatures at higher elevations, the disease will expand upslope, further constricting the range available to the native forest birds (Benning et al. 2002). Other

introduced organisms threatening the native birds include mammalian predators, invasive plants, and feral ungulates (Scott et al. 1986).

Priorities for the conservation of the Hawaiian forest birds focus on mitigation against the threat of avian disease and climate change (United States Fish and Wildlife Service 2006; VanderWerf 2012). On the ground, this manifests in the restoration of habitat and the establishment, maintenance, and/or increase of native bird populations (Warren et al. 2015; Peck et al. 2015; Mounce et al. 2015). To monitor populations, researchers initiated the Hawaiian Forest Bird Survey (HFBS) in the 1970s. This monumental effort provided the first population estimates for all of Hawai'i's forest birds, and established a sampling design that is still used today (Scott et al. 1986). Unfortunately, subsequent surveys have not been comprehensive, and some areas have never been resampled (Camp et al. 2009).

One of these neglected areas is the Kula Forest Reserve on Maui (hereafter the KFR). Three transects were surveyed in 1980, but none have been done since. This has resulted in this area's exclusion from recent literature on Hawai'i's bird populations, and range maps for some species are incomplete (VanderWerf 2012; Paxton et al. 2013a; Fortini et al. 2015). A wildfire in 2007 alerted managers to the vulnerability of the native forest birds that occupy the KFR, and highlighted a need to better understand the bird populations and their ecology in the area (Mounce et al. 2007).

Non-native plants dominate the forested habitat in the KFR and their families include Pinaceae, Myrtaceae, Fabaceae, Rosaceae, and Oleaceae. Not coincidentally, these families represent the most widely planted trees and shrubs in the world, and researchers have raised concern over their invasive properties (Richardson & Rejmánek 2011; Richardson et al. 2011). Birds worldwide, including some in Hawai'i, are known to use non-native trees and shrubs

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(Waring et al. 1993; Aslan & Rejmánek 2010; Schlaepfer et al. 2011), and native birds can occupy habitats, such as tree plantations, that are almost exclusively exotic (Estades & Temple 1999; Lindenmayer et al. 2003a; De la Hera et al. 2013). This confirms that non-native plants can potentially provide the structure and functions required for occupancy by birds. Conservation managers are now considering the ecological functions that non-native species can offer, instead of simply discounting them because of their non-native origins (Shackelford et al. 2013; Buckley & Catford 2016).

Not all birds respond to changes in the ecosystem the same way (Lindenmayer et al. 2003b), and in general, species with a higher degree of specialization are more sensitive (Cody 1974). The native forest birds of Hawai'i have displayed a high diversity of bill forms to exploit a wide range of food resources, especially nectar (Banko & Banko 2009a). The more specialized Hawaiian forest birds have displayed an intolerance to anthropomorphic change, as they are either extinct, or are at high risk of extinction (Pimm & Pimm 1982; Banko & Banko 2009a; Banko et al. 2013), while 10 species of non-specialized forest birds remain extant in Hawai'i that are still not considered threatened (Banko & Banko 2009a; Banko et al. 2013). It is apparent that degree of specialization and foraging guild are relevant to the birds' success in a novel environment, therefore I reviewed these factors in the four native forest birds that are known to occupy the KFR. I also included three introduced bird species to investigate more community-wide patterns.

The four native Hawaiian forest birds that occupy the KFR are Maui 'alauahio (*Paroreomyza montana*), 'i'iwi (*Drepanis coccinea*), 'apapane (*Himatione sanguinea*), and Hawai'i 'amakihi, (*Chlorodrepanis virens).* Recent literature has defined three degrees of specialization in the Hawaiian honeycreepers and labeled them as generalist, intermediate, and

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specialist (Banko & Banko 2009a). They also defined three food guilds and labeled them nectar-eating, fruit-and seed-eating, and arthropod and snail-eating (Banko & Banko 2009a), although in this paper, I will refer to them as nectarivores, frugivores, and insectivores, respectively. The four honeycreepers that occur in the KFR each represent a unique combination of specialization and food guild.

Maui ʻalauahio represents an intermediate insectivore, and is now restricted to only the forests of East Maui (Banko & Banko 2009a; Warren et al. 2015) . Global population estimates are 52,729-57,921 birds ([95% CI], mean 55,262) (Brinck et al. 2012). Maui ʻalauahio typically occurs in family groups and mixed-species flocks while gleaning insects in the understory of native forest, and studies have documented them occupying, nesting, and foraging in non-native vegetation (Carothers 1982; Waring et al. 1993; Baker & Baker 2000). This species is listed as endangered with decreasing populations (Birdlife International 2016).

ʻIʻiwi represents an intermediate nectarivore that occurs on the five largest Hawaiian islands (Banko & Banko 2009a; Paxton et al. 2013a). Global population estimates are 550,972 - 659,864 birds ([95%CI], mean 605,418) and they are not evenly distributed across their range, with 90% of the entire population occurring on the island of Hawaiʻi (Paxton et al. 2013a). ʻIʻiwi will take nectar from exotic eucalyptus flowers, but the extent of this association is unknown (Scott et al. 1986). This species is listed as vulnerable with decreasing populations (Birdlife International 2016).

ʻApapane is Hawaiʻi's most abundant and widespread honeycreeper, and represents a generalist nectarivore that occurs on all major Hawaiian islands (Camp et al. 2009; Banko & Banko 2009a). Global population estimates are greater than 1,000,000 birds (Camp et al. 2009) and they appear to be increasing in abundance in portions of their range (Gorresen et al. 2009).

'Apapane have also been documented taking nectar from eucalyptus flowers (Scott et al. 1986). This species is listed as least concern with stable populations (Birdlife International 2016)

Hawai'i 'amakihi is one of three distinct species in the Hawaiian 'amakihi complex, (Tarr & Fleischer 1993), although for my comparisons across islands, I pooled all these into one group named 'amakihi. These birds have been described as Hawai'i's most generalist species foraging on arthropods, nectar, fruit, and sap (Lindsey et al. 1998), yet they are categorized as a generalist insectivore (Banko & Banko 2009a). Summing the abundance estimates for 'amakihi across Hawai'i results in estimates of greater than 1,000,000 birds (Gorresen et al. 2009). This species is listed as least concern with stable populations (Birdlife International 2016).

The two more threatened native birds, Maui 'alauahio and 'i'iwi, are highly susceptible to avian malaria, and consequently the disease effectively restricts their range (Scott et al. 1986; Camp et al. 2009). 'Apapane and 'amakihi, on the other hand, are less susceptible and are displaying distributional and genetic patterns of survival and resistance to avian malaria (Woodworth et al. 2005; Spiegel et al. 2006; Foster et al. 2007).

A suite of introduced birds also occur in the KFR. The most abundant species are Japanese white-eyes (*Zosterops japonicas*), red-billed leiothrix (*Leiothrix lutea*), and house finches (*Haemorhous mexicanus*). Other rare, but conspicuous non-native birds include Japanese bush warblers (*Horornis diphone*), melodious laughing thrushes (*Garrulax canorus*), and northern cardinals (*Cardinalis cardinalis*). I included the white-eyes, leiothrix, and house finches in my analyses to compare patterns across native and non-native birds. These three species are omnivorous generalists (Scott et al. 1986), and are listed as species of least concern (Birdlife International 2016).

This study investigated the birds of the KFR on multiple levels. First, I estimated total abundances and densities, and mapped distributions. These data will contribute to more complete reporting of the population status and occurrence ranges of the native forest birds. To investigate the birds' response to variable habitat conditions at a smaller scale, I compared bird densities across structures and plant compositions. In studies of birds in non-native tree plantations, native bird numbers are often lower when non-native trees dominate, and correlated with the amount of, or proximity to, native vegetation (Estades & Temple 1999; Lindenmayer et al. 2003b). Although, the KFR is different in that native plants and non-native plants do not offer similar structures. The native vegetation is mostly restricted to the low-stature scrub habitat, and native plants rarely occur under the canopy of the non-native trees (Mascaro et al. 2008). I expected that when comparing forested versus non-forested habitats, this difference in structure will be more important to the forest-adapted birds than the distinction between native and non-native plants.

The original Hawai'i Forest Bird Survey reported that all seven of the bird species in my study occurred at lower density in the treeless habitat than forested habitat, showing that structure is important (Table 1) (Scott et al. 1986). Three native bird species and one introduced bird species occurred at higher densities in the native koa-ohia forest. Surprisingly, the other native bird species, Maui 'alauahio, occurred at slightly higher densities in the introduced trees than in the native koa-ohia forest (Scott et al. 1986). The authors offered no explanation or discussion of this phenomenon, but I interpreted this as suggesting that the introduced trees may not be of considerably lesser quality than native habitat.

I sought to determine if the native plants were facilitating the presence of the native birds, or if the non-native plants were providing the necessary functions for occupancy. Due to the scarcity of the native plants in the forest, I expected that the native birds were able to exploit the

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functions of the non-native trees; therefore I observed the foraging and nesting habits of Maui

'alauahio. I chose this species because they occur in noisy social groups that nest and forage

closer to the ground than the other species, making them easier to catch and observe (Scott et al.

1986; Baker & Baker 2000), and as a more specialized species, their habitat associations in the

non-native forest may help inform those of other species as well.

Understanding the status and habitat associations of the native birds in the KFR will help

inform efforts to conserve them. A lack of high-elevation forest with a reduced threat of avian

malaria is a limiting factor for the native forest birds of Hawai'i (United States Fish and Wildlife

Service 2006), and my study highlighted the potential of non-native trees to fill this role and

provide the resources required by the native forest birds.

2. Methods

2.1 Study area

The 20 km² Kula Forest Reserve (KFR) lies on the leeward southwestern flank of

Haleakala, a 3052 m high volcano on the eastern side of Maui, Hawai'i (26°42'N, 156°18'W).

The area receives ~900–1000 mm of rainfall per year, whereas some native forests on windward

Maui receive up to ten times more than that (Giambelluca et al. 2013). The political boundary of

the reserve occurs between 1550 m and 2700 m in elevation and includes two disjunct patches of

habitat. (Fig. 1 and 2). These areas of state-managed land are separated by a strip of private land

that is mostly dominated by a thick monoculture of non-native black wattle (*Acacia mearnsii*). I

did not conduct surveys on this private land.

I observed 22 varieties of tree and shrub in KFR (Table 2), and categorized them into

native trees: 'ohia (*Metrosideros polymorpha*) and koa (*Acacia koa*), non-native trees: Monterey

pine (*Pinus radiata*), cluster pine (*Pinus pinaster)*, redwood (*Sequoia sempervirens*), Monterey

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cypress (*Cupressus macrocarpa*), tropical ash (*Fraxinus uhdei*), eucalyptus (*Eucalyptus* spp.), tsugi pine (*Cryptomeria japonica)*, western red cedar (*Thuja plicata*), native shrubs: mamane (*Sophora chrysophylia*), pukiawe (*Styphelia tameiameiae*), 'a'ali'i (*Dodenaea viscosa*), 'ohelo (*Vaccinium* spp.), pilo (*Coprosma montana),* 'akala (*Rubus hawaiensis*), and non-native shrubs: cape wattle (*Pariserianthes lopantha*), black wattle (*Acacia mearnsii*), blackwood acacia (*Acacia melanoxylon*), firetree (*Morella faya*), mysore raspberry (*Rubus niveus*), and banana poka (*Passiflora mollissima*).

Three habitats types with distinct physical structures occur in the KFR (Fig. 2), and I named them consistently with the habitat scheme used in the original Hawai'i Forest Bird Survey (HFBS) (Scott et al. 1986). The "forest" had a closed canopy (> 60% cover) that stood over 10 meters tall and included a patchy array of understory vegetation throughout. The forest covered a total of 5.67 km².

The "burned woodland" was the result of a high intensity fire that occurred in 2007. It was characterized by a variable mix of scattered live trees and many standing dead snags with the lower understory composed of a nearly impenetrable matrix of vegetation thickets and fallen trees. This fit definitions included in both "woodland" and "savanna" from the HFBS (Scott et al. 1986). They defined a "woodland" as having an open canopy (25-60% cover) that stands 5 – 10 meters tall, and "savanna" as having a very open canopy (5-25% cover) standing < 5 meters tall, or scattered trees (<5% cover) standing 5 - 10 meters tall. All of these conditions were included in the burned woodland, and this habitat type covered 5.03 km² of contiguous area.

The third area in the KFR is the "scrub," defined by the HFBS as having scattered trees (< 5% cover) standing less than five meters tall or including shrubland, grassland, or barren rock (Scott et al. 1986).This habitat type covers 6.46 km².

2.2 Transect surveys

I placed a grid of 123 points (survey stations) into 10 transects over the accessible habitat within the boundary of the KFR. The transects included and ran parallel to transects 29, 30, and 31 from the original HFBS (Scott et al. 1986) and were approximately 800 m apart with points occurring in 150 m increments (Figure 2). Of the 123 survey points that I analyzed, 52 occurred in the forest, 26 occurred in the burned area, and 45 occurred in the scrub. All points were sampled with the same effort.

My field team sampled each station for birds five times over two years: In 2013, we surveyed March 21-26, April 4-11, June 5-11, and June 18-20. In 2014, we surveyed March 10-13. These dates were chosen to coincide with the peak of the breeding season. Surveys were conducted between 30 minutes before sunrise and 1100 to capture peak bird activity, and one transect was completed per day per observer. Surveys were eight minutes long at each station, following standard protocols for Hawaiʻi that aim to optimize survey length and number of birds sampled (Camp et al. 2011).

Upon detection of a bird during a survey, the observer identified it to species and measured the horizontal distance to the bird using a laser-range finder. These distances were recorded because distance sampling theory states that the detectability of a bird relates to its distance from the observer (Buckland et al. 2001). The analysis can also account for differential detectability caused by various influences. To test and evaluate these potential influences on detectability, I recorded the following: date, time, observer, detection type (seen, heard, or both), and weather (cloud cover, rain, wind speed, and gust speed).

I then recorded ocular estimates of the relative abundance of all tree and shrub species present within a 50 meter radius of each station.

2.3 Data analyses of transect surveys

I calculated densities and abundance of birds using program Distance 6.2 (Thomas et al. 2010). Detection functions for each species were chosen by considering AIC, visual inspection of the model, various goodness-of-fit tests, and parsimony (Buckland et al. 2001, Anderson and Burnham 2004). Differences among covariates and also various adjustment parameters were tested using AIC (Buckland et al. 2001). After selecting models and detection functions for each species, I then stratified the sample by the three habitat types (forest, burned woodland, and scrub) and calculated a density in each. Then I averaged densities from the three strata and weighted them by the area of the habitat type (Buckland et al. 2001). This stratified random sampling design produced variance estimates for each stratum, which ultimately reduced the variance in the final estimate of average density, which I then bootstrapped to calculate 95% confidence intervals. I estimated the number of birds per square kilometer at three levels; an average across the entire KFR, an average for each habitat type, and finally I estimated a per-point density at each of the 123 survey stations.

To determine if native or introduced birds dominate the avian community, I compared the abundances of the four native birds and the three most abundant non-native birds. I considered overlapping confidence intervals to indicate no significant differences in relative abundance.

To compare bird density in native versus non-native forest, I collected results from four different publications that reported estimates from a variety of other study sites across Hawai'i (Appendix A). I gleaned point estimates and 95% confidence intervals for each of the four native birds in seven other study sites. Data for non-native birds in Hawai'i were scarce and I did not include them in this analysis. Overlapping confidence intervals indicate no significant differences in bird density.

To investigate vegetation differences across the three habitat types within KFR, I plotted relative abundances of plant species in an NMDS ordination using the vegan package in R (Oksanen et al. 2015). Each point on the ordination represents a survey station, and placement on the plot is determined using the Bray-Curtis dissimilarity index based on the plant composition of that survey station relative to others. Points closer to each other are more similar in plant composition than points further away. Permanova analysis indicated whether there were significant differences in plant composition across the three habitat types. I then compared the density of each bird species across the three habitat types. Again, overlapping confidence intervals indicate no significant differences in bird density.

To observe the spatial distribution of the different plant and bird species within the KFR. I used the kriging tool in Arcmap 10.1.1 to extrapolate data across gaps between survey transects. Raster pixels were given a value based on the average of the eight nearest survey points.

To test whether the native birds were associated more with native plants or non-native plants, I grouped each plant species into either non-native trees, native shrubs, or non-native shrubs and ran a Poisson generalized linear model in R (R Core Team 2014). Native trees were excluded from the analysis because of very low occurrence. Significance was determined with a p-value, and the coefficient determined the strength of the positive or negative association.

To determine if areas with higher or lower bird density were associated with particular plant compositions, I conducted an indicator species analysis using PC-ORD (Dufrene & Legendre 1997). I was particularly interested in habitat associations in the forest habitat, where the non-native trees dominate; therefore my analysis only included the forest survey points. For each bird species, I divided these survey points into three groups depending on the density of

birds recorded there, and labeled the groups "high", "average", and "low." I used a non-parametric ranking method to list the densities at 52 forest points, and divided the list into three approximately equal-sized groups. For example, the top third of points with the highest density were put into the "high" group. This indicator species analysis calculates the relative abundance of each plant species given that it occurs in that group, and also the relative frequency of that plant species, given it is in that group. These values combine to produce an indicator value (IV) and a p-value to determine significance (Dufrene & Legendre 1997).

2.3 Habitat selection of Maui 'alauahio

To assess the specific non-native trees and shrubs used by Maui 'alauahio, I observed their foraging and nesting in three plots with distinct plant compositions (Fig.2). Plot A was dominated by eucalyptus and Monterey cypress in the canopy, and a mixture of acacias and young eucalyptus in the understory. Plot B was dominated by tropical ash and redwood in the canopy with some occasional western red cedar. The understory was composed of young tropical ash, cape wattle, and firetree. Plot C was mostly Monterey pine mixed with occasional cluster pine and redwood. The understory included firetree and black wattle, but was often a dense thicket of mysore raspberry.

In each plot, birds were mist-netted and color-banded for identification of individuals. Birds were then released, to be later observed with binoculars. Each time a banded bird was observed, I took a GPS point and recorded a behavior and the plant species on which it occurred. Home range analyses of these data were reported by Warren et al. (2015), and are not discussed further here. Observations were filtered for foraging behavior, and then pooled across all birds in each plot. Survey effort was not the same across plots because bird abundance and ease of catching them varied greatly across the sites.

Ocular estimates of plants in each plot were pooled to produce the percentage of total available foraging substrate that was represented by each plant species. This produced the metric of what was available. Total bird observations per plant species per plot produced my metric of what was used. I then ranked these values and compared the difference between ranks of use and ranks of availability (Johnson 1980). A positive difference in rank dictated a preference for that plant, and negative difference in rank dictated avoidance (Johnson 1980).

Observers searched for active Maui ʻalauahio nests both within the three study plots and the surrounding areas. When the nest found was confirmed to be active, we recorded the tree or shrub species that is was placed in. When possible, these nests were monitored for fate. I defined a fledged nest as one where the new young were observed beyond the rim of the nest.

3. Results

3.1 Birds observed and model selection

I recorded 8848 detections of 6 native bird species and 20 non-native bird species during transect surveys (Table 3), but my study focuses only on the four native forest birds and the three most abundant introduced passerines. When choosing detection functions to model bird densities, I found that detection type was the covariate of the best model for all birds, except the house finch, highlighting the difference in detectability when a bird is seen versus heard. Models and detection functions for each species are shown in Appendix B.

3.2 Bird abundances

I found that abundances of native birds overlapped with those of the introduced birds (Figure 3), with ʻapapane (9665 birds (95% CI: 3972-21958)) and Hawaiʻi ʻamakihi (9339 birds (95% CI:7422-12586)) being the most abundant, followed in decreasing order by red-billed leiothrix (7182 birds (95% CI:4869-10596)), Japanese white-eye (4797 birds (95% CI: 3396-

6777)), Maui ʻalauahio (4395 birds (95% CI:2695-7169)), house finch (3735 birds (95% CI: 2659-5250)), and ʻiʻiwi (2399 birds (95% CI: 1617 – 3561)).

3.3 Native bird density in native versus non-native habitat in Hawaiʻi

Native forest bird densities were highly variable across the eight areas chosen as comparison sites (Figure 4), but most often, densities were lower in the KFR than at native sites. For all species, my results show no significant differences from those found in exotic forest by Foster (2005). Maui ʻalauahio occurred at significantly lower density in the KFR than in the two native sites on Maui and did not occur in sites on other islands. ʻIʻiwi densities in the KFR were lower than in four native sites, and higher than in one site, and showed no difference with one site. For ʻamakihi, densities in the KFR were lower than in three native sites, but significantly higher than in two others. Confidence intervals were not available for ʻamakihi in Waikamoi. ʻApapane densities in the KFR were lower than in three native sites, and showed no difference from three other native sites.

3.4 Distribution of birds and plants across the Kula Forest Reserve

Distribution maps for the birds show variable and heterogeneous patterns (Fig. 5). Hawaiʻi ʻamakihi displayed the most homogenous and widespread distribution, and the other three native species displayed their highest densities in the forested habitat. All species show a decline in abundance approaching the upper limit of the reserve, where vegetation becomes scarce. ʻApapane and ʻiʻiwi show a patch of high density in the middle of the forest, whereas Maui ʻalauahio displays slightly lower densities in this same patch. Red-billed leiothrix also occurs at lower densities in the middle of the forest. One patch, at the northeastern edge of the

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forest overlapping with the burned woodland, appears to support relatively high densities of all species.

Maps of plant distributions show that each plant species typically dominated a portion of the reserve, but that no single species was present throughout the entire area (Fig. 6 and 7). Native plants were mostly restricted to the scrub habitat, and the two native trees, koa and 'ohia, are rare in the reserve, and do not occur in the forest where the non-native trees dominated. Monterey pine and cluster pine dominated the burned woodland and were the two non-native plants that occurred most often in the scrub. These species are displaying vigorous regrowth after the fire of 2007, but have not yet matured into tall trees. 'akala, the native raspberry, was the native plant the occurred most often in the forest habitat. Plant compositions differed significantly between the three habitat types (Permanova, $p < 0.05$) (Fig. 8). Native plant species were more abundant in the scrub than in the forest, and the reverse was true of non-native plants.

3.5 Bird – habitat associations

Two native bird species showed a significant difference in density across habitat structures (Fig. 9). 'I'iwi densities averaged 20 times higher in closed-canopy forest compared to the scrub habitat, where only scattered trees occur, and Maui 'alauahio densities averaged 30 times higher in forest than in the scrub. 'Apapane and 'amakihi showed no significant differences in density across habitat structures.

All native birds showed significant negative correlations with native shrubs, and significant positive correlations with non-native trees and shrubs (Table 5). Native tree occurrence was too low to include in analyses. The introduced red-billed leiothrix showed similar patterns, and Japanese white-eye showed negative associations with trees and native

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shrubs, but positive associations with non-native shrubs. House finch showed negative associations with all shrubs, but positive associations with trees.

Indicator species analyses results were different for each species (Table 4). For Maui 'alauahio, significant indicators of high density were Monterey cypress, eucalyptus, and cape wattle, and low densities were indicated by cluster pine, black wattle, firetree, pukiawe, ohelo, and banana poka. For 'i'iwi, redwood was a significant indicator of high density, and black wattle and banana poka were significant indicators of low density. For 'apapane, mysore raspberry indicated high density and firetree and pukiawe indicated low density. No significant indicators emerged for the most generalist species, Hawai'i 'amakihi. For Japanese white-eyes, black wattle and banana poka indicated high density, and tropical ash and Monterey cypress indicated low density. For red-billed leiothrix, eucalyptus and 'akala were indicators of high density and redwood was an indicator of low density. No plants emerged as indicators of high density for house finches, but cluster pine, firetree, and pukiawe indicated low density.

3.6 Habitat selection of Maui 'alauahio in non-native forest

I recorded 745 observations of 46 individually marked Maui 'alauahio foraging on 13 different trees and shrubs (Table 6). The three plants species used most often for foraging were cape wattle, eucalyptus, and tropical ash, with the total number of observations for each being 203, 122, and 101, respectively. Eucalyptus and tropical ash were used in proportion to their availability, yet cape wattle was used slightly more than I expected given availability, denoting preference (Johnson 1980). Western red cedar and black wattle were also preferred, and Monterey cypress, firetree, and mysore raspberry were used less than expected, or avoided. Redwood was preferred in Plot C, but avoided in Plot B. Maui 'alauahio used every tree and shrub species available in each plot, except in one case where the birds were not observed using

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any firetree available in Plot C. Birds showed a slight avoidance of firetree in Plot B as well. Other species were used in proportion to their availability.

Of the 49 active Maui ʻalauahio nests that I found in the KFR, 19 successfully fledged young, 17 failed, and I was unable to confirm the fate of 13. Nests were most often found in Monterey cypress (14), followed in decreasing order by Monterey pine (9), eucalyptus (8), blackwood acacia (4), redwood (4), tropical ash (3), firetree (2), black wattle (2), cluster pine (2), and tsugi pine (1). No nests were found in cape wattle or mysore raspberry. Sample sizes were too low to draw inference about nest success per species, but notable patterns were found in black wattle, where all nests failed, and in blackwood acacia, where all nests successfully fledged young.

4. Discussion

4.1 Non-native trees provide habitat for native birds

Over 25,000 native Hawaiian forest birds occupy the Kula Forest Reserve, despite it being dominated by non-native plants. Studies have shown that native Hawaiian plants typically occur at low abundances, or are unable to recruit in non-native forests in Hawaiʻi (Mascaro et al. 2008; Ostertag et al. 2008; Mascaro 2011). Even with the absence of native plants, these novel forests have been shown to maintain a list of valuable ecosystem functions that includes providing aboveground biomass, nutrient cycling, and watershed protection, and they often contain more plant diversity than the native Hawaiian forests (Ewel & Putz 2004; Mascaro et al. 2012). My study shows that these novel forests can potentially provide native bird habitat as well.

Due to niche partitioning, different species are adapted to different habitat structures, and this structure is often more important than floristics (Grinnell 1917; MacArthur & MacArthur

1961; Lindenmayer et al. 2003a). For example, Botteri's sparrow (*Peucaea botteri*) has adapted to grasslands, and displayed no reduction in reproductive success when nesting among non-native grasses (Jones & Bock 2005), the federally endangered southwest willow flycatcher (*Empidonax traillii extimus*), which is adapted to riparian shrubs, will nest in non-native tamarisk (Paxton et al. 2013b), and even Swainson's warbler (*Limnothlypis swainsonii*), which was originally thought to be a canebrake specialist, is now expanding its breeding range because pine plantations offer the appropriately structured habitat (Graves 2015). In Hawai'i, Baker and Baker (2000) documented Maui 'alauahio nesting in non-native trees, and I found the same in my study. Despite the non-native origins of the plants in the KFR, these trees and shrubs collectively provide the appropriate structure and ecological functions that the native Hawaiian forest birds need to persist.

Forest bird species are also known to reoccupy forests that were once cleared, and then reforested (Lack 1933) , even if the reforestation occurs with non-native trees (Lindenmayer et al. 2003a; De la Hera et al. 2013). This is precisely what occurred in the KFR, as the forest was cleared historically, and then reforested with non-native trees in the early 1900s (Woodcock 2003). The source of the birds that repopulated the area is currently unknown, and I argue this question warrants research. Regardless, it is clear that the native birds are responding positively to the presence of trees, especially the more specialized species, Maui 'alauahio, and 'i'iwi. The simple presence of forest is valuable to the birds, and therefore valuable to their conservation.

4.2 Densities in KFR and native habitat

With a few exceptions, the native birds occurred at lower densities in the KFR than in native forests elsewhere in Hawai'i. A major caveat to this finding is that the KFR densities that I used to compare across sites were pooled across all habitats, including the scrub, where densities

for some species were much lower, skewing the mean. If only densities from the forest in the KFR were compared, the results would have shown fewer differences (fig. 4 and 9), but because scrub habitat was included in some of the other sites in our comparison, I included it in my estimates as well.

Lower densities could suggest that the non-native trees provide lesser-quality habitat than native trees, yet this inference cannot be fully supported with my data because to properly assess the habitat quality of an area, a robust measure of fitness is required (Van Horne 1983; Johnson 2007). The non-native plants of the KFR may create an ecological trap, where despite supporting high abundances of native birds, those birds experience reduced fecundity and survival. This study confirms that at least one species, Maui ʻalauahio, is successfully nesting and reproducing in the non-native trees, and nests of other native species were observed anecdotally. Acquiring a robust measure of fecundity for these species was beyond the scope of this study, so habitat quality could not be inferred. A study comparing the fitness of native birds in KFR and in native habitat at similar elevation would be valuable and informative.

Other factors besides habitat quality and fitness may have influenced bird numbers in the KFR relative to native habitat. For example, firefighters reported finding dead birds after the high- intensity wildfire of 2007 (Mounce et al. 2007), so populations may still be recovering from that fire, or perhaps from some other catastrophic event, such as a hurricane, which island species are particularly prone to (Foster et al. 2004). Some factor unrelated to habitat may be limiting populations as well, such as disease or predators. Models suggest that avian malaria is absent from the KFR because of its elevation above 1500 meters (Atkinson et al. 2014; Fortini et al. 2015), but the birds that live there have never been tested for the pathogen.

4.3 Habitat associations and degree of specialization

As expected, Hawai'i 'amakihi, the most generalist of the native bird species, occurred with the most homogenous distribution, and showed no significant associations with any specific plant or habitat type. By contrast, the insectivorous Maui 'alauahio showed strong patterns of selection for certain habitat conditions. Other studies have also found that insectivores represent the foraging guild most sensitive to habitat structure (Mansor & Sah 2012). Although I calculated stronger associations for some plant species than others, I believe the structure, including the diversity, distribution, and architectural complexity of the habitat, is most important to the birds (Lawton 1987).

The diversity of plants that occur in the KFR has also occurred elsewhere as non-native species, and was used by native birds. In Portugal and Brazil, native birds have been observed using non-native eucalyptus trees (Proença et al. 2010; Brockerhoff et al. 2013). Anecdotally, I observed native Hawaiian birds foraging directly on eucalyptus flowers (Figure 10), confirming observations from Scott et al. (1986). Tropical ash is not as widespread as the other tree species and I could not find direct use by native birds outside of the tree's native range, although native Hawaiian birds are known to persist in ash forests outside of the KFR (Foster 2005). Cape wattle, along with many other Australian wattles, is considered invasive in most of its non-native range (Richardson et al. 2011; Impson et al. 2011), yet in New Zealand, a population of bellbirds, a bird that feeds on nectar like some Hawaiian honeycreepers, was known to persist in a stand of non-native cape wattle for over a hundred years (Lee 2005). Redwood trees have been cultivated elsewhere in the world, but are rarely considered invasive, and I could not find reports of birds using these trees outside of its native range. The deep recesses in the bark of redwood trees provide habitat for many arthropods and snails in the KFR (Figure 11), and this may provide a

food source to the native birds. Beyond foraging substrates, non-native trees in the KFR also offered appropriate nesting structure for native birds like the Maui ‘alauahio.

In an urban park in Mexico, native house finches nested in non-native Monterey cypress trees (Zuria & Rendón-Hernández 2010). On the island of Mauritius, native birds preferred to nest in the non-native tsugi pines, to the extent that restoration efforts for the conservation of the birds include planting more of these non-native pines (Safford & Jones 1998). These plants offer a diverse array of ecosystems functions, and collectively in the KFR, they provide heterogeneous habitat, which birds have been shown to respond positively to (Tews et al. 2004) .

Habitat structure is particularly important to insectivores because it influences arthropod communities (Gardner et al. 1995; Jokimäki et al. 1998). Unfortunately, the arthropod community of the KFR has never been studied, so any discussion of prey base for birds is purely speculative. Some relevant points to consider are 1) the wattles of the KFR are taxonomically similar to the native Koa tree, and therefore may support similar arthropod communities, and 2) Maui ‘alauahio is known to shift the composition of its arthropod prey base in non-native habitat (Foster 2005). Arthropod surveys have been done in multiple sites harboring forest bird habitat on Maui (Peck et al. 2015), and I recommend they also be done in the KFR.

Estimates for ‘apapane produced very large confidence intervals and I believe significant plant associations to be spurious. ‘Apapane are known to travel long distances to find flowering trees, and their occurrence in an area depends on phenology, a metric I did not record (Ralph & Fancy 1995). ‘Apapane and ‘i‘iwi relied on the nectar resources provided by the eucalyptus and the wattles (Fig. 10) (Scott et al. 1986). ‘I‘iwi’s positive association with redwood may be spurious as well, unless perhaps they prefer the tallest canopy in the forest, which the redwoods provide. Associations with specific plant species were inconclusive for these species, yet ‘i‘iwi,

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which is more specialized than other birds, showed a strong preference for forest overall compared to scrub habitat; the same as Maui 'alauahio.

I could not explicitly explain the distribution of Maui 'alauahio within the forest. The highest density of this species is in the southwestern portion of the reserve, at the lowest elevation edge of the forest. Beyond that edge of forest is treeless ranchland. In contrast, 'i'iwi and 'apapane occurred at highest densities in the middle of the forest, relatively far from the edge, a distribution consistent with forest-interior species in other fragmented landscapes (Temple & Cary 1988; Laurance & Yensen 1991). Potential explanations for the distribution of Maui 'alauahio include 1) intolerance for the colder temperatures at higher elevations, 2) variable arthropod abundance, 3) a finer response than we could detect to habitat structure within the forest, as 'alauahio may be influenced by understory plant density (Scott et al. 1986), 3) a negative association with feral pigs that can be restricted from very steep slopes, as was found in Scott et al. (1986), 4) competitive exclusion by non-native birds (Foster 2005; Freed & Cann 2009), or 5) sampling bias because transects were only conducted in a downhill direction, meaning that lower elevation stations were always surveyed later in the morning than upper elevations. Due to the cold-temperatures at the high-elevations, these insectivorous birds may become more active and detectable later in the day, when warmer temperatures facilitate movement of both them and their arthropod prey.

4.4 Habitat selection by Maui 'alauahio

My observations of Maui 'alauahio highlight the different functions each non-native plant species may provide native birds. The wattles, and particularly cape wattle, were used often for foraging, although the black wattle showed a significant negative association with the distribution of 'alauahio. This may be because black wattle occurred more often as monotypic

stands, whereas cape wattle occurred as an understory component of a structurally diverse habitat. Birds in the Western Cape of South Africa occupied thickets of non-native acacias, which are closely related to the wattles of the KFR, but the birds were less common in areas where acacias occurred in more dense stands with reduced plant diversity (Rogers & Chown 2014). I observed that black wattles in the KFR were often thin-stemmed and susceptible to surging undulations during high winds, which created potentially catastrophic conditions for birds attempting to nest there. Both nesting attempts by 'alauahio in black wattle failed. In contrast, blackwood acacia, a congener of black wattle, occurs as a sturdier structure, and all nesting attempts by 'alauahio in this plant successfully fledged young. Likewise, more active nests were found in Monterey cypress than any other tree species, and these trees too had large, sturdy branches and thick clumps of vegetation, which offered both support and cover for the nest. Therefore, both the structure of the stand and the structure of the individual tree may be important characteristics to which birds respond. These examples highlight that the structural characteristics of plants, independent of their taxonomic affinity, may be the features that make non-native plants suitable habitat for native birds

4.4 Conservation implications

Today, less than 10% of Hawai'i's native forest remains undisturbed (Gagné 1988; Pratt & Jacobi 2009). In 2006, The Hawai'i Gap Analysis Project calculated that 446 km² of land on the island of Maui fit their criteria for potential native bird habitat, based on vegetation cover, elevation, and bird observations (Gon et al. 2006; Price et al. 2009). Although only 127 km² (28%) of this area is currently receiving some level of active management for the conservation of forest birds. Another 154 km² (35%), which includes the KFR, is designated for conservation, but is not currently receiving any management (Price et al. 2009). The remaining 165 km² (37%)

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of the potential bird habitat on Maui contains only scattered trees, or is treeless. This area is similar, or even less vegetated than the scrub in the KFR, where I found very low numbers of Maui ʻalauahio and ʻiʻiwi. Therefore, I expect densities of these species to be low or zero in more than one-third of the area designated as potential bird habitat. The ability of the birds to reach much higher densities in the forest highlights value of the trees, and further emphasizes the need for forest restoration.

Considering management within the forest, The US Fish and Wildlife Service has recommended replacing the non-native trees of the KFR with native trees (United States Fish and Wildlife Service 2006), and conservation and maintenance of bird populations has been shown to coincide with other forest management practices as well (Pejchar & Press 2006; Pejchar et al. 2007; Goldstein et al. 2008). Conversion of the forest to native would be a labor and resource-intensive project, although collaborations between conservation managers, state foresters, and the timber industry could potentially benefit all parties involved. Consider the case of ʻakiʻapolaʼau, a federally endangered native Hawaiian honeycreeper that has been shown to use habitat provided by a commercial Koa plantation on the island of Hawaiʻi (Pejchar et al. 2005). The KFR may offer another unique opportunity for conservation management to coincide with industry practices.

Restoring additional habitat that can support native forest birds is a priority for their conservation (United States Fish and Wildlife Service 2006; Flaspohler et al. 2010; VanderWerf 2012; Warren et al. 2015), but increasing connectivity among forested areas should be a conservation goal as well. Many native Hawaiian forest birds suffer from low genetic diversity due to small population sizes and population bottlenecks (Motyka et al. 2012; Mounce et al. 2015), and isolated populations face an increased threat from catastrophes, such as fires (Mounce

et al. 2007) and hurricanes (Foster et al. 2004). Establishing connectivity between these isolated populations would increase the amount available habitat while allowing for gene flow, and would also create a route to facilitate recolonization of newly restored habitat or of areas where populations were reduced or extirpated by catastrophe (Beier & Noss 1998; Root 1998; Tewksbury et al. 2002; Flaspohler et al. 2010). For the native birds in the KFR, 'apapane and 'i'iwi are known to travel long distances to find flowering trees (Ralph & Fancy 1995), while 'amakihi has a high tolerance for non-forest habitats, so these species may not be isolated from other populations on Maui. In contrast, The Maui 'alauahio of KFR may be geographically and genetically isolated from other populations,

Although it has been suggested that 'alauahio's ability to use a broad range of habitats may facilitate its natural dispersal to restored forest (Scott et al. 1986), my data indicate Maui 'alauahio occurs at very low density in scrub habitat, and numbers approach zero with increasing distance from tall trees. This suggests that Maui 'alauahio may be unlikely to travel into the extensive area of treeless scrub that separates the KFR from other forests on Maui, and therefore would be facilitated by increased habitat connectivity or translocations (VanderWerf 2012). Further research is needed to determine the dispersal and migration patterns of the birds.

Novel forests occur elsewhere in Hawai'i as well, but at lower elevations where avian malaria is prevalent (Mascaro et al. 2008). Some native forest birds, such as Hawaii 'amakihi, have shown evidence of repopulating lowland forests due to a resistance to avian malaria (Woodworth et al. 2005; Spiegel et al. 2006; Foster et al. 2007). If Hawai'i's native forest birds continue to increase in numbers at low elevations, my data suggests that they will likely inhabit these novel forests, and non-native trees will further facilitate their conservation.

In a world where habitats void of non-native species are becoming increasingly rare,

identifying conditions that can potentially facilitate the native species is becoming more valuable (Hobbs et al. 2009; Schlaepfer et al. 2011). I argue that an ecosystem-based approach, where the functional diversity of a habitat is more important than the origins of its constituents, is needed to simultaneously deal with the presence of non-native species and the conservation of native species (Lindenmayer et al. 2003b). With current limitations on conservation resources and funding (Restani & Marzluff 2002; Leonard 2008; Luther et al. 2016), the potential value of habitats containing non-native species must be considered (Hobbs et al. 2009; Schlaepfer et al. 2011; Shackelford et al. 2013). I hope this study will help inform the conservation management of Hawai'i's native forest birds and their habitat, and also other habitats worldwide that are being impacted by non-native species.
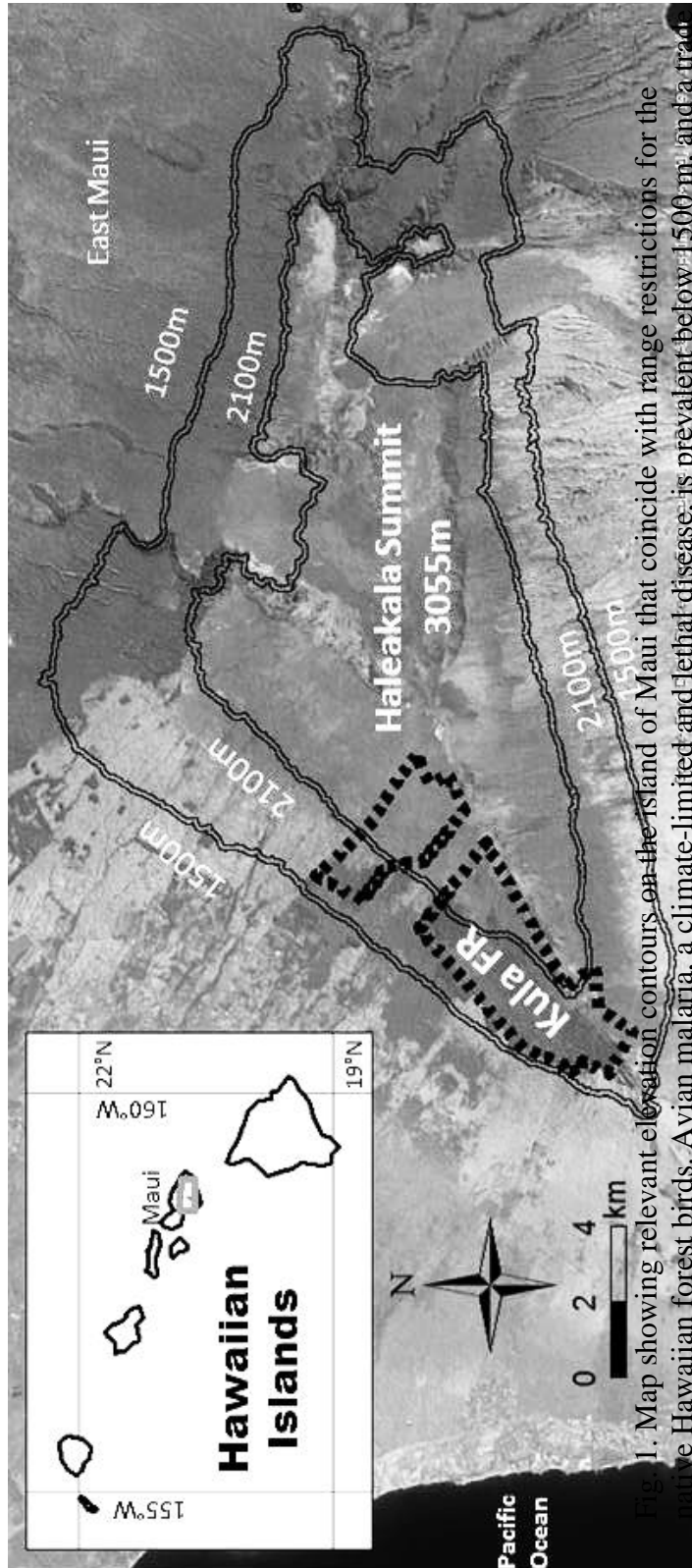
Fig. 1. Map showing relevant elevation contours on the island of Maui that coincide with range restrictions for the native Hawaiian forest birds. Avian malaria, a climate-limited and lethal disease, is prevalent below 1500 m, and a tree wind inversion, which restricts the growth of tall native trees, occurs near 2100 m. Much of the Kula Forest Reserve lies between these elevations, allowing for a forested refuge from disease and occupancy by native forest birds. A lack of disease-free forest is limiting to the native Hawaiian forest birds, highlighting the conservation value of the area.
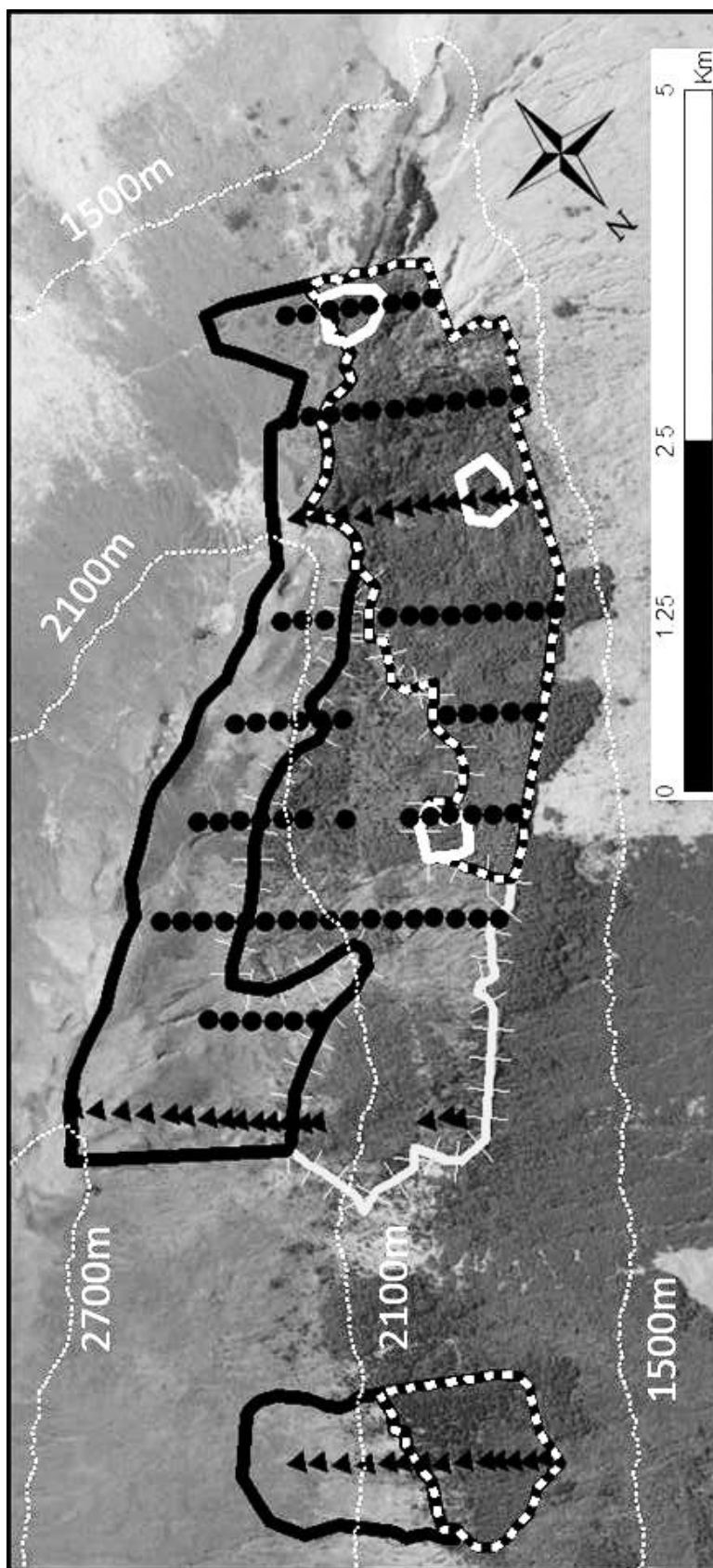
Fig. 2. Map of the study site in the Kula Forest Reserve displaying survey transects (black circles and triangles), which included, and ran parallel to, Hawai'i Forest Bird Survey transects done in 1980 (triangles). Three areas with distinct structures were surveyed: forest (checkered outline), scrub (solid black outline), and burned woodland (gray outline with hashes). Foraging and nesting of Maui 'Alauahio was observed in three plots (outlined in white). Background imagery shows the general distribution of vegetation (darker areas) and contours coincide with rangerestrictions for the native Hawaiian foret birds.
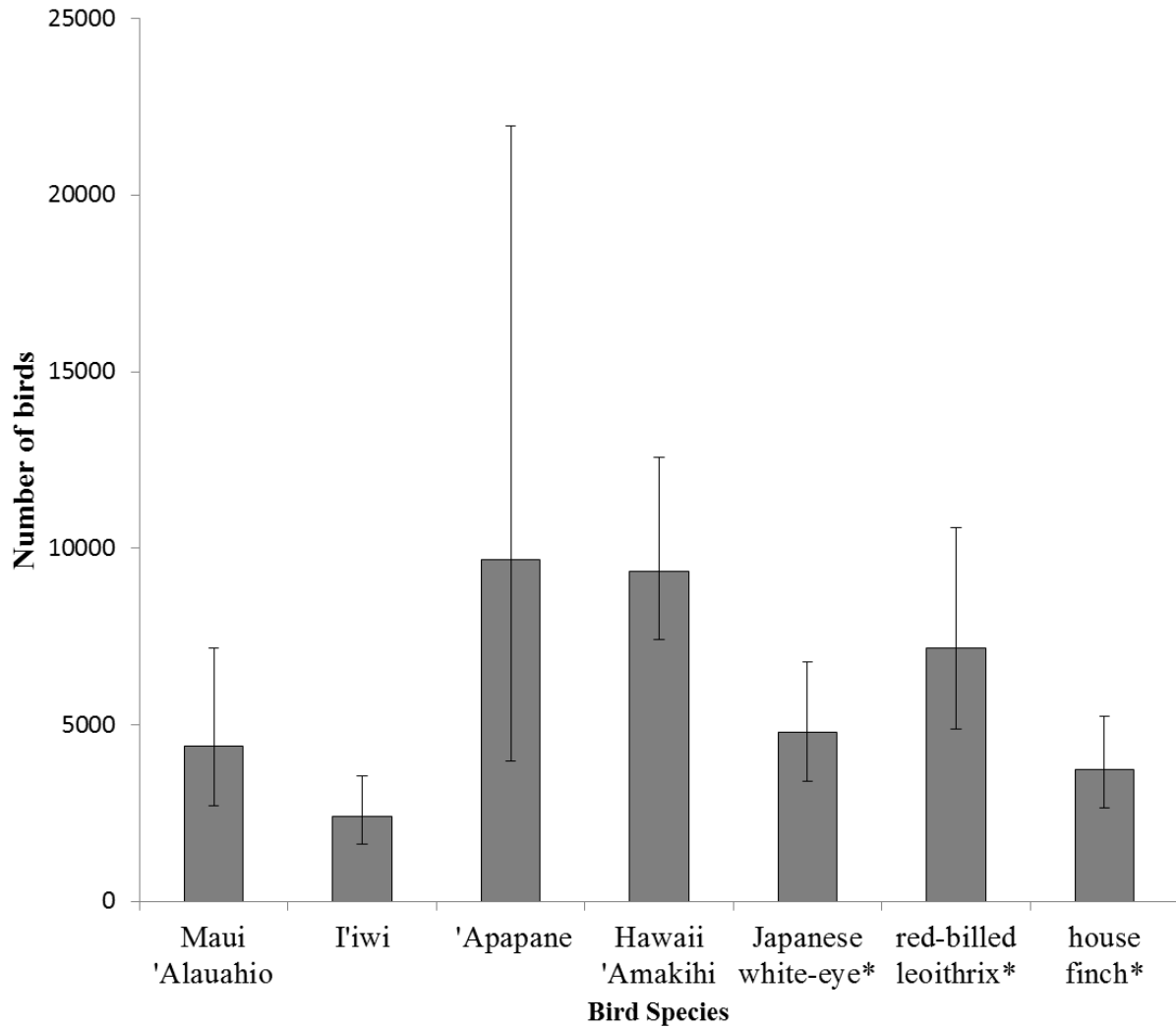
Fig. 3. Bird abundance estimates and 95% confidence intervals for four native birds and three non-native birds(*) in the Kula Forest Reserve, Hawai'i. Collectively, native birds occurred at similar abundances as non-native birds.
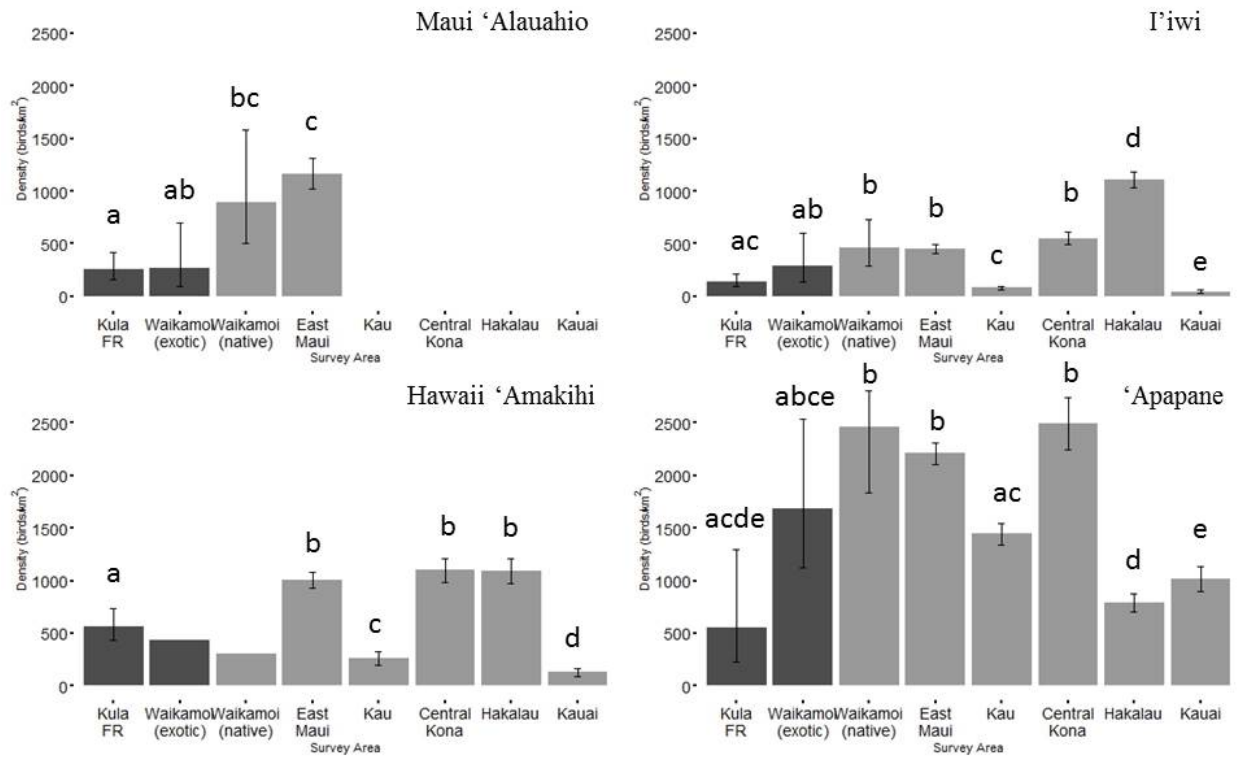
Fig. 4. Native bird densities in the Kula Forest Reserve and in native (light gray) and non-native (dark gray) sites across Hawai'i. Letters over bars convey statistical significance determined by overlapping 95% confidence intervals. In general, densities in the Kula Forest Reserve fell within the range of variability found across other sites in Hawai'i. Data sources are shown in Appendix A.
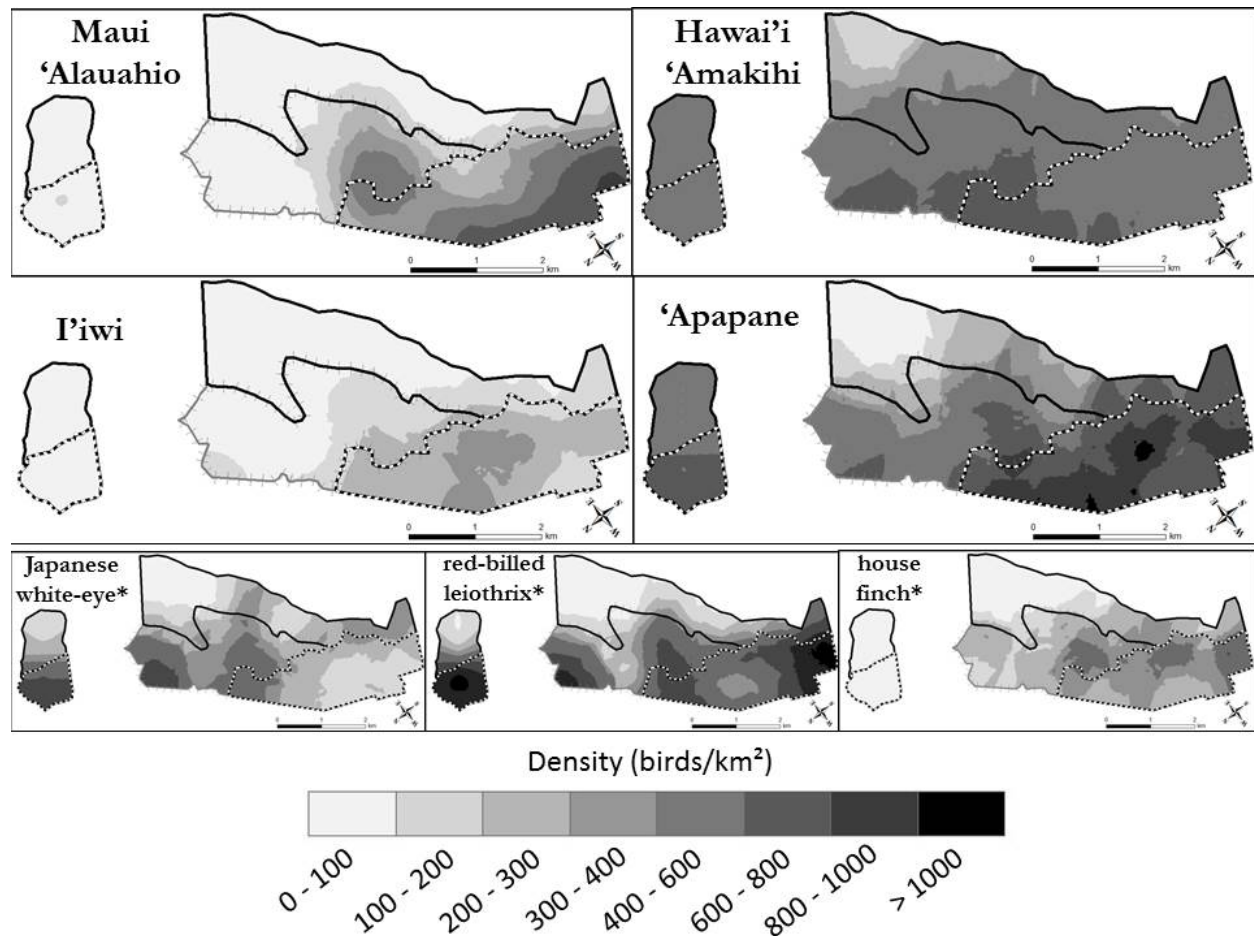
Fig. 5. Maps of the spatial distribution of four native Hawaiian forest birds and three non-native birds (*) relative to different habitat structures in the Kula Forest Reserve, Maui. The scale of shading is consistent for all species. Darker shading represents areas with a higher density of that species, and lighter shading represents lower densities. Three distinct habitat structures occur in the reserve: Closed-canopy forest is outlined with the checkered line, the low-stature scrub is outlined in the solid black line, and the open and variable burned woodland is outlined with a gray hatched line. White shown on the map was not surveyed. Maps display raster output of kriging model that extrapolated data from 123 survey points throughout the study site.
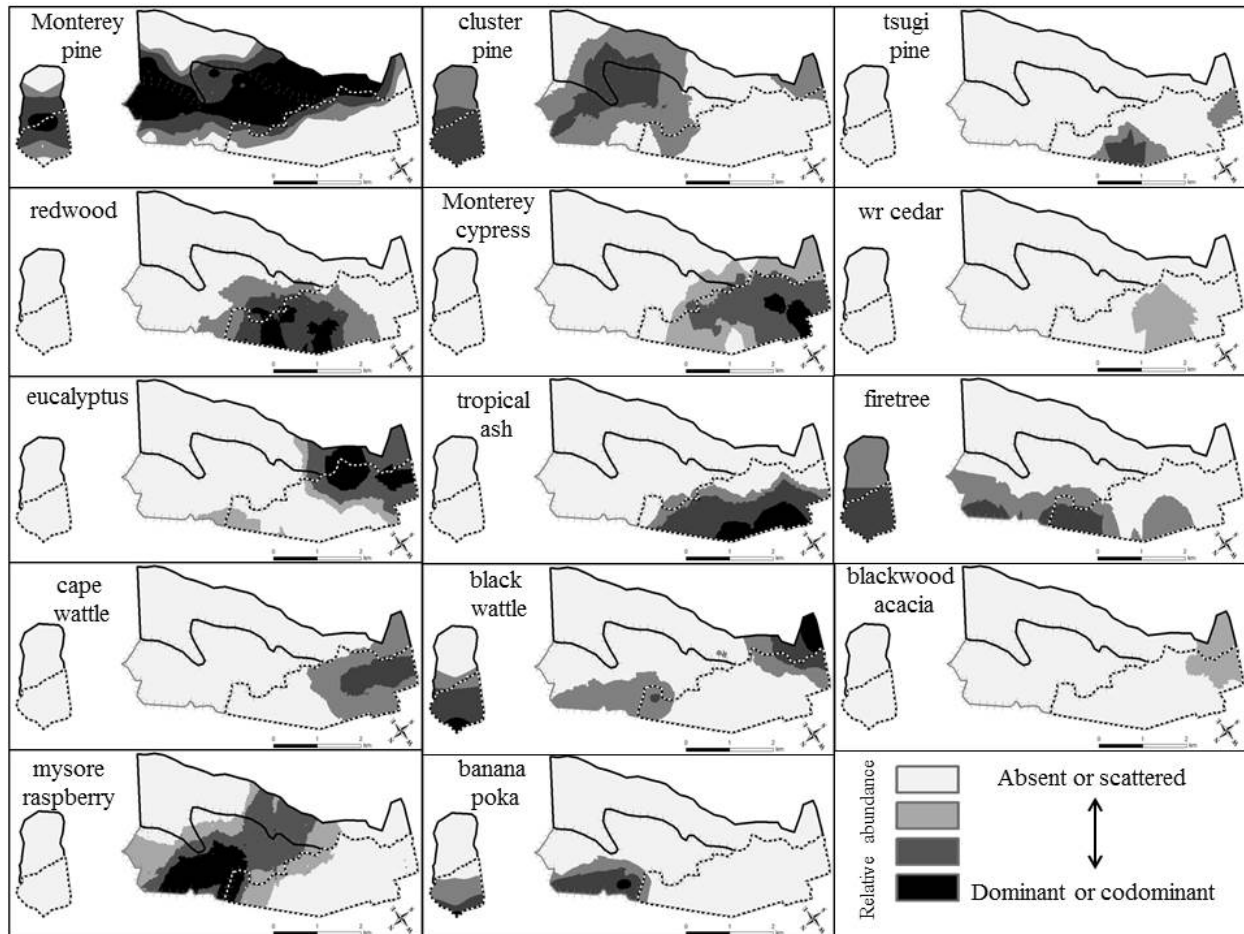
Fig. 6. Maps of the spatial distributions of fourteen non-native plants in the Kula Forest Reserve on Maui. Relative abundance compared to other plant species is indicated by shading with black indicating the plant is dominant or codominant to light gray indicating the plant is absent or very scattered. Plant species are listed in order by the number of survey stations at which they occurred (out of 123 total stations), from most to least. A) Monterey pine (*Pinus radiata*), n = 68 stations, B) mysore raspberry (*Rubus niveus*), n = 54, C) cluster pine (*Pinus pinaster*), n = 45, D) redwood (*Sequoia sempervirens*), n = 36, E) black wattle (*Acacia mearnsii*), n = 32, F) firetree (*Morella faya*), n = 32 G) Monterey cypress (*Cupressus macrocarpa*), n = 29, H) tropical ash (*Fraxinus uhdei*), n = 24, I) cape wattle (*Periserianthes lopantha*), n = 20, J) eucalyptus (*Eucalyptus* spp.) n = 20, K) (banana poka (*Passiflora mollissima*), n = 18, L) tsugi pine (*Cryptomeria japonica*), n = 16, M) western red cedar (*Thuja plicata*), n = 11, N) blackwood acacia (*Acacia melanoxylon*), n = 5. Maps display raster output of kriging model that extrapolated data from 123 survey points throughout the study site.
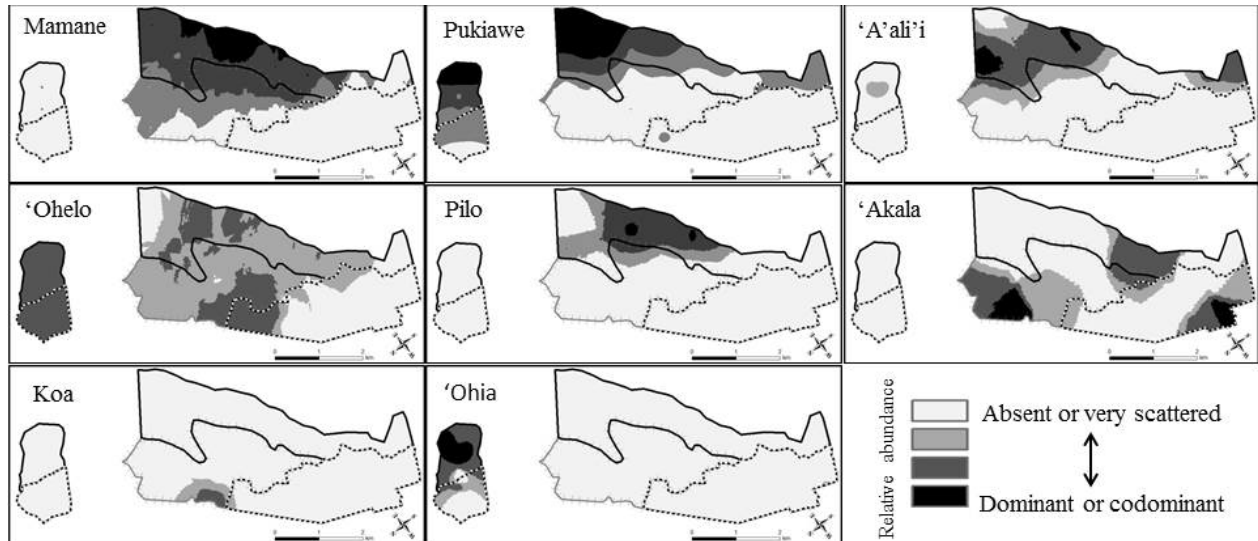
Fig. 7. Maps of the spatial distributions of eight native plants in the Kula Forest Reserve on Maui. Relative abundance compared to other plant species is indicated by shading with black indicating the plant is dominant or codominant to light gray indicating the plant is absent or very scattered. Plant species are listed in order by the number of survey stations at which they occurred (out of 123 total stations), from most to least. A) Mamane (*Sophora chrysophylia*), n = 65 stations B) Pukiawe (*Styphelia tameiameiae*), n = 62, C) 'A'ali'i (*Dodenaea viscosa*), n = 38, D) 'Ohelo (*Vaccinium* spp.) n = 34, E) Pilo (*Coprosma montana)*, n = 33, F) 'Akala (*Rubus hawaiensis*), n = 18, G) Koa (*Acacia koa*), n = 7, H) 'Ohia (*Metrosideros polymorpha*), n = 6. Maps display raster output of kriging model that extrapolated data from 123 survey points throughout the study site.
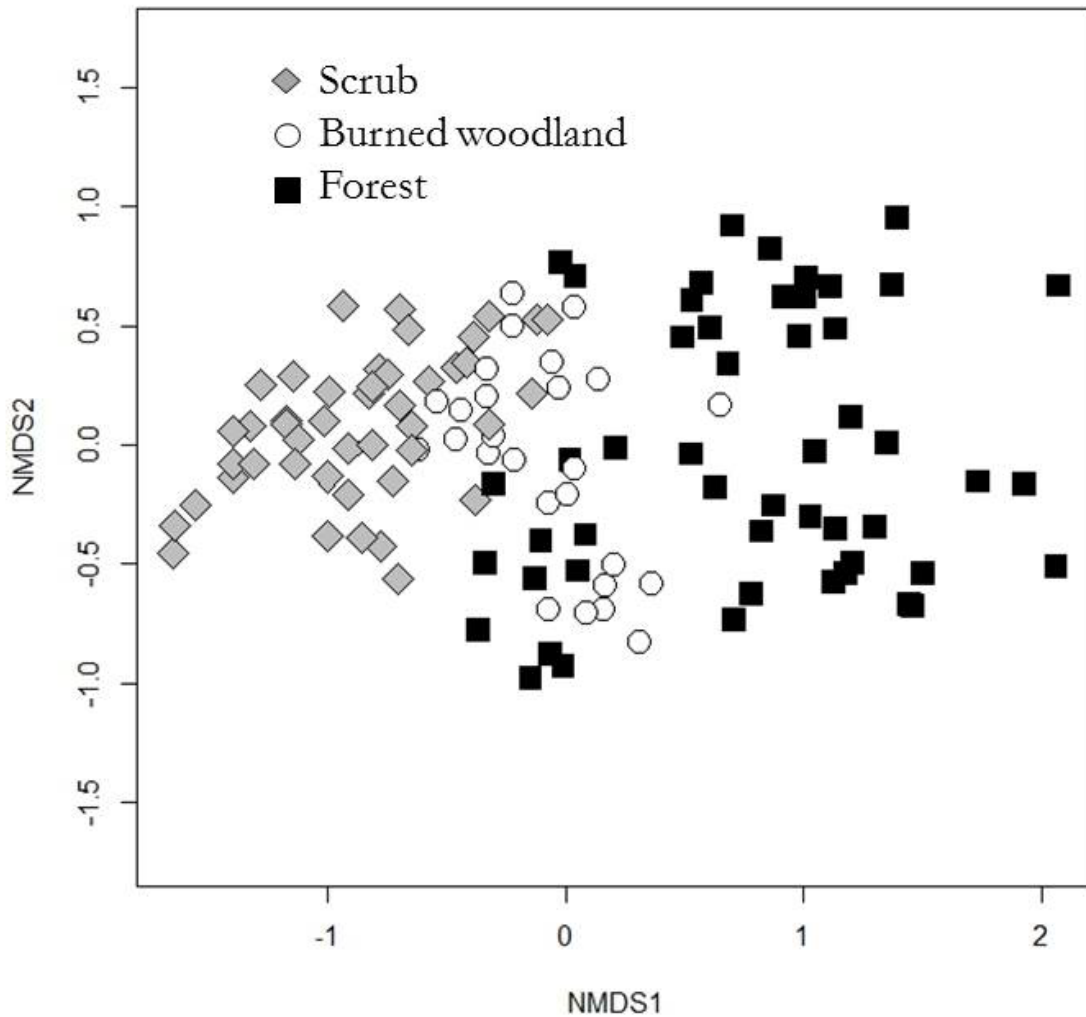
Fig. 8. Plant compositions of 123 survey stations in the Kula Forest Reserve plotted onto NMDS ordination using Bray-Curtis dissimilarity index to determine distances between points. Groups of points and those closer to each other are more similar than those further away. Symbols represent which of three habitat types the point occurs in: gray diamonds display scrub points, white circles display burned woodland points, and black squares display forest points. Permanova analysis shows that differences in plant composition between the three habitat types are significant ($p < 0.001$).
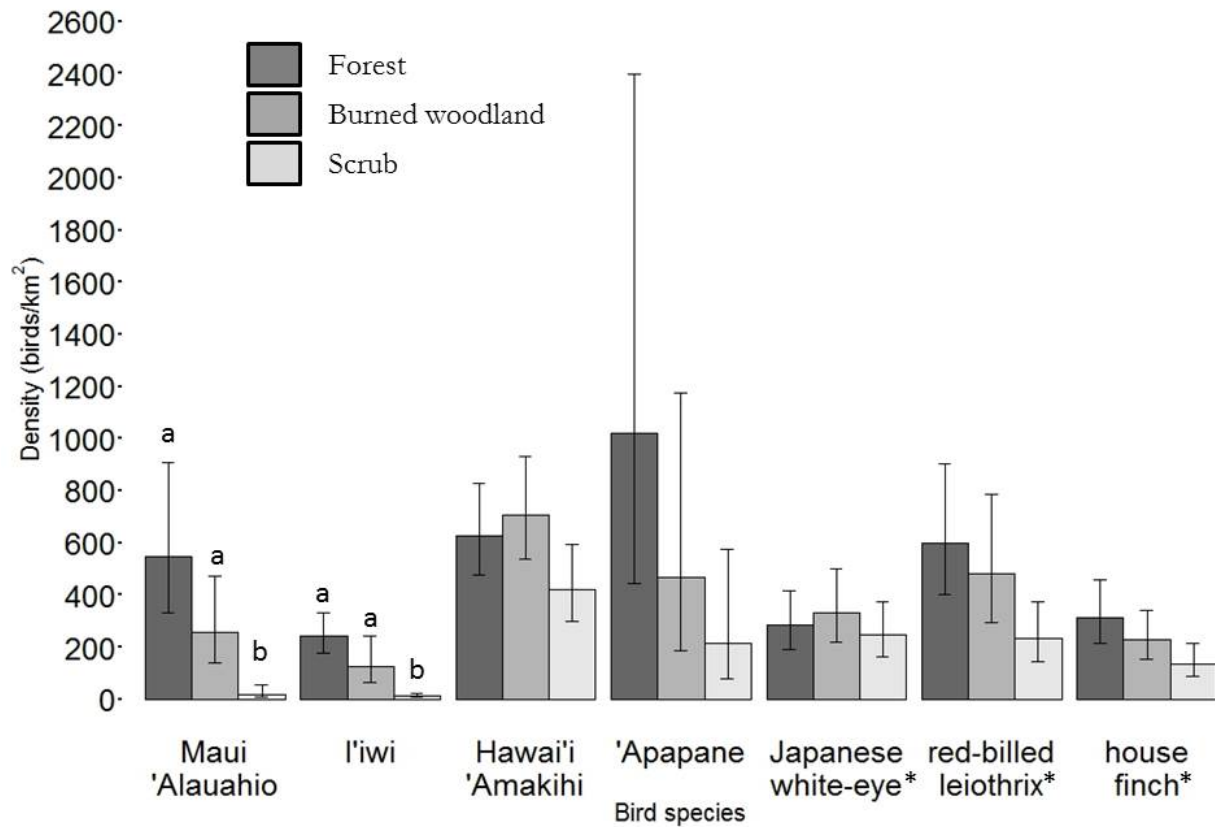
Fig. 9. Densities and 95% confidence intervals for four native Hawaiian forest birds and three non-native birds (*) across three habitat types in the Kula Forest Reserve on Maui. The three habitat types were the closed canopy forest (dark gray bars), the open burned woodland (middle grey bars), and the scrub (light gray bars). Letters over bars convey statistical significance determined by overlapping 95% confidence intervals. Species with no letters showed no significant differences across habitat types, and bird species were not tested against other birds

Fig. 10. Photograph showing ʻapapane (*Himatione sanguinea*), a native Hawaiian forest bird, feeding on the nectar of a non-native eucalyptus flower in the Kula Forest Reserve on Maui. The native nectarivores in the area sequestered food resources from non-native trees.
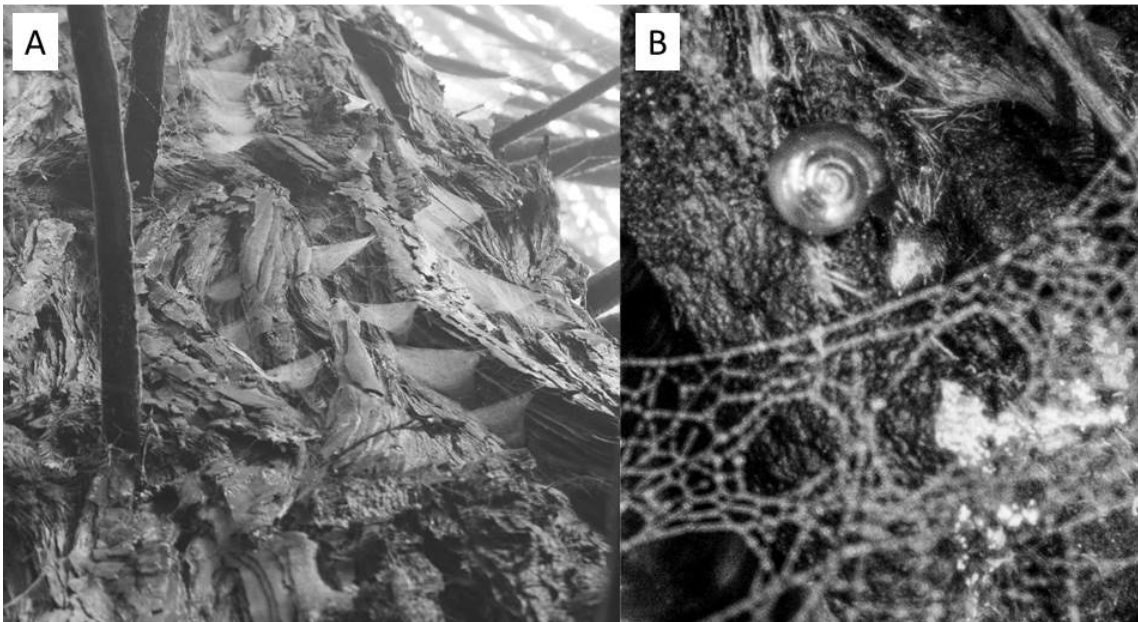
Fig. 11. Photographs showing the deep grooves in the bark of a redwood tree (*Sequoia sempervirens*) in the Kula Forest Reserve on Maui. Although sampling for bird diets has not yet been done in this area, I found evidence of A) arthropods and B) snails, suggesting that food resources for insectivores may be abundant.

Tables

Table 1. Data from the original Hawaiʻi Forest Bird Survey displaying the densities of seven forest bird species in various habitat structures and plant compositions in Hawaiʻi. The koa-ohia habitat was dominated by native Hawaiian trees, whereas the introduced forest was dominated by non-native trees. The treeless area included scrub habitat dominated by low stature shrubs (Scott et al. 1986).

Habitat	Bird density (birds/km² (SE))						
	Maui 'alauahio	ʻiʻiwi	Hawaiʻi ʻamakihi	ʻapapane	red-billed leiothrix	Japanese white-eye	house finch
koa-ohia	110 (32)	82 (12)	143 (12)	328 (23)	100 (7)	555 (37)	103 (34)
introduced trees	141 (34)	24 (11)	139 (15)	111 (20)	100 (13)	325 (38)	209 (33)
treeless	77 (34)	7 (3)	32 (2)	96 (16)	8 (1)	99 (15)	4 (1)

Table 2. Twenty-two trees and shrubs listed in order of their occurrence in the Kula Forest Reserve on Maui.

Common name	Scientific name	Native range	Number of survey stations where plant is present (123 total)	Percentage of total survey stations where plant is present
Monterey pine	*Pinus radiata*	California	68	55%
Mamane	*Sophora chrysophylla*	Hawai'i	65	53%
Pukiawe	*Leptecophylla tameiameiae*	Hawai'i	62	50%
mysore raspberry	*Rubus niveus*	Asia	54	44%
cluster pine	*Pinus pinaster*	Mediterranean	45	37%
A'ali'i	*Dodonaea viscosa*	Hawai'i	38	31%
redwood	*Sequoia sempervirens*	California	36	29%
Ohelo	*Vaccinium sp.*	Hawai'i	34	28%
Pilo	*Coprosma montana*	Hawai'i	33	27%
black wattle	*Acacia mearnsii*	Australia	32	26%
firetree	*Morella faya*	Macronesia/Portugal	32	26%
Monterey cypress	*Cupressus macrocarpa*	California	29	24%
tropical ash	*Fraxinus uhdei*	Mexico	24	20%
Eucalyptus	*Eucalyptus* spp.	Australia	20	16%
cape wattle	*Paraserianthes lophantha*	Australia	20	16%
banana poka	*Passiflora tarminiana*	South America	18	15%
Akala	*Rubus hawaiensis*	Hawai'i	18	15%
tsugi pine	*Cryptomeria japonica*	Japan	16	13%
western red cedar	*Thuja plicata*	Western North America	11	9%
Koa	*Acacia koa*	Hawai'i	7	6%
Ohia	*Metrosideros polymorpha*	Hawai'i	6	5%
blackwood acacia	*Acacia melanoxylon*	Australia	5	4%

Table 3. Bird species detected in the Kula Forest Reserve on Maui during surveys conducted in 2013-2014. A grid of 123 points were sampled five times each to determine the status and ecology of the bird populations. I analyzed the seven most abundant bird species, which includes four native Hawaiian forest birds.

Common name	Scientific name	Number of detections
Hawaii 'Amakihi*	*Chlorodrepanis virens*	1720
red-billed leoithrix	*Leiothrix lutea*	1367
'Apapane*	*Himatione sanguinea*	1262
Japanese white-eye	*Zosterops japonicus*	879
house finch	*Haemorhous mexicanus*	852
I'iwi*	*Drepanis coccinea*	728
Maui 'Alauahio*	*Paroreomyza montana*	601
northern cardinal	*Cardinalis cardinalis*	288
Japanese bush-warbler	*Horornis diphone*	237
northen mockingbird	*Mimus polyglottos*	173
ring-necked pheasant	*Phasianus colchicus*	167
sky lark	*Alauda arvensis*	102
chukar	*Alectoris chukar*	60
mourning dove	*Zenaida macroura*	25
spotted dove	*Spilopelia chinensis*	16
California quail	*Callipepla californica*	15
melodious laughing thrush	*Garrulax canorus*	9
gambel's quail	*Callipepia gambelii*	6
black francolin	*Francolinus francolinus*	4
gray francolin	*Francolinus pondicerianus*	4
Pacific golden plover*	*Pluvialis fulva*	3
short-eared owl*	*Asio flammeus sandwichensis*	3
zebra dove	*Geopelia striata*	3
common myna	*Acridotheres tristis*	2
rock dove	*Colomba livia*	2
scaly breasted munia	*Lonchura atricapilia*	1

* native to Hawaii

Table 4. Indicator species values for 22 trees and shrubs occurring in forest of the Kula Forest Reserve. For each of the seven bird species analyzed, the 52 survey points were ranked by the birds density at each point, and then categorized in to a high, average, or low density group. Significant associations (p < 0.05) are shaded in gray.

Plants	Maui 'Alauahio density group	IV	p	'I'iwi density group	IV	p	'Apapane density group	IV	p	Hawai'i 'Amakihi density group	IV	p	Japanese white-eye density group	IV	p	red-billed leiothrix density group	IV	p	house finch density group	IV	p
Native trees																					
Koa	low	3.2	0.7796	average	11.1	0.3193	low	3.6	0.6687	average	3.2	0.8698	low	3	0.8332	low	3.4	0.5477	average	3	1
'Ohia	low	3.9	1	low	4.6	0.5439	average	13.3	0.0828	low	13.3	0.077	high	8.4	0.5055	high	11.1	0.3133	low	5.5	0.5237
Native shrubs																					
'A'ali'i	low	5.6	1	low	6.2	0.2967	low	5.9	0.6067	low	6.7	0.2925	average	4.5	1	average	5.9	0.6529	low	7.1	0.2637
'Akala	average	12.4	0.3817	average	20	0.0692	low	10.2	0.5767	high	12.1	0.4017	high	9.5	0.6915	high	25	0.027	high	13.7	0.3041
'Ohelo	low	25.5	0.019	average	10.2	0.5971	low	13.5	0.3185	low	9.1	0.6813	average	12.1	0.4269	average	7.2	0.831	low	18	0.0712
Pilo	low	8.9	0.2811	low	10.5	0.5815	low	7.1	0.2609	average	7.1	0.5785	high	11.3	0.2258	high	4	0.9174	low	6.3	0.6833
Pukiawe	low	35.3	0.0078	average	14.8	0.2609	low	29.6	0.0298	low	23.9	0.113	high	16.2	0.4887	average	21.8	0.1644	low	28.3	0.0386
Mamane	average	7.8	0.7546	average	12.6	0.2973	low	9.5	0.5869	low	19.1	0.0892	average	9.5	0.6417	high	9.7	0.5317	average	12	0.3377
Non-native trees																					
Monterey cypress	high	37.2	0.057	average	23.3	0.757	average	31	0.2142	low	36.5	0.073	low	42.6	0.0286	high	25.6	0.5645	high	29.1	0.3149
Monterey pine	low	22.4	0.2426	low	17.1	0.6005	low	27	0.1008	average	13	0.9212	average	27.8	0.1118	average	33.9	0.021	low	21.6	0.2881
cluster pine	low	38.7	0.002	low	18.9	0.2298	low	10.4	0.862	high	22.8	0.1124	high	23.4	0.1284	average	15.1	0.4667	low	29.5	0.0324
redwood	average	18.3	0.7744	high	34	0.0458	low	20.8	0.5631	high	16.7	0.9	low	25	0.3095	low	49.9	0.0012	high	16.1	0.932
tsugi pine	high	16.9	0.5567	average	13.7	0.8278	low	15.3	0.6989	high	15.1	0.7181	low	24	0.2052	low	11.7	0.9606	average	26.7	0.106
western red cedar	average	17.2	0.2647	high	13.5	0.5345	high	12.2	0.6381	low	18.4	0.2254	low	10.7	0.7774	low	14.3	0.4449	average	13	0.5657
tropical ash	average	21.8	0.4693	high	24.4	0.3055	low	24.4	0.3121	high	21.8	0.4863	low	35	0.0492	low	29.1	0.1146	high	20.7	0.5779
eucalyptus	high	37	0.0098	high	15.5	0.7243	high	16.1	0.6551	average	21.7	0.2659	average	28.5	0.0884	high	30.2	0.043	high	27.1	0.1018
Non-native shrubs																					
blackwood acacia	average	6	0.764	low	9.6	0.3073	average	10.5	0.2667	high	7.2	0.5409	average	18.2	0.0666	average	9.5	0.2609	low	6.1	0.7251
black wattle	low	31.2	0.0206	low	34.1	0.0098	average	15.1	0.6385	average	16	0.5383	high	42.8	0.0042	high	22.6	0.1564	low	25.8	0.0834
cape wattle	high	55.5	0.0002	high	14.3	0.961	high	27.3	0.1346	average	15.7	0.875	average	23	0.3345	high	23.3	0.2751	high	20.2	0.4897
firetree	low	53.4	0.0006	low	24.2	0.3009	low	33.8	0.0412	low	15.6	0.9566	high	26.4	0.2262	low	25.6	0.2342	low	40.2	0.0078
mysore raspberry	high	28.5	0.0958	average	13	0.9244	high	36.9	0.0148	high	11.7	0.9816	average	13.8	0.8892	high	23	0.2468	high	23.3	0.2384
banana poka	low	36.7	0.001	low	32.9	0.0034	average	11.2	0.5085	high	12.7	0.4027	high	44.8	0.001	high	15.6	0.238	low	20.8	0.0664

Table 5. Poisson generalized linear models showing associations of native and non-native(*) birds with native and non-native trees and shrubs. Coefficient estimates display the strength of a positive or negative association, and the p-value determines statistical significance ($p < 0.05$). Native trees were not included in analyses because they occurred too infrequently in the study site.

Species	Variable	Estimate	Std. Error	z value	p
Maui 'Alauahio					
	non-native trees	0.83136	0.03248	25.59	<2e-16
	native shrubs	-1.5736	0.03247	-48.46	<2e-16
	non-native shrubs	0.76632	0.04091	18.73	<2e-16
I'iwi					
	non-native trees	2.27199	0.04776	47.567	< 2e-16
	native shrubs	-0.1906	0.04346	-4.387	1.15E-05
	non-native shrubs	1.15307	0.05871	19.639	< 2e-16
'Apapane					
	non-native trees	0.83707	0.02245	37.29	<2e-16
	native shrubs	-0.9805	0.02055	-47.71	<2e-16
	non-native shrubs	0.78483	0.02821	27.82	<2e-16
Hawai'i 'Amakihi					
	non-native trees	0.16085	0.02462	6.533	6.43E-11
	native shrubs	-0.6569	0.0204	-32.195	< 2e-16
	non-native shrubs	0.14553	0.03178	4.579	4.66E-06
red-billed leiothrix*					
	non-native trees	-0.1399	0.02545	-5.496	3.88E-08
	native shrubs	-1.4579	0.02351	-62.02	< 2e-16
	non-native shrubs	0.82464	0.03212	25.673	< 2e-16
Japanese white-eye*					
	non-native trees	0.54885	0.03782	14.512	< 2e-16
	native shrubs	-1.3639	0.03493	-39.044	< 2e-16
	non-native shrubs	-0.1626	0.04936	-3.293	0.00099
house finch*					
	non-native trees	0.54885	0.03782	14.512	< 2e-16
	native shrubs	-1.3639	0.03493	-39.044	< 2e-16
	non-native shrubs	-0.1626	0.04936	-3.293	0.00099

Table 6. Non-native plants used by a native Hawaiian forest bird, Maui Alauahio (*Paroreomyza montana*), in three plots in the Kula Forest Reserve on Maui. Comparing the ranks of use and availability produces a "difference in rank." A positive difference in rank means the plant was used more often than expected based on availability, or preference. A negative difference in rank denotes general avoidance of that plant.

Plot A

	Plants		Bird detections (n = 475)				Nests (n = 29)			
Species	Percent of available foraging substrate in plot	Rank of availability	Foraging observations per plant	Percent of total detections in plot	Rank of use	Difference in rank	Fledged	Failed	Fate unknown	Total
Monterey cypress	30%	1	66	14%	3	-2	7	4	3	14
eucalyptus	27%	2	122	26%	2	0	2	4	2	8
cape wattle	20%	3	160	34%	1	2				0
black wattle	11%	4	66	14%	3	1	0	2	0	2
blackwood acacia	7%	5	51	11%	5	0	4	0	0	4
sugi pine	3%	6	8	2%	6	0	0	0	1	1
cluster pine	1%	7	1	>1%	7	0				0
Monterey pine	1%	7	1	>1%	7	0				0

Plot B

	Plants		Bird detections (n = 216)				Nests (n = 8)			
Species	Percent of available foraging substrate in plot	Rank of availability	Foraging observations per plant	Percent of total detections in plot	Rank of use	Difference in rank	Fledged	Failed	Fate unknown	Total
tropical ash	36%	1	101	47%	1	0	1	1	1	3
redwood	23%	2	26	12%	4	-2	2	1	0	3
cape wattle	19%	3	43	20%	2	1				0
firetree	11%	4	17	8%	5	-1	0	1	1	2
western red cedar	10%	5	28	13%	3	2				0
Monterey pine	1%	6	1	0%	6	0				0

Plot C

	Plants		Bird detections (n = 54)				Nests (n = 14)			
Species	Percent of available foraging substrate in plot	Rank of availability	Foraging observations per plant	Percent of total detections in plot	Rank of use	Difference in rank	Fledged	Failed	Fate unknown	Total
Monterey pine	52%	1	33	61%	1	0	3	2	4	9
mysore raspberry	17%	2	2	4%	5	-3				0
cluster pine	13%	3	7	13%	3	0	0	1	1	2
redwood	8%	4	9	17%	2	2	0	1	0	1
firetree	6%	5	0	0%	6	-1				0
black wattle	4%	6	3	6%	4	2				0

CHAPTER 3. RECOMMENDATIONS FOR FUTURE RESEARCH

Being a curious naturalist can be a blessing and a curse in regards to ecological research. While keen observation skills and a solid understanding of theoretical bases can facilitate good data collection, ecology offers many challenges in the form of interesting distractions. While observing the ecology of the birds in the KFR, many questions came to mind that were not directly in line with my initial inquiries. Some of them I pursued with further data collection, and some of them I did not. Here is a review of some patterns I observed that I believe warrant future research:

1) Reproduction and survival of Maui ʻalauahio in native vs. non-native forest. Habitat quality and sink dynamics.

- For a real measure of habitat quality, an estimate of fitness is required. Reproductive rate can be obtained from a study of nest success, and survival can be measured with continued resighting of marked birds.

2) Arthropod sampling in the Kula Forest Reserve

- Food availability is a major contributor to habitat quality. The KFR should be sampled following methods carried out in other protected areas in Hawaiʻi, but also new developing techniques, such as pyrosequencing, can be used to investigate bird diets.

3) Population genetics in a territorial cooperative breeder: Family dynamics of Maui ʻalauahio and implications for translocations and evolved disease resistance

- Large family groups of Maui ʻalauahio, including aunts, uncles, and cousins, may dominate large patches of habitat, and may be breeding within these groups. This may have relevant implications for the genetic diversity of the population. Birds can be captured, then marked and bled to identify individuals and measure relatedness to other birds. Monitoring marked birds and nests will yield information on these social dynamics.

- The origins of the Kula population of Maui ʻalauahio are also unclear. A study of mitochondrial DNA from birds across the island could provide great insight into the multiple isolated populations that the species maintains.

4) Mosquito-borne disease dynamics in the Kula Forest Reserve

- Due to the presence of the birds, and species distribution models depicting the range of mosquitos and avian disease, I suspect that little to no avian disease persists in the KFR. Blood drawn from captured birds can be tested across variable weather patterns, and a more precise estimate of the "malaria line" could be obtained.

5) Native bird response to habitat restoration: experiments in converting a non-native forest to native.

- Research on small scale conversion of non-native forest to native can provide insight into potential larger scale operations. Experiments with various forestry applications and the continued monitoring of my point transects could capture trends that may correlate with the conversion of habitats.

Appendix A. Years covered by estimate and data sources for Figure 4

Site	Maui 'Alauahio	Iiwi	'Apapane	'Amakihi
Waiakmoi (exotic)	2002-2004 (Foster 2005)	2002-2004 (Foster 2005)	2002-2004 (Foster 2005)	2002-2004 (Foster 2005)
Waikamoi (native)	2002-2004 (Foster 2005)	2002-2004 (Foster 2005)	2002-2004 (Foster 2005)	2002-2004 (Foster 2005)
East Maui	1997-2001 (Camp et al. 2009)	2011 and 2012 (Paxton et al.2013)	1997-2001 (Camp et al. 2009)	1997-2001 (Camp et al. 2009)
Kau	N/A	2004, 2008, 2010 (Paxton et al.2013)	2005 (Camp et al. 2009)	2005 (Camp et al. 2009)
Central Kona	N/A	2009 and 2010 (Paxton et al.2013)	2001 (Camp et al. 2009)	2001 (Camp et al. 2009)
Hakalau	N/A	2012 (Camp et al. 2016, Closed-canopy)	2012 (Camp et al. 2016, Closed-canopy)	2012 (Camp et al. 2016, Closed-canopy)
Kauai	N/A	2012 (Paxton et al.2013)	2008 (Camp et al. 2009)	2008 (Camp et al. 2009)

Appendix B

Appendix B. Models tested to determine detection functions for seven bird species.

Maui 'alauahio

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Detect*	4	0.00	3406.25	27.96	280.35	224.38	350.27	0.11
Detect24	3	10.83	3417.08	31.98	214.39	172.72	266.12	0.11
Observer 2	4	36.51	3442.76	31.37	222.84	179.73	276.28	0.11
Observer	5	38.48	3444.73	31.33	223.35	180.14	276.94	0.11
Detect14	3	38.66	3444.91	30.18	240.63	193.66	299.00	0.11
Cloud	4	46.92	3453.17	31.55	220.18	177.65	272.89	0.11
Gust	4	47.51	3453.76	30.52	235.42	189.80	292.01	0.11
Habitat	4	47.52	3453.78	31.89	215.55	173.91	267.16	0.11
Key	2	48.18	3454.43	31.72	217.82	172.66	274.79	0.12
Time	4	49.47	3455.73	31.36	222.97	179.91	276.32	0.11
Survey Period 15	5	51.49	3457.74	30.99	228.31	184.11	283.13	0.11
Survey Period	6	53.09	3459.35	30.63	233.59	188.32	289.76	0.11
Wind	4	53.89	3460.14	32.68	205.30	165.80	254.20	0.11

'apapane

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Detect+Habitat+Observer	8	0.00	5983.26	25.55	602.51	502.61	722.27	0.09
Detect+Habitat	6	2.78	5986.04	25.11	623.77	520.74	747.18	0.09
Detect*	4	15.47	5998.73	25.11	623.73	522.52	744.53	0.09
Detect24	3	25.50	6008.75	24.40	660.52	554.04	787.48	0.09
Detect14	3	173.44	6156.70	26.46	561.65	472.73	667.30	0.09
Habitat	4	198.36	6181.62	28.63	479.80	407.71	564.64	0.08
Observer 2	4	198.48	6181.73	27.25	529.64	449.83	623.61	0.08
Observer	5	198.57	6181.83	27.10	535.27	454.24	630.76	0.08
Key	2	203.70	6186.96	24.15	674.31	462.19	983.77	0.19

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Time	4	204.07	6187.33	28.76	475.32	403.92	559.33	0.08
Wind	4	205.74	6189.00	27.62	515.55	438.19	606.56	0.08
Cloud	4	209.86	6193.12	29.24	460.08	391.26	541.02	0.08
Survey Period 15	5	217.17	6200.43	29.09	464.75	395.01	546.80	0.08
Survey Period	6	218.70	6201.96	28.97	468.60	398.13	551.54	0.08
Key HN	1	229.86	6213.12	33.45	351.55	295.60	418.10	0.09

'i'iwi

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Detect24*	3	0.00	4614.84	41.73	158.27	128.31	195.24	0.11
Detect	4	1.94	4616.78	41.48	160.19	129.70	197.85	0.11
Detect 24 + Habitat	5	2.52	4617.37	41.04	163.63	132.39	202.24	0.11
Detect14	3	54.17	4669.02	45.06	135.79	110.82	166.39	0.10
Observer	5	82.62	4697.46	46.58	127.05	104.62	154.30	0.10
Cloud	4	83.21	4698.06	45.48	133.25	109.74	161.80	0.10
Wind	4	85.28	4700.13	46.37	128.19	105.67	155.51	0.10
Key	2	85.90	4700.75	47.16	123.93	97.21	158.00	0.12
Time	4	85.96	4700.80	47.56	121.87	100.47	147.82	0.10
Observer 2	4	88.65	4703.50	46.91	125.28	103.29	151.96	0.10
Habitat	4	90.15	4705.00	46.94	125.10	103.16	151.71	0.10
Survey Period 15	5	92.07	4706.91	47.78	120.75	99.58	146.41	0.10
Survey period	6	92.90	4707.75	48.16	118.86	98.03	144.12	0.10

Hawai'i 'amakihi

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Detect + Habitat + Observer	8	0.00	10487.32	34.29	583.00	518.94	654.96	0.06
Detect + Habitat*	6	20.81	10508.13	34.84	564.92	503.96	633.26	0.06
Detect	4	24.48	10511.80	34.87	563.94	503.23	631.97	0.06
Detect 24	3	30.38	10517.70	35.43	546.28	488.68	610.67	0.06
Detect 14	3	70.20	10557.52	35.89	532.19	475.29	595.91	0.06
Observer	5	170.28	10657.60	37.06	499.16	449.93	553.78	0.05
Observer 2	4	171.59	10658.91	37.77	480.70	433.38	533.18	0.05
Habitat	4	171.65	10658.97	38.53	461.72	416.60	511.74	0.05
Gust	4	179.98	10667.30	39.43	441.01	398.14	488.51	0.05
Key	2	182.07	10669.39	39.05	449.72	392.56	515.20	0.07
Time	4	182.49	10669.81	39.58	437.68	395.15	484.79	0.05
Wind	4	182.81	10670.13	39.72	434.65	392.42	481.41	0.05
Survey period	6	185.97	10673.29	40.01	428.33	386.70	474.43	0.05
Survey Period 15	5	186.65	10673.97	40.03	427.94	386.40	473.95	0.05
Cloud	4	187.76	10675.08	40.08	426.89	385.49	472.75	0.05

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Japanese white-eye

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Detect24*	3	0.00	4539.77	31.46	320.67	272.50	377.37	0.08
Detect	4	1.09	4540.86	35.03	258.65	220.94	302.79	0.08
Detect14	3	39.61	4579.38	34.77	262.54	224.40	307.17	0.08
Time	4	70.71	4610.48	35.60	250.44	214.95	291.80	0.08
Key	2	74.93	4614.71	36.09	243.67	202.85	292.69	0.09
Gust	4	75.51	4615.28	35.44	252.71	216.94	294.38	0.08
Observer 2	4	76.34	4616.11	36.22	241.95	207.79	281.73	0.08
Observer	5	77.33	4617.11	36.20	242.18	207.96	282.02	0.08
Survey period 15	5	77.43	4617.20	36.14	242.96	208.62	282.96	0.08
Habitat	4	77.84	4617.61	35.58	250.75	215.29	292.04	0.08
Cloud	4	78.07	4617.84	35.93	245.84	211.12	286.28	0.08
Wind	4	78.87	4618.64	35.83	247.28	212.34	287.97	0.08
Survey period	6	79.47	4619.24	35.62	250.13	214.69	291.43	0.08

red-billed leiothrix

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Detect*	4	0.00	6940.79	31.67	452.76	382.32	536.17	0.09
Detect24	3	2.73	6943.51	27.98	580.05	486.75	691.23	0.09
Detect14	3	162.57	7103.36	34.65	378.27	320.52	446.42	0.08
Survey period	6	221.21	7162.00	35.94	351.58	301.72	409.67	0.08
Key	2	222.63	7163.42	36.08	348.94	287.93	422.88	0.10
Survey period 15	5	225.02	7165.80	38.58	305.18	262.33	355.01	0.08
Habitat	4	225.92	7166.71	38.41	307.80	264.62	358.03	0.08
Time	4	228.61	7169.39	39.18	295.86	254.42	344.05	0.08
Gust	4	229.40	7170.19	39.03	298.16	256.39	346.73	0.08
Cloud	4	229.41	7170.20	39.01	298.50	256.68	347.12	0.08
Observer 2	4	229.68	7170.47	39.12	296.76	255.20	345.08	0.08
Wind	4	229.78	7170.57	39.05	297.80	256.09	346.30	0.08
Observer	5	231.67	7172.45	39.12	296.77	255.20	345.11	0.08

house finch

Model	# par.	Delta AIC	AIC	EDR	D	D LCL	D UCL	D CV
Key*	2	0.00	5732.35	40.20	216.25	178.04	262.67	0.10
Detect14	3	8.99	5741.34	43.01	188.89	159.95	223.07	0.08
Detect24	3	8.99	5741.34	43.01	188.89	159.95	223.07	0.08

Gust	4	10.99	5743.34	43.01	188.89	159.94	223.08	0.08
Detect	4	10.99	5743.34	43.01	188.89	159.95	223.08	0.08
Cloud	4	10.99	5743.34	43.01	188.89	159.95	223.08	0.08
Wind	4	10.99	5743.34	43.01	188.89	159.94	223.08	0.08
Time	4	10.99	5743.34	43.01	188.89	159.94	223.08	0.08
Habitat	4	10.99	5743.34	43.01	188.89	159.95	223.08	0.08
Observer 2	4	10.99	5743.34	43.01	188.89	159.95	223.08	0.08
Survey period 15	5	12.99	5745.34	43.01	188.89	159.94	223.09	0.08
Observer	5	12.99	5745.34	43.01	188.89	159.94	223.09	0.08
Survey period	6	14.99	5747.34	43.01	188.89	159.93	223.10	0.08

Appendix C

Appendix C. Detection functions used to estimate bird abundances. The hazard-rate model was chosen for all birds. A) Maui alauahio, B) Iiwi, C) Apapane, and D) Hawaii Amakihi. Exotic birds included E) Japanese white-eye, F) Red-billed leiothrix, G) house finch.
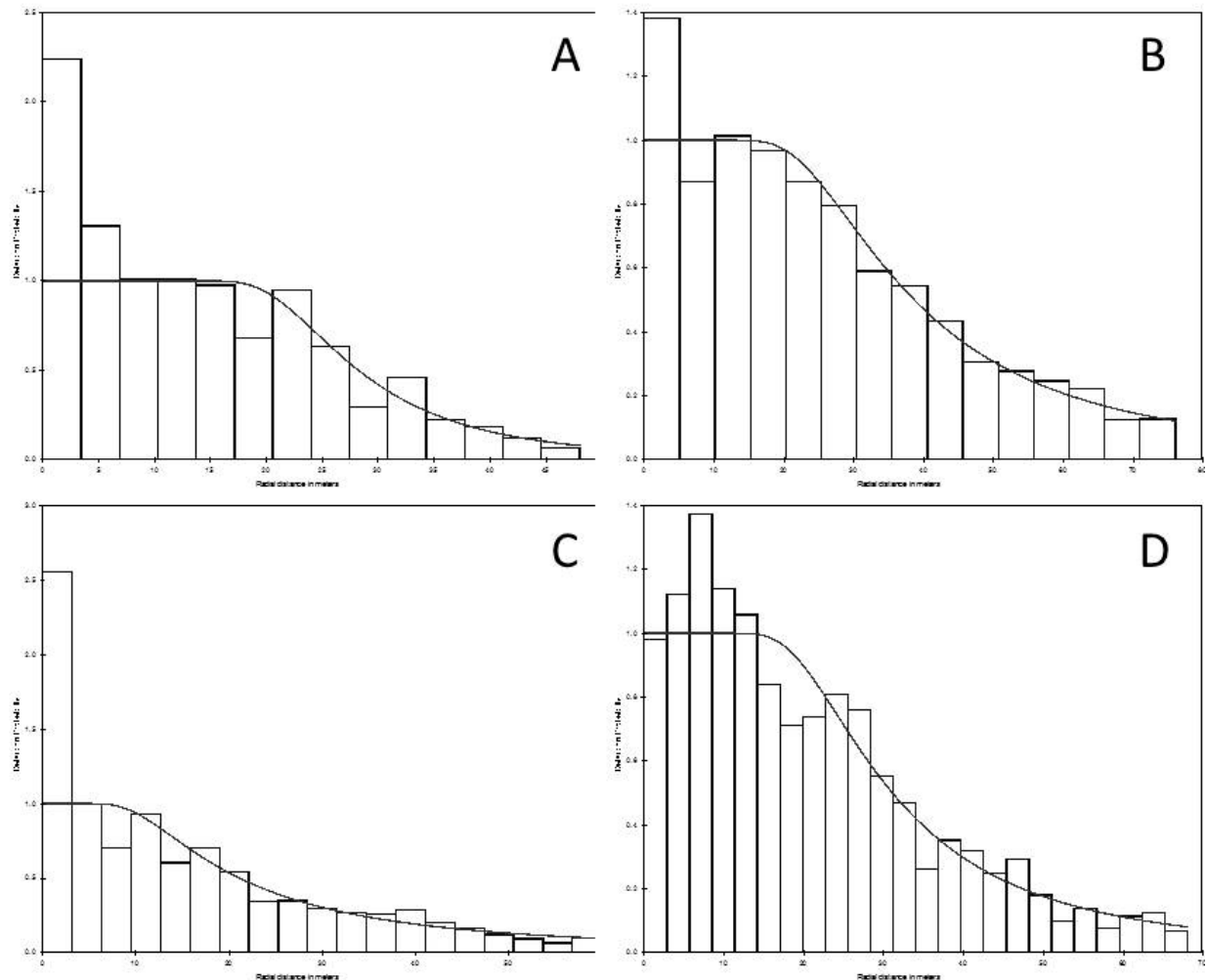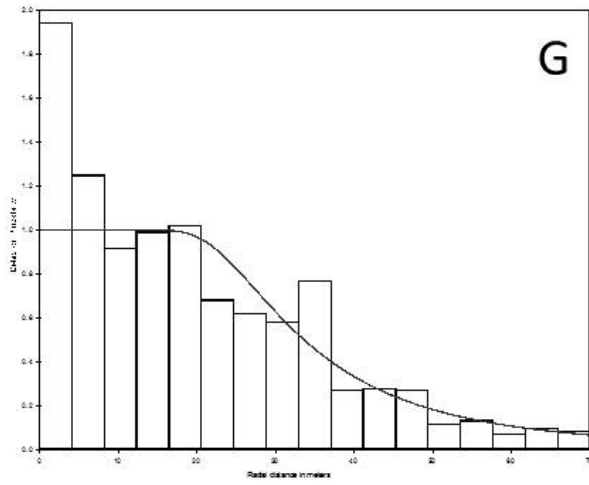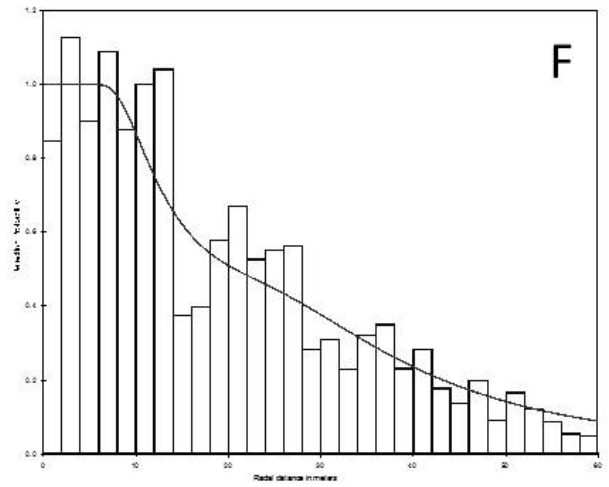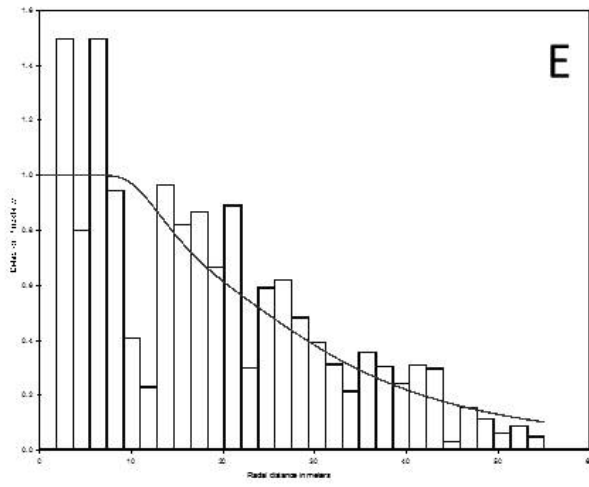
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