FINAL REPORT

Seed Dispersal Networks and Novel Ecosystem Functioning in Hawaii

SERDP Project RC-2434

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14. ABSTRACT

The Hawaiian Islands are both the extinction and invasive species capitals of the world. The result has been Hawaiian ecosystems fundamentally changed in form; that is, ecosystems replete with a mix of novel and native species. Most native Hawaiian plant species are bird-dispersed, yet no native avian dispersers remain in most Hawaiian ecosystems. Thus, ecosystem functioning will only be maintained by the handful of invasive vertebrate dispersers that now reside on the islands, most of which are birds.

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Nonnative invasive species, islands, invasion biology, plant communities, introduced bird communities, seed dispersal, movement ecology

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List of Acronyms

ARU: Automated Receiving Units
DoD: Department of Defense
DLNR: Department of Land and Natural Resources, State of Hawaii
EKA: Ekahanui field site
ERDC-CERL: U.S. Army Engineer Research & Development Center, Construction Engineering Research Laboratory
IPR: In-Progress Review
KAH: Kahanahaiki field site
MOA: Moanalua field site
MTK: Mt. Kaala field site
NARS: Natural Areas Reserve System
NIS: non-native invasive species (can refer to either plants or vertebrates)
OANRP: Oahu Army Natural Resource Program
OISC: Oahu Invasive Species Committee
PAH: Pahole field site
SDN: seed dispersal network
SEMS: SERDP and ESTCP Management System
TAN: Tantalus field site
WAI: Waimea Valley field site

Keywords

Nonnative invasive species, islands, invasion biology, plant communities, introduced bird communities, seed dispersal, movement ecology

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Objectives

The Hawaiian Islands are both the extinction and invasive species capitals of the world. The result has been Hawaiian ecosystems fundamentally changed in form; that is, ecosystems replete with a mix of novel and native species. Most native Hawaiian plant species are bird-dispersed, yet no native avian dispersers remain in most Hawaiian ecosystems. Thus, ecosystem functioning will only be maintained by the handful of invasive vertebrate dispersers that now reside on the islands, most of which are birds. In this context, research efforts must shift focus to non-native bird species (and potentially rats) and the potential for these species to maintain native plant communities under current and predicted environmental conditions. To successfully manage and preserve Hawaiian terrestrial ecosystems, it is necessary to identify and characterize non-native invasive species that are dispersers of desired plant species, determine their role in ecosystem function, and improve non-native plant management plans, while facilitating the recovery of native threatened, endangered, and at-risk plants. The overarching objective of this project is to determine the effects of plant disperser traits, competition, predation, and landscape features on native and non-native plant dispersal and recruitment. This will be accomplished through the integration of field-based data collection, field experiments, and ecological modeling to describe and quantify seed dispersal in novel Hawaiian communities. Essential outcomes of the research include determining how well different species of non-native birds disperse native plant species across environments, whether non-native rat species have a cumulative positive (via seed dispersal) or negative (via predation on bird seed-dispersers and/or via seed predation) impact on communities, and creating predictive models to be used for management in novel environments and under future abiotic and biotic scenarios. The proposed research will provide DoD and the scientific community with the essential tools for managing and maintaining native plant communities in Hawaii and other Pacific Islands.

Technical Objectives

Overall Objective: Quantify and predict how novel communities of seed dispersers structure plant communities across environmental gradients. To address this overall objective, we:

1. **Determined how environmental variables affect networks of non-native seed dispersers.** We accomplished this by documenting variation in SDN structure (number and type of plant and disperser species) across ecological contexts, estimated the effects of abiotic factors and species interactions on the persistence of disperser species, and determined the impacts of competition on seed preference and dispersal.
2. **Determined how the movement of non-native dispersers, the availability of fruits, and seed dispersal affects plant communities.** We accomplished this by assessing how traits of seed dispersers influence seed viability and seedling recruitment and constructed agent-based movement ecology models to examine how disperser behavior and landscape features affect seed movement and plant community structure.
3. **Predicted the effect of changing environmental conditions on the networks of non-native seed dispersers and plant communities.** We constructed predictive ecosystem functioning models using output from Objectives #1 and #2. This extends the benefits of the research beyond our study sites on Oahu to inform future management action in new landscapes and under future scenarios of biotic and abiotic (e.g., climate change) shifts in other locations in Hawaii and the Pacific. Examples include the potential for new dispersal events given the landscape composition, risk of invasion, and changes to functioning with the addition or deletion of dispersers.

Technical Approach

Multi-species interactions are crucial to the maintenance of ecosystem structure and function. This is especially true for seed dispersal networks, where interactions among seed dispersers, plants, and predators influence the efficacy of seed dispersal and ultimately, community structuring. Research on seed dispersal by birds has largely been restricted to individual species and focused on the identification of seeds in their diets and their role in plant dispersal. Thus, most current research does not reflect the reality of multiple interacting native and non-native species (birds and rats), relative disperser effectiveness, and the capability of non-native dispersers to maintain native plant communities in severely altered ecosystems. This project incorporated these interactions through the comprehensive examination of seed dispersal networks comprised of seven non-native invasive bird species, two common non-native invasive rat species, seven non-native invasive plant species, and eight ecologically important native plant species. Collection of field-based variables included species abundance, reproduction, predation, inter- and intra-specific competition, diet preferences, disperser behavior, gut passage times, and seed germination rates to create and parameterize movement ecology models for assessing seed dispersal across heterogeneous landscapes. When integrated with high resolution vegetation and elevation data in a landscape modeling framework, these individually-based movement ecology models can be used to estimate and predict how interactions within seed dispersal networks influence dispersal and recruitment probability of native and non-native plants.

Benefits

This project examined multiple seed dispersal networks comprised of interacting native and non-native plant and vertebrate species across several trophic levels and ecological contexts in order to develop predictive models for assessing recovery and maintenance of key ecological processes including dispersal, recruitment, and establishment of threatened, endangered, and at-risk plant species. These predictive models, capturing a range of elevation and precipitation gradients and utilizing generic bird (e.g. mass, life history, dietary) and plant (e.g. size, color, fruiting height) traits, are particularly useful as they can be applied to other similar Pacific Island habitats with different bird and plant species. Importantly, our work will provide DoD and adjacent resource managers with the tools to go beyond current non-native invasive species (NIS) control and eradication efforts in Hawaii by providing meaningful predictive measures of native and non-native plant dispersal and establishment. In this context, our results will put DoD in a powerful position to match environmental objectives with agency needs, and to provide leadership on responses to global climate change and the recovery of native threatened, endangered, and at-risk plants in the Pacific Islands.

Background

Multi-species interactions are crucial to the maintenance of ecosystem services. This is especially true for seed dispersal networks, where interactions among seed dispersers, plants, and predators influence the efficacy of seed dispersal and community structure and dynamics (Levin et al. 2003, Stanton et al. 2003, Strauss and Irwin 2004, Gosper et al. 2005). Prior research on seed dispersal by avian species has largely been restricted to individual species and has focused on the identification of seeds in the diets of birds and preference (in the absence of interactions) for native versus non-native plants (Gosper et al. 2005, Aslan and Rejmánek 2010, Schupp et al. 2010). In addition, these efforts have not explored the typical situation of multiple interacting native and non-native plant, disperser, and predator species. Nor have they tested whether, in the absence of native dispersers, invasive dispersers increase the spread of non-native plants, or can maintain native plant communities in severely altered ecosystems (Gosper et al. 2005, Schupp et al. 2010). An understanding of the mechanisms driving seed dispersal behavior and population demography of dispersers is required to assess the effectiveness of seed dispersers and predict the long-term ability of species to maintain ecosystem functioning in different ecological contexts (Schupp et al. 2010). In our project we quantified the effects of disperser traits, competition, predation, and landscape features on native and non-native plant distributions to determine and predict the effectiveness of non-native vertebrates as seed dispersers in different ecological contexts in the highly altered Hawaiian Islands.

Globally, invasive species rank as one of the most serious threats to native biodiversity and their effects are the strongest on oceanic islands (Millennium Ecosystem Assessment Board 2005, Sax and Gaines 2008). Since human arrival at least a millennium ago, and particularly in the last two centuries, the Hawaiian Islands have fundamentally changed with the colonization of invasive species and extinction of native ones. This has resulted in novel communities across all the islands, with a mix of invasive and native species (Vitousek et al. 1987a), and novel interactions among species from five continents. Perhaps the most profound changes to the ecosystem are the loss of half of all native plant species (Wagner et al. 1999, Sakai et al. 2002, Foster and Robinson 2007) as well as the extinction of nearly all native bird species that once maintained ecosystem functioning through seed dispersal (Foster and Robinson 2007). Bird research on Hawaii continues to focus on native bird species, although there are few native plant dispersers remaining, and yet the vast majority of native plants are bird-dispersed (Foster and Robinson 2007). Only one native bird species, the Omao (*Myadestes obscurus*) on the island of Hawaii, still effectively disperses native seeds over large areas. Thus, the only seed dispersers that remain in most ecosystems are non-native birds and rats (Medeiros 2004, Foster 2009, Shiels and Drake 2011), and these are now the only species potentially capable of dispersing seeds of native plants. Thus, if native plant communities are to be maintained in Hawaii, research efforts must shift to focus on how and which non-native dispersers will be effective at maintaining ecosystem functioning. Our research aimed to address these issues and provide realistic and effective management options.

Seed dispersal effectiveness, and, by extension, ecosystem function, is influenced by a variety of mechanisms including disperser traits (e.g., fruit handling techniques, gut passage, disperser movement, and food preference), seed/fruit traits (e.g., mass, shape, and number), landscape features (e.g., vegetation, topography, land cover, and climate), inter- and intra-specific competition, and predation on seeds and seed dispersers (Howe and Smallwood 1982, Gosper et al. 2005, Schupp et al. 2010). Single species studies of disperser traits and the effects of landscape features have been examined across a variety of systems, but the influence of multi-species interactions has received much less attention (Gosper et al. 2005). Disperser effectiveness or efficiency is defined as the number of adult plants produced by the dispersal activities of a disperser relative to other dispersers (Schupp 1993, Schupp et al. 2010). Because disperser effectiveness is strongly influenced by species interactions, effective management and predictions of future communities cannot be made without knowledge of how species interactions alter dispersal. For example, competition, both interspecific and intraspecific, can affect seed disperser behavior, foraging ability, and diet (Howe and Estabrook 1977, Gautier-

Hion et al. 1985), yet most studies assess disperser behavior in isolation (Westcott et al. 2005, Aslan and Rejmanek 2012). Dominant or more efficient species may exclude less competitive species (Shochat et al. 2004), thus limiting their effectiveness as seed dispersers. Predation can also impact the effectiveness of seed dispersers in a community both through behavioral modifications of foraging prey (Verdolin 2006) and through direct predation on adults and young (Wilcove 1985, Côté and Sutherland 1997), thereby influencing seed disperser abundance and probability of persistence in a habitat. The next step, and that which we took in our project, was to quantify the effects of multi-species interactions on seed dispersal and, ultimately, on plant community composition across environmental gradients.

In the context of SDNs, the role of invasive rats in Hawaiian ecosystems is unclear. Evidence of deleterious effects abound, with many species being documented consumers of native plants and seeds (Nogueira-Filho et al. 2009, Chimera and Drake 2010) and rats as nest predators of many avian species (Atkinson 1977), including avian seed dispersers. Rats have been implicated in the declines of many endemic plant (Chimera and Drake 2010) and avian species (Blackburn et al. 2004, Woodworth and Pratt 2009), resulting in programs to reduce the effects of rats on native species (VanderWerf and Smith 2002). However, rats are also documented seed dispersers (Chimera and Drake 2011, Shiels and Drake 2011) and may play integral roles in the formation of plant community structure. The complex relationship among rats, avian seed dispersers, and the resulting plant community needs to be assessed in order to determine appropriate future invasive species management. We present data on rodent (rats and mice) abundance and seed caching behaviors although this is limited because our work suggests that rodents play a minor role in seed dispersal in our sites.

In our project we integrated empirical field-based data collection, field experiments, and multi-scale (individual movement to landscape) ecological modeling to describe and quantify seed dispersal in Hawaiian novel communities, with a focus on determining which non-native species may serve the greatest roles in ecosystem function. Here we generally define SDNs based on the species involved in seed dispersal, and we examine how the number and type of species and the strength and direction of interactions among species vary across environments. The extensive existing resource management programs on Oahu allowed for a well-replicated design that enabled us to explicitly test the additive and synergistic influence of unique community structuring and ecological contexts on seed dispersal and recruitment. We used existing conservation and restoration infrastructure, including plant monitoring, and native outplanting areas, along natural environmental gradients to quantify context-dependency of seed dispersal and inform predictive models. We also examined seed dispersal across ecological contexts, both biotic and abiotic. Biotic contexts included presence and abundance of invasive plant species, and non-native and native bird species. Abiotic contexts included elevation, rainfall, habitat patch size (and other fragmentation characteristics), and distance to human development.

<u>We evaluated the following research hypotheses:</u>

1. Structure of SDNs will change across different ecological contexts.
2. Probability of long-term persistence of seed dispersers within the SDN will change across ecological contexts.
3. Competition impacts seed preference of disperser species.

4. Variation in seed viability and seedling recruitment will be observed across ecological contexts and will depend upon seed and disperser functional traits.
5. Seed dispersal will be affected by disperser behavior and landscape features.
6. Future dispersal competence and maintenance of ecosystem functioning will be governed by changes in local climate, landscape, disperser behavior, and SDN dynamics.

These research hypotheses were addressed using six unique but related steps (Fig. 1):
For Step I, we quantified seed dispersal networks by documenting which vertebrate species consume seeds, the species and quantity of seeds consumed, the importance of vertebrate dispersal for plant species, and how structure of the SDN (number and type of plant and disperser species) varies across ecological contexts. The primary tasks associated with this step were to determine diet composition of free-ranging vertebrate seed dispersers by capturing individuals to examine diet through gut and fecal samples and by radio-tracking individuals to observe foraging. Documenting the role of each individual species as seed consumers, in a natural context, is a necessary first step in understanding SDNs as a whole. We also conducted seed rain experiments to assess fruit consumption, seed fall, and the importance of vertebrate dispersal across the plots. This first step indicates what is observed in nature and the outcome of the mechanisms influencing seed dispersal. Subsequent steps are the specific mechanisms of seed dispersal and are designed to examine the *effectiveness* of particular bird and rat species to disperse seeds, based on intrinsic and extrinsic factors.

For Step II, we determined potential effectiveness of seed dispersers based on their abundance and potential for persistence across environments. For example, species that are either in very low abundances or have low productivity in an environment will not likely contribute substantially, at least in the long-term, to seed dispersal effectiveness (Jordano and Schupp 2000). Species abundance, in combination with traits of the disperser, such as body mass, is directly related to the number of fruits consumed, and, consequently, the potential for the species to be a major seed disperser (Schupp et al. 2010).

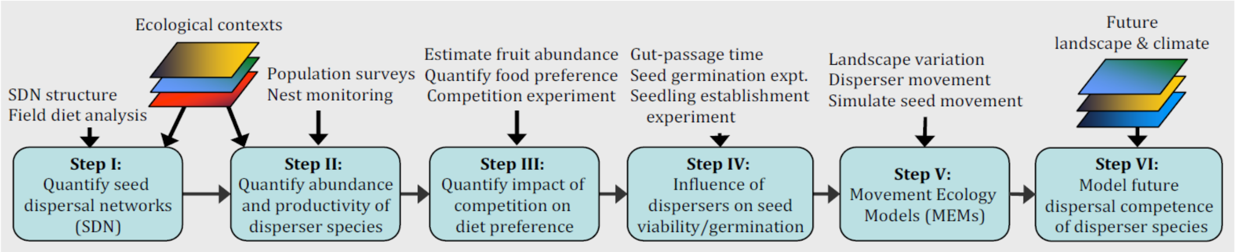


Fig. 1. Flowchart of study, including ecological assessments, field and laboratory experiments, and modeling approaches to address factors influencing ecosystem functioning across novel ecological contexts. Blue boxes indicate research Steps I-VI.

For Step III, we determined seed preferences for each disperser species and how competition alters diet across ecological contexts. This step assessed preference for native and non-native plant species, what functional traits of seeds dispersers prefer, and how competitive interactions alter diet. Dispersers are typically attracted to functional traits of seeds/fruits, such as color, size, and pulp to seed ratio (Aslan and Rejmanek 2012). Evidence for whether non-native dispersers prefer non-native plants is equivocal and varies depending upon the experimental protocol

(Aslan and Rejmanek 2012). Different results arise depending on whether functional traits of native and non-native seeds are matched or not (by color, size, etc.) in the experiment (Aslan and Rejmanek 2012). Moreover, studies often only assess preference using aviary experiments of single birds in isolation, yet competitive interactions and the abundance of fruits in the natural environment alter preference under different ecological contexts. For example, a competitively dominant species' ability to monopolize a food source may reduce the effectiveness of a less efficient species (Shochat et al. 2004). Therefore, to address the potentially confounding factors associated with preference, we used field and aviary experiments, and observational field data (using radio telemetry) of birds in the presence and absence of competitors and estimate relative abundance of fruits to determine seed preferences of each potential seed-disperser.

In Step IV, we examined variation in seed limitation, seed viability, seedling establishment, and recruitment across different ecological contexts and for bird and rat dispersers. Although a species may be consuming seeds, its effectiveness as a seed disperser is dependent on the ability of the seeds to germinate following ingestion (Traveset 1998, Paulsen and Hogstedt 2002, Schupp et al. 2010). The ability of seeds to germinate depends upon the abiotic and biotic factors associated with the location at which the seed was defecated/regurgitated and the gut-passage time (Meyer and Witmer 1998). Gut-passage time influences the level of mechanical or chemical scarification of the ingested seeds (Figuerola et al. 2002), with longer retention times associated with decreased seed weight and inconsistent changes in germinability (Traveset et al. 2001). Furthermore, seed addition experiments allowed us to disentangle the roles of seed limitation versus seedling establishment limitation in recruitment of key plant species. All of the data collected in Steps I-IV, in conjunction with high-resolution vegetation maps and satellite imagery were used to populate the models in Steps V and VI below.

For Step V, we integrated all data collected in Steps I-IV into movement ecology models (MEMs) that describe how disperser behavior and landscape features influence potential seed dispersal. Movement ecology models (Getz and Saltz 2008, Nathan et al. 2008) allow for the examination of how individual movement patterns are driven by an individual's internal state, current location, and local environmental variables (e.g., climate and landscape features). This family of models had been used successfully to model seed dispersal across complex landscapes (Bolker 2003, Levey 2005) and across large spatial scales (Levey et al. 2008) where seed dispersal events (i.e., defecation or regurgitation) are rarely observed. We adopted this framework because it incorporates bidirectional interactions of fruits/seeds and their vertebrate dispersers. Seed dispersal is directly affected by disperser movement and behavior, but initial ingestion and excretion by disperser species is directly influenced by fruit and seed traits (Gautier-Hion et al. 1985, Gosper et al. 2005)(quantified in Steps II-III). Likewise, the predicted seed dispersal kernels (defined as the probability density function of dispersal distances from individual plants) are influenced by traits of the disperser and the plant species. By first quantifying variation in vegetation across fine spatial scales and then testing the influence of vegetation structure and local climate conditions on disperser movement patterns, we created a generalized mechanistic framework for estimating spatial distributions of seed dispersal in a variety of ecological contexts. We integrated these movement ecology models with empirically derived data on seed preference, gut passage, and germination probability to (i) simulate seed movement and germination potential across landscapes, and (ii) assess the relative impact of each disperser species on seedling recruitment. This enabled a realistic examination of dispersal competence and the ability of particular disperser species to influence plant community structure. Finally, in Step VI, we estimated the robustness of seed dispersal network to climate change. Specifically, we estimated and compared the rates of coextinction (i.e. loss of plants following bird extinction) and how they differ between a scenario where birds are lost by random versus when most climatically vulnerable birds are lost first. This step was a modification of the initial plans for Step VI of developing landscape models to be used to predict future dispersal competence and maintenance of ecosystem functioning in novel environments. Due to our advances in network analyses, it was strongly suggested during the 2019 IPR that take a network approach for this task of the project rather than use agent-based modeling, at least in the short term. We are continuing to work on these agent-based models but do not detail them here. These models are critical to: (i) predicting how ecosystem functioning will vary across different environments and under future scenarios of climate and land use change and (ii) allowing results to be expanded beyond the spatial and temporal scope of this project. For example, we will be able to predict species distributions and the probability of colonization/extinction of native and invasive plant species with shifts in abiotic (climate change) and biotic factors (the disperser species present). These models can be applied to new SDNs in novel environments, such as other sites in Hawaii and the Pacific, by using the functional traits of dispersers and seeds and the relationship between these functional traits and landscape features (based on modeling output from Step V). Using functional traits to address broad scale ecological questions has proven effective, particularly in addressing how environmental changes (climate, land use, and other disturbances) influence seed dispersal and community dynamics (Cornelissen et al. 2003, Gosper et al. 2005, Schupp et al. 2010).

By focusing on the effects of multi-species interactions on ecosystem functioning across different ecological contexts, the research provides a realistic assessment of the future of Hawaiian ecosystems under current and predicted conditions. Understanding the bird species that are effective seed dispersers, under a variety of environmental scenarios, is a critical tool for land managers attempting to maintain native plant communities in increasingly altered habitats. Identifying the effectiveness of dispersers can be used to determine which non-native dispersers need to be monitored or managed to maintain ecosystem functioning. Furthermore, by including a wide range of habitats/biotic conditions and by examining functional traits associated with seed disperser competence, the results of this project should be broadly applicable to other systems and DoD installations. The Pacific Islands are an ideal system for testing our methods of predicting the response of SDNs and plant communities to environmental change owing to their lower biodiversity compared to mainland tropical systems. Ideally, our approach would serve as a model on how to adequately incorporate species interactions and network theory into ecosystem functioning under current conditions and future climate change scenarios in more complex systems. Moreover, we use individual-based models to scale up to the population level and to the community. There is increasing recognition of the importance of individuals in population dynamics and community structure (Clobert et al. 2009) and taking this multi-scale approach is essential for understanding the mechanisms of seed dispersal and for predicting the outcomes on ecosystem functioning.

Tasks

Task 1. All Subtasks Due (using SEMS reporting terminology).

This Task can be seen as an administrative one. Island-based field research can be logistically challenging. Perhaps overlooked by many are the additional challenges faced by researchers working on islands, particularly when handling vertebrates and when endangered species may be involved. Our work required 15 permits from state and federal agencies, as well as private landowners. Thus, substantial administrative work was required for the work to start. Fortunately, most of our research could proceed without delay although the hurdles were substantial. These results are potentially informative for future SERDP projects indicating that one must be realistic with how quickly the project can commence and accounting for logistical complexity. Furthermore, we feel our success came from our ability to work together as a team. With numerous investigators, students, and staff on the project, constant communication among team members was imperative. It was not perfect. For example, establishing authorship criteria early on would have been highly beneficial. Finally, building and maintaining solid working relationships with land managers has been essential and we will continue to make and bolster these connections.

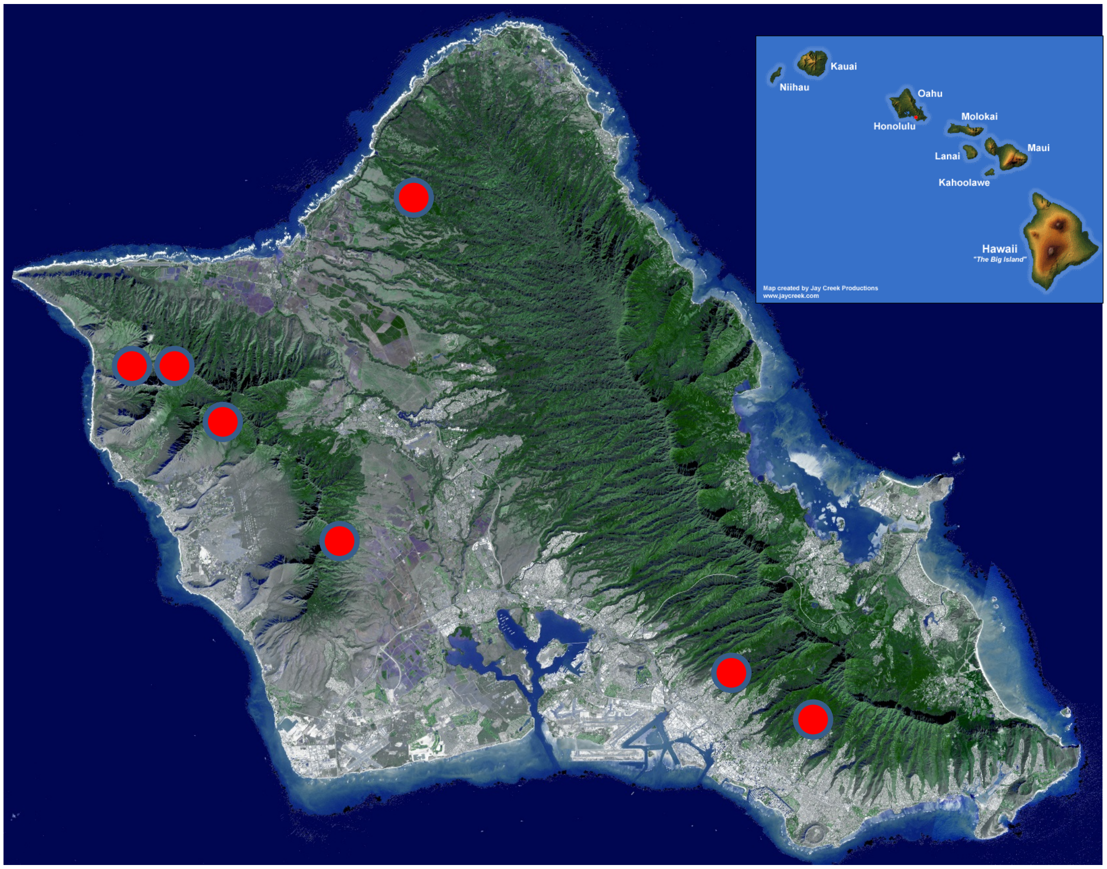


Fig. 2. Locations of seven field sites established on Oahu.

In the first year of the project we established seven field sites across an elevation and precipitation gradient (Fig. 2). We continued work at all of these sites through the end of the project in year 5, although the majority of field work concluded in year 3. Throughout this report we have abbreviated the site names as follows: Ekahanui (EKA), Kahanahaiki (KAH), Moanalua (MOA), Mt. Kaala (MTK), Pahole (PAH), Tantalus (TAN), and Waimea (WAI). As detailed in our proposal and timelines, our work in the first three years of the project focuses on data collection and corresponds to Tasks 2–5 for SERDP reporting. Note that our project proposal worded this as Steps I–IV, rather than Tasks 2–5, but the overall work remains the same. The final two tasks, Task 6: Constructing movement ecology models of seed dispersal and Task 7: Determining climate effects on dispersal competence are data analysis and modeling were conducted in years 4 and 5 of the project.

Task 2. Quantifying disperser abundance and potential

We generated an enormous amount of data to address this task. In many ways, the data for this task are the heart of the project, forming the basis for subsequent work and analyses. This task included point-counts and mist-netting to estimate bird abundance, fecal collection and analysis of the seeds from mist-netted birds, and radio-tracking and ARU-based telemetry of birds with transmitter attachments. The abundance data from point-counts and mist-netting are the most intensive and extensive work ever done on the introduced bird community ever done in Hawaii. Our fecal sample collection contains seed identifications for over 4,000 fecal samples and represents one of the most comprehensive seed dispersal datasets in the world.

Study species—vertebrates: We are examining seed dispersal networks comprised primarily of two common non-native invasive rat species, black rat (*Rattus rattus*) and Polynesian rat (*R. exulans*), and six non-native invasive bird species including Japanese white-eye (*Zosterops japonicus*), red-billed leiothrix (*Leiothrix lutea*), red-vented bulbul (*Pycnonotus cafer*), red-whiskered bulbul (*Pycnonotus jocosus*), spotted dove (*Spilopelia chinensis*), and Kalij pheasant (*Lophura leucomelanos*). These rat species are well established consumers of fruits and seeds of plants but the extent of their seed dispersal is poorly known (Shiels 2011, Shiels and Drake 2011). Three of these bird species we predicted to be critical seed dispersers in our study sites due to either their ubiquity or dependence on fruit in their diet (Islam and Williams 2000a, b, Foster and Robinson 2007): Japanese white-eye, red-vented bulbul, and red-billed leiothrix. Although Japanese white-eyes and red-billed leiothrix eat a wide variety of food, their high abundance on other islands in Hawaii and their consumption and dispersal of a broad range of native and non-native fruits suggests they may be major seed dispersers on Oahu (Foster and Robinson 2007). Red-vented and Red-whiskered bulbuls likely play a role in long-distance dispersal of seeds due to their large home ranges compared to many other non-native birds and they are recognized as effective seed dispersers on other islands where they have been introduced (Mandon-Dalger et al. 2004, Linnebjerg et al. 2010). There are no known native seed dispersers remaining on Oahu. The Oahu elepaio (*Chasiempis sandwichensis ibidis*), apapane (*Himatione sanguinea*), and Oahu amakihi (*Chlorodrepanis flava*) are native species that still persist on Oahu, but they are not frugivorous. Nonetheless, we have been sampling the diets of any native birds captured in mist-netting efforts to verify their lack of fruit consumption and seed dispersal abilities. For native frugivores from Oahu, all of which have gone extinct, we are conducting morphometric analyses on bill and wing morphologies from museum specimens to estimate potential limits on seed/fruit size and their dispersal potential for native plants following protocols detailed in Meehan et al. (2002).

Methods–Bird abundance

Mist-netting

We used two primary methods, mist-netting and point-counts, for determining the abundance of birds as dispersers. For the first of these methods, mist-netting, we captured 4400 birds in 2+ years, of which 16.5% were recaptures (Table 1). A total of 19 species were captured. As expected, red-billed leiothrix and Japanese white-eye were the most abundant species with 1862 and 1175 captures, respectively. Red-whiskered bulbuls were captured in higher numbers, n = 301, than red-vented bulbuls, n = 33 despite a seemingly higher abundance of red-vented bulbuls, likely driven by behavioral differences.

Table 1. Mist-netting capture totals by year, including recaptures, from 7 sites.

	Year			
Species	**2014**	**2015**	**2016**	**Total**
Apapane		72	55	127
Common Waxbill	17	52	35	104
Common Myna		1		1
House Finch	11	86	58	155
Hwamei	1	2	2	5
Japanese Bush-Warbler	6	30	36	72
Japanese White-eye	116	735	324	1175
Northern Cardinal	15	50	17	82
Oahu Amakihi	5	10	13	28
Oahu Elepaio		3	1	4
Red-billed Leiothrix	302	1015	545	1862
Red-crested Cardinal		16	7	23
Red Avadavat	2			2
Red-vented Bulbul	4	16	13	33
Red-whiskered Bulbul	41	154	106	301
Scaly-breasted Munia	24	27	30	81
Spotted Dove	5	22	8	35
White-rumped Shama	29	152	81	262
Zebra Dove	7	32	9	48
	585	2475	1340	4400

Point counts

For the second estimator of bird abundance we used point counts. Summary results of our bird detections from point-counts include number of stations, number of visits to each station in each year, total number of point count surveys conducted, number of unique species detected at each site, number of individuals detected at each site, and a derived estimate of number of birds per survey. Additional bird capture results such as densities per site for each species were generated during the analysis phase of our project (see below). One site was visited per week and every point was surveyed on a single day making the time between counts seven weeks per site. On the day of the surveys, the first points were surveyed at dawn (approximately thirty minutes before sunrise) and all surveys were completed within 5.5 hours of the sunrise. Surveys were not conducted in heavy rain or high winds (>7 on the Beaufort scale), and if a survey was not able to be conducted due to weather, it was conducted on the next day. The surveys followed a two-minute acclimatization period and lasted eight minutes. During the survey, every bird heard or seen was recorded, with species identity, estimated distance, and bearing also recorded. Immediately after the survey, the following point-level abiotic conditions were recorded: intensity of rain (none, light, moderate, heavy), cloud cover (percent of visible sky obscured by clouds), and wind speed (Beaufort Scale: 0-7). If wind gusts were observed during the counts, the average between the strengths of the sustained wind and gusts was used.

Habitat Measurements

To describe the habitat around each survey point, we measured the plant community and four vegetation structure variables (i.e. canopy height, canopy cover, forest openness, and vegetation density of the shrub layer) at four points around each survey point (one at the survey point and three 10m from the survey point at bearings of 0, 120, and 240 degrees). In order to characterize the plant community at and around each point, the stem density of each woody species and the estimated percent cover of each herbaceous species was recorded within a two-meter radius. The clonal tree *Hibiscus tiliaceus* and the vine species observed have sprawling growth structures making it difficult to obtain good stem counts, and therefore, we estimated the cover of these species. The vegetation structure at each point was determined by recording the canopy height measured with a graduated two-meter pole (for canopies < 4m) or a range finder, visual estimation of canopy cover (percent of visible sky obscured by vegetation), and the presence of vegetation within two-meter increments of the forest column. The presence of vegetation in the forest column was then converted into a variable of forest openness by subtracting the proportion of two-meter increments that had vegetation from one (as in Wilcox and Tarwater *in review*; hereafter "openness"). Additionally, a Robel pole was used to determine the density of vegetation in the shrub layer. The stem counts and vegetation structure data were then averaged across the four points around each survey point.

In addition to the point level habitat metrics, we also calculated site level habitat variables. Every meter along each transected, the plants that intersect a vertical line were recorded. Information on the detected plants' reproductive ecology (bearing fleshy or non-fleshy fruit) and its origin (native or non-native) was obtained from Wagner et al. (1999). The herbaceous, non-fleshy fruited plant species were combined into categories based on their growth form (i.e. tree fern, other fern, short grass, tall grass, sedge, and forb). The level of invasion was calculated by dividing the number of non-native species by plant species richness for each site (as recommended by Catford et al. (2011); hereafter labeled "invasion level"). Similarly, the proportion of fruiting species (hereafter "fruit proportion") was calculated by dividing the number of species that bore fleshy fruit by plant species richness for each site.

Statistical analyses

All statistical analyses were conducted in R (version 3.5.1; R Core Team 2018). The abundance of the common species was estimated using n-mixture models with the "pcount" function of the "unmarked" package (Fiske and Chandler 2011). The covariates for the detection function were wind, rain, time since sunrise, month of survey, presence of flock, and observer. The variable 'flock' was determined to account for the rare occasions that large groups were observed which can influence the estimation of a species' detection probability and was determined if an observation of a species during a survey was of five or more individuals (< 1% of all observations). The observers were condensed into fourteen categories based on the number of surveys they conducted. Observers that conducted at least 90 surveys were kept as individuals (6 observers) and the rest were grouped into the following classes based on how many surveys they conducted: 70-85, 60-69, 50-59, 40-49, 30-39, 20-29, 10-19, and <10 surveys. Since running a model for every combination of detection variables would be computationally intensive, we only ran twenty models that included both an intercept only and full model as well as models with each detection variable by itself. Because weather during our study was variable and the season can influence detection through seasonal changes in behavior, we ran models of each weather variable with month. For the other ten models, we included both weather variables and varied the other detection variables including month when more than one variable other than the weather variables were considered. The detection model with the lowest AIC was then selected to estimate the abundance of the bird species at each point. Only birds detected within 40 meters of the point were used in analyses. For each species, the points that did not have any observations during the entire study were assumed to have an abundance of zero for that species and not included in the n-mixture models since they would artificially reduce the probability of detection. N-mixture models do not perform well for naturally rare species by artificially reducing the probability of detection (Banks-Leite et al. 2014). Therefore, the abundance of rare bird species (< 50 observations during the length of study and detected at less than 25% of the survey points; 8 species of the 24 detected) was calculated by averaging the number of observations at each point across surveys.

To describe the heterogeneity of the bird communities, we conducted a non-parametric multidimensional scaling ordination (hereafter NMDS) of the bird communities at each survey point. In an NMDS, the Bray-Curtis distance between points is determined based on the bird communities at each point (i.e. dissimilarity in bird community), which is different from the Euclidean distance in a principal components analysis in that it uses rank orders and, therefore, does not have the same assumptions. The NMDS was performed using the "metaMDS" function 1000 iterations to obtain the lowest stress value which indicates how well the ordination represents the dispersion of survey points with lower stress meaning suggesting a better fit. The axes were then rotated (PC rotation) so that the first dimension describes the most variation among the bird communities at each point. To determine the drivers of bird community composition, we fit the average stem count or cover of each plant species at each point and the other environmental variables (i.e. S, invasion level, fruit proportion, canopy cover, canopy height, openness, Robel score, S_F, patchiness, elevation, and annual rainfall) onto the NMDS with the "envfit" function with 999 permutations within the "vegan" package (Oksanen et al. 2018).

We selected the most abundant non-native and native bird species to determine their species-specific habitat and plant species associations. For the non-native bird species, four bird species were selected, including *Zosterops japonicus* (Japanese white-eye, hereafter JAWE), *Leiothrix lutea* (red-billed leiothrix, hereafter RBLE), *Pycnonotus jocosus* (red-whiskered bulbul, hereafter RWBU), and *Pycnonotus cafer* (red-vented bulbul, hereafter RVBU). In a separate study, these four species accounted for 97.6% of avian seed dispersal events in the same sites used as this study (Vizentin-Bugoni et al. 2019). We also selected two of the three remaining native passerines (Oahu amakihi, OAAM and apapane, APAP), which are primarily insectivorous and nectarivorous, respectively. The Oahu elepaio (*Chasiempis ibidis*) was omitted because it is very rare and under intense conservation. To evaluate if and how specific plant species are associated with bird species, we selected both non-native and native plant species that are known to be important in the diet of bird species or are widespread at our sites. We selected the three most common non-native and the three most common native plant species in the diet of the forest bird community of Oahu. The non-native plant species included *Clidemia hirta*, *Trema orientalis*, and *Rubus rosifolius*, and the three native plant species included *Pipturus albidus*, *Psydrax odorata*, and *Ilex anomala*. The plants selected because they are the most widespread species across our sites are two non-native plants - *Psidium cattleyanum* and *Schinus terebinthifolius* - and two native plant species - *Acacia koa* and *Metrosideros polymorpha*. While all of the non-native plant species we selected bear fleshy fruits, *A. koa* and *M. polymorpha* do not bear fleshy-fruit.

We used linear mixed models with a Gaussian error distribution to relate the abundance of the frugivores to the environmental variables that were fitted to the NMDS and the quadratic effect of elevation since some species may have mid-elevation peaks in their abundance. Additionally, using linear mixed models with a Gaussian error distribution, we related the abundance of the bird species with the stem density or cover of the selected plant species. Site was included as a random variable in all of the species-specific models. Based on their dimension loadings, most of the selected bird species did not seem to relate strongly with the environmental variables or selected plant species in the NMDS, and therefore, we could not build models *a priori*. Because of this, we used an information criterion approach to determine the models that best explained the variation in each species abundance out of a model set that included every combination of predictors possible using the "dredge" function and then averaged the estimates of the models that accounted for 95% of the cumulative model weight using the function "model.avg" in the "MuMIn" package (Barton 2019). The mixed models were performed using the function "glmer" in the "lme4" package (Bates et al. 2015).

Results–Bird abundance

Bird Community Structure: We detected 19,316 birds of 24 species from 15 families during 1501 surveys across approximately three years (Fig. 3). Of these species, two were endemic to Oahu (Oahu amakihi and Oahu elepaio, hereafter OAAM and OAEL, respectively), another endemic to Hawaii (apapane, hereafter APAP), and another non-endemic native species (black-crowned night heron, *Nycticorax nycticorax*) that is typically found near ponds, streams, and marshes. From the NMDS (final stress = 0.1617), the bird communities across the sites showed substantial variation with EKA and Mt. Kaala (hereafter MTK) being the most different (Figs. 3 and 4A). Moanalua Valley (hereafter MOA) and Waimea Valley (hereafter WAI), and Pahole NAR (hereafter PAH) and Kahanahaiki (hereafter KAH) had the most similar bird communities (Figs. 3 and 4A). Additionally, the sites in the Waianae Mtns. (i.e. PAH, KAH, MTK, and EKA) separated from the sites in the Koolau Mtns. (i.e. MOA, WAI, and Tantalus – hereafter TAN) in the NMDS (Fig. 4A).

Many bird species were found in every site, and therefore, their loadings were near the origin in the NMDS; these included the main frugivores on the island (i.e. JAWE, RBLE, RVBU, and RWBU; Figs. 3 and 4B). The species that separated out the MTK, PAH, and KAH bird communities were apapane and Japanese bush-warbler (*Horornis diphone*), with the PAH and KAH bird communities separating from MTK due to the higher abundances of Erckel's francolin

(*Pternistis erckelii*), Kalij pheasant (*Lophura leucomelanos*), rock pigeon (*Columba livia*), and the one observation of the black-crowned night heron at the former two sites (Figs. 3 and 4B). EKA had more scaly-breasted munias (*Lonchura punctulata*), common mynas (*Acridotheres tristis*), and the only observations of the Oahu elepaio (Figs. 3 and 4B) and the rest of the sites (MOA, WAI, and TAN) had similar communities with MOA and WAI having more spotted doves (*Spilopelia chinensis*), zebra doves (*Geopelia striata*), and red-crested cardinals (*Paroaria coronata*) than TAN (Figs. 3 and 4B).

Drivers of Bird Community Composition: Eight environmental variables had significant relationships with the NMDS dimensions and R^2 values ranging from 0.14 – 0.86 (Fig. 4C). These variables included, in order of decreasing R^2, elevation, invasion level, annual rainfall, fruit proportion, species richness, fruit species richness, and canopy height (Fig. 2C). Of these eight variables, elevation, fruit proportion, and fruit species richness had positive relationships with the first dimension (i.e. the dimension that describe the most variation in community structure) greater than 0.50 and canopy height, and invasion level had a negative relationship greater than 0.50 in magnitude. The second dimension had positive relationships greater than 0.50 with fruit proportion, and annual rainfall and negative correlations greater than 0.50 in magnitude with elevation, fruit species richness, and species richness. Twenty-three out of 82 plant species and categories had significant relationships with the NMDS axes and R^2 values ranging from 0.07–0.53 (Fig. 2D). Ten of these species or categories had positive correlations with the first dimension, seven of which were native species. The other two native species (of the 23 important plant species) were negatively correlated with the second dimension.

Species-Specific Habitat Relationships: Overall elevation was the most important variable influencing the abundance of the selected bird species. However, the influence of the environmental variables tended to vary between native and non-native bird species. For instance, elevation or its square term had a negative relationship with JAWE, RBLE, RVBU, and RWBU abundances, all of which are non-native frugivores, although, the 95% confidence interval for the effect of elevation on JAWE abundance did overlap zero (Fig. 5A). However, the abundance of both native species selected, APAP and OAAM, had a positive relationship with elevation or its square term (Fig. 5A). Additionally, OAAM had a negative relationship with the square of elevation even though it had a positive relationship with elevation meaning the highest abundance of OAAM was found at mid-elevation sites (Fig. 5A). Invasion level had a negative relationship with RVBU abundance and a positive relationship with OAAM (Fig. 5A). APAP was the only species to have a relationship with the Robel variable which was positive (Fig. 5A). Canopy cover had a negative relationship with JAWE and RVBU abundances (Fig. 5A). Plant species richness had a positive relationship with JAWE but a negative relationship with RWBU abundance (Fig. 5A). Additionally, average annual rainfall had a negative relationship with JAWE (Fig. 5A).

The amount of the selected plant species only had a relationship with three bird species we selected (Fig. 5B). Of the three most connected native plant species in the Oahu seed dispersal network, *Pipturus albidus* had a positive relationship with the abundance of one frugivore species, RVBU, and one native species, APAP (Fig. 5B). The amount of *Trema orientalis* also had a positive relationship but only on RVBU abundance (Fig. 5B). The abundance of APAP had a positive relationship with *Metrosideros polymorpha* (Fig. 5B). Additionally, the only negative relationship that did not have a confidence interval that encompassed zero was between *M. polymorpha* and RBLE (Fig. 5B). The effects of plant species on the abundance of JAWE, RWBU, and OAAM all had a 95% confidence interval that encompassed zero (Fig. 4B). However, the relationships of JAWE loosely mirrored those of RBLE and RVBU (3 out of 11 in the same direction) and the relationships of OAAM loosely mirrored that of APAP (2 out of 11 in the same direction). Approximately 4 out of 11 relationships of the non-native bird species generally mirror those of the native species. However, 3 of the relationships of the non-native bird species are generally opposite to those of the native species. Specifically, the relationship with *M. polymorpha* is positive with native bird species and negative with non-native species (Fig. 5B).

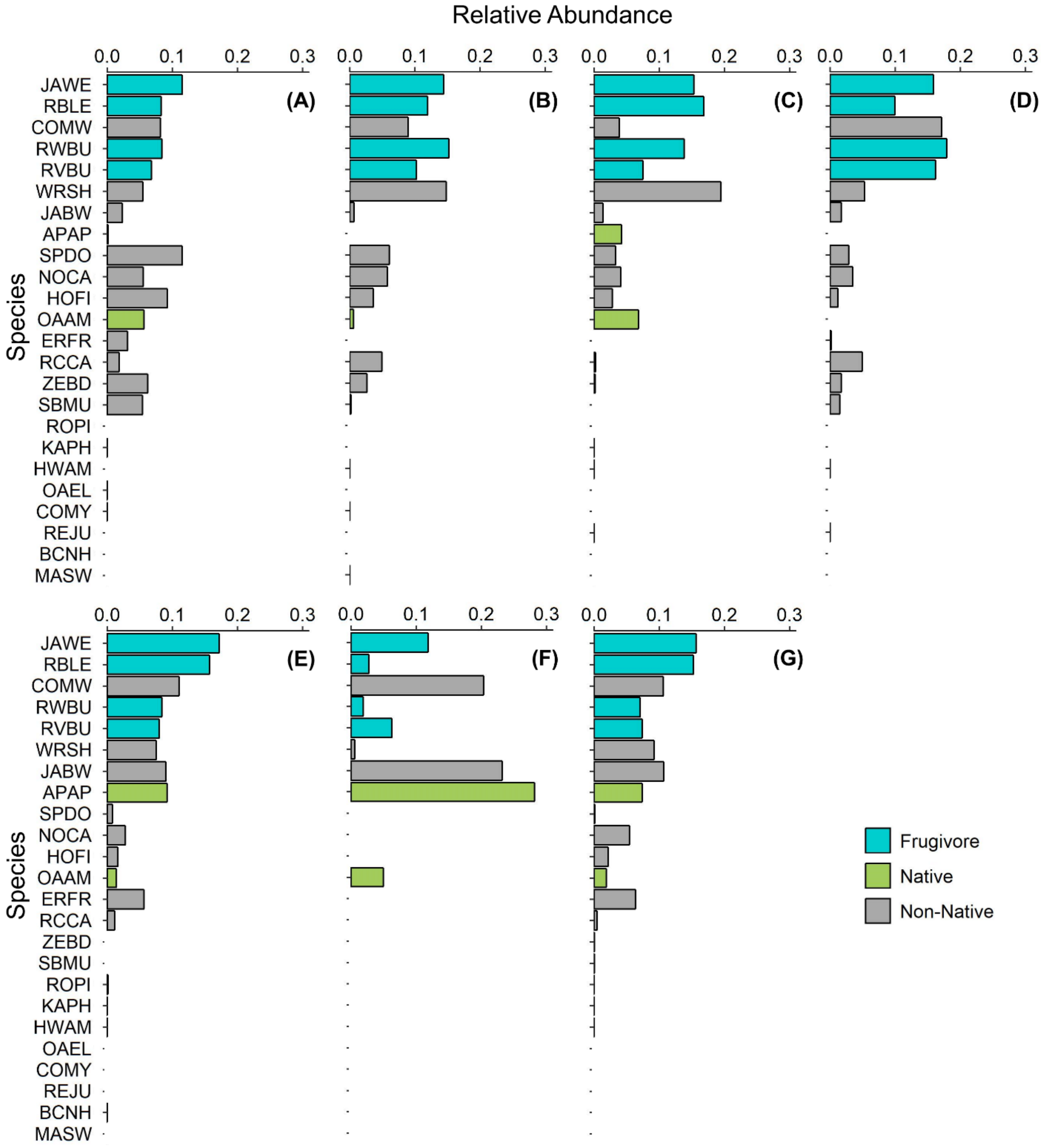


Fig. 3. Relative abundances of bird species at 7 sites. Bird species observed at (A) Ekahanui, (B) Moanalua Valley, (C) Tantalus, (D) Waimea Valley, (E) Kahanahaiki, (F) Mt. Kaala, and (G) Pahole Natural Area Reserve. Graphs A-D are the sites that have the highest proportion of non-natives in their plant communities, and E-G are have more native plant communities.

Fig. 4. Ordination of survey points by site and species. The dispersion of survey points within a 2-dimensional, non-metric multidimensional scaling ordination. (A) shown are the ellipses for each site based on a normal distribution. (B) the bird species loadings are represented by the position of the species code. The species that are in the direction of one of the ellipses is a species that is more unique to that site. The fit of the environmental variable (C) and plant species abundance (D) is represented by the arrows where the length of the arrow is proportional to the strength of correlation. In (D) the red arrows represent non-native plant species, the blue arrows represent native plant species, and the gray arrows represent plant species categories where origin is indeterminable.

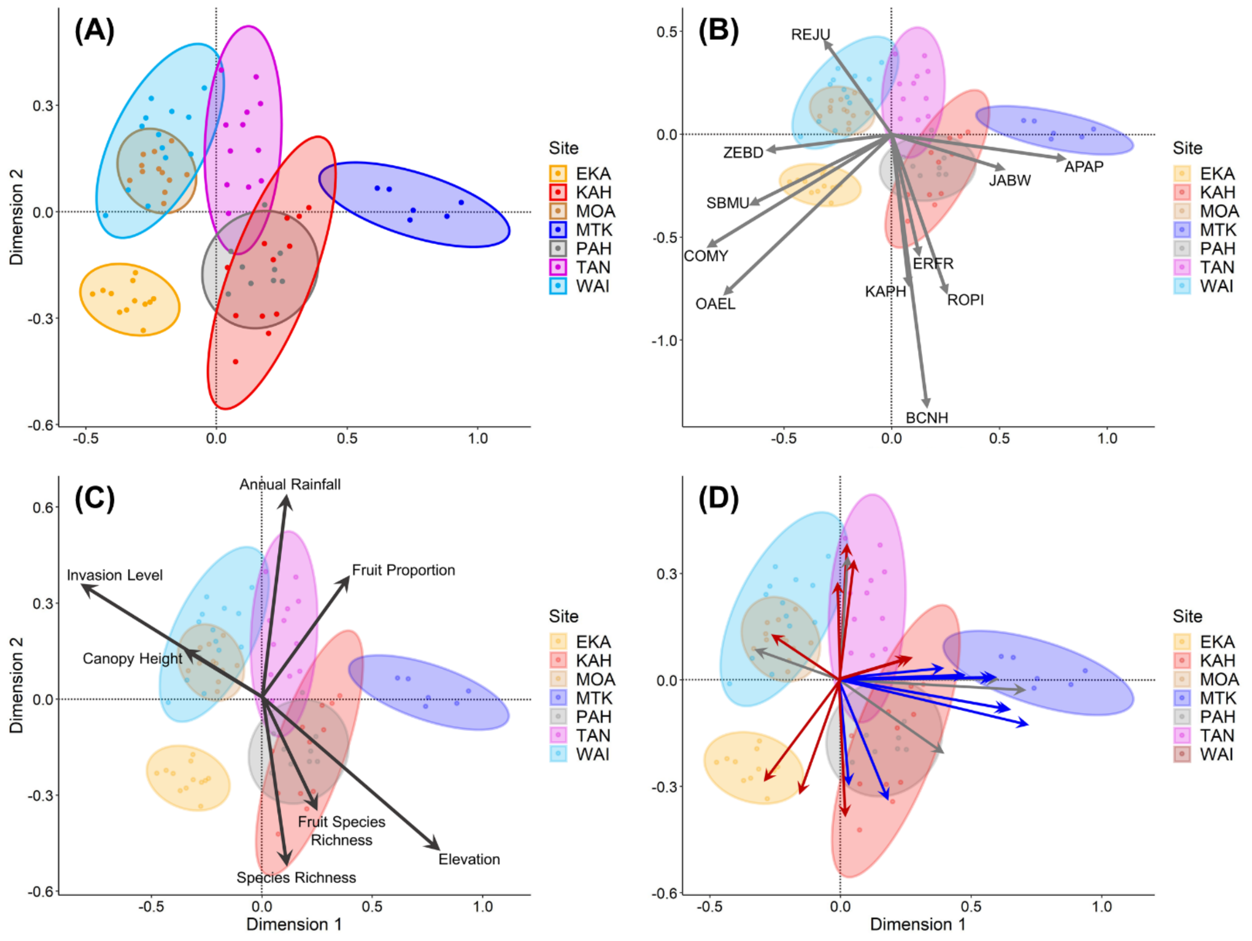
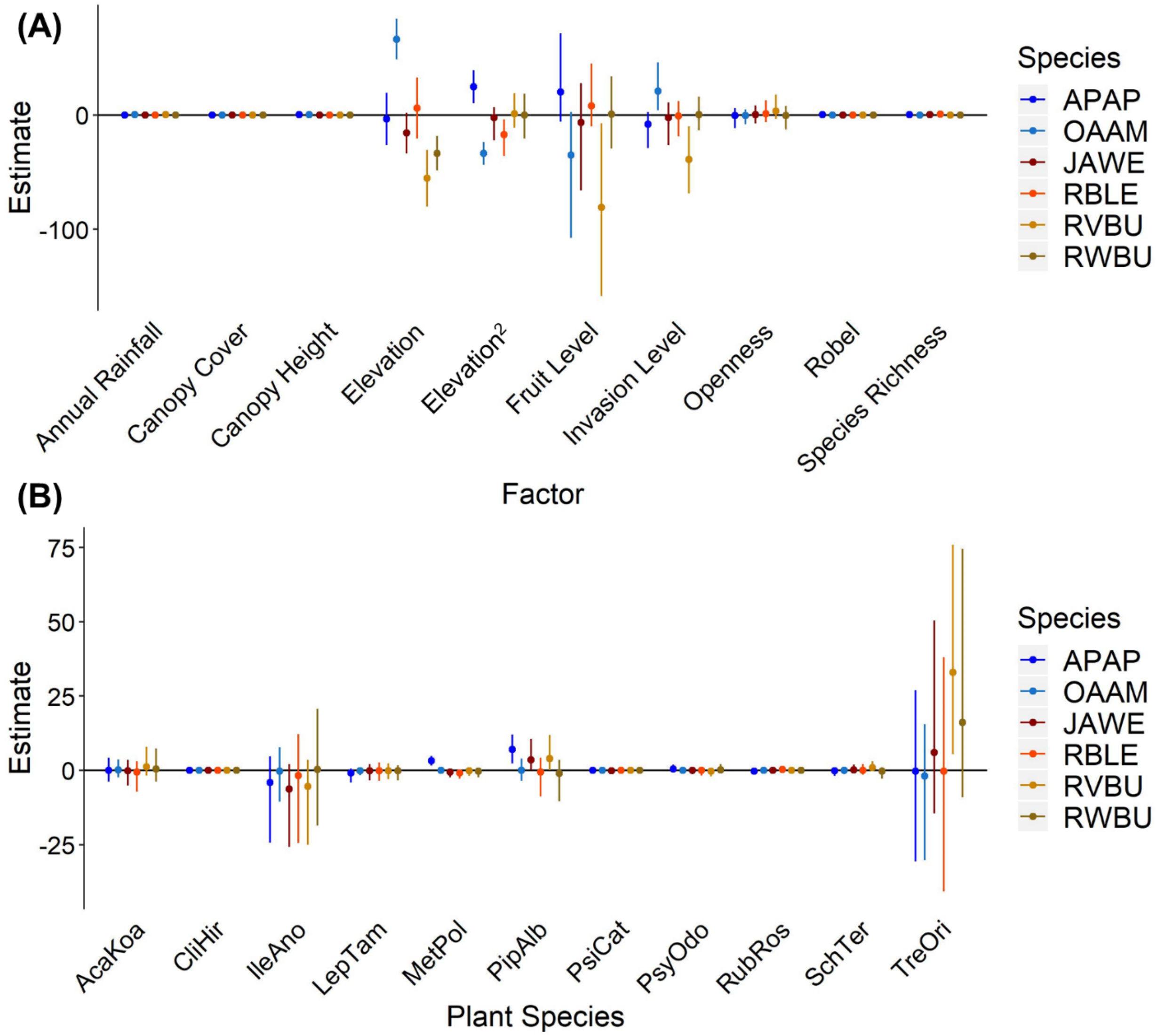


Fig. 5. Model averaged estimates for (A) habitat characteristics and (B) selected plant stem densities. Estimates were averaged over the top liner mixed models (i.e. having a cumulative weight of 95% of a complete model set) predicting each bird species abundance. Blue colors represent native bird species and orange colors represent non-native bird species. Error bars represent 95% confidence intervals for each estimate. See text for bird and plant species' codes, respectively.



Radio-Telemetry

Radio-telemetry was a key component of our data collection for the movement ecology models. We summarize our data collection of birds that had transmitters attached here (Table 2). Results of activity of these birds is detailed in subsequent tasks.

Table 2. Radio-telemetry of birds with transmitters occurred at two sites (WAI and PAH) from August 2015 to December 2017.

Species	Transmitter life (months)	Individuals Tagged	Number of Observation Hours
Japanese white-eye	3–4	39	278
red-billed leiothrix	4–6	34	229
red-whiskered bulbul	7–9	17	250
red-vented bulbul	7–9	7	37
zebra dove	12–18	5	50
spotted dove	12–18	2	15

Avian Activity from radio-telemetry: We documented the home ranges of birds using radio-transmitters as a measure of seed dispersal potential (Fig. 6). Initial home range estimates were made by the tracking of birds using hand-held antennas. Subsequent estimates of bird locations have also included detections from our Automated Receiving Units (ARUs)—a telemetry system involving an array of towers that take continuous (detection period determined by user) recording of transmitter locations, day and night. ARU tracking allowed us to drastically increase our bird locations from 2,443 points using hand tracking of 16 birds of three species to 590,295 points tracking 36 birds of three species (Table 3).

Table 3. Summary of telemetry data by species.

	JAWE	RBLE	RWBU
# of hand tracking locations	701	798	944
# of days on ARU	390	649	796
# of activity points	194,800	194,345	201,150

ARU tracking also allowed us to model the activity profile for each of three common bird species, all dominant seed dispersers in our study: Japanese white-eye, red-billed leiothrix, and red-whiskered bulbul. We present the activity profile for a single bird for each of these species (Fig. 8). Data indicate inactivity or activity—based on a calibrated threshold of transmitter signal strength—over a consecutive multiday period (*Zosterops*=14d, *Leiothrix* = 20d, *Pycnonotus* =14d). Data were modeled using a generalized additive mixed model with day as a random factor and a binomial error distribution. Data used in the model were obtained using our three-tower automated radiotelemetry system. Note the small signal of nocturnal activity ~2300h for all three species.

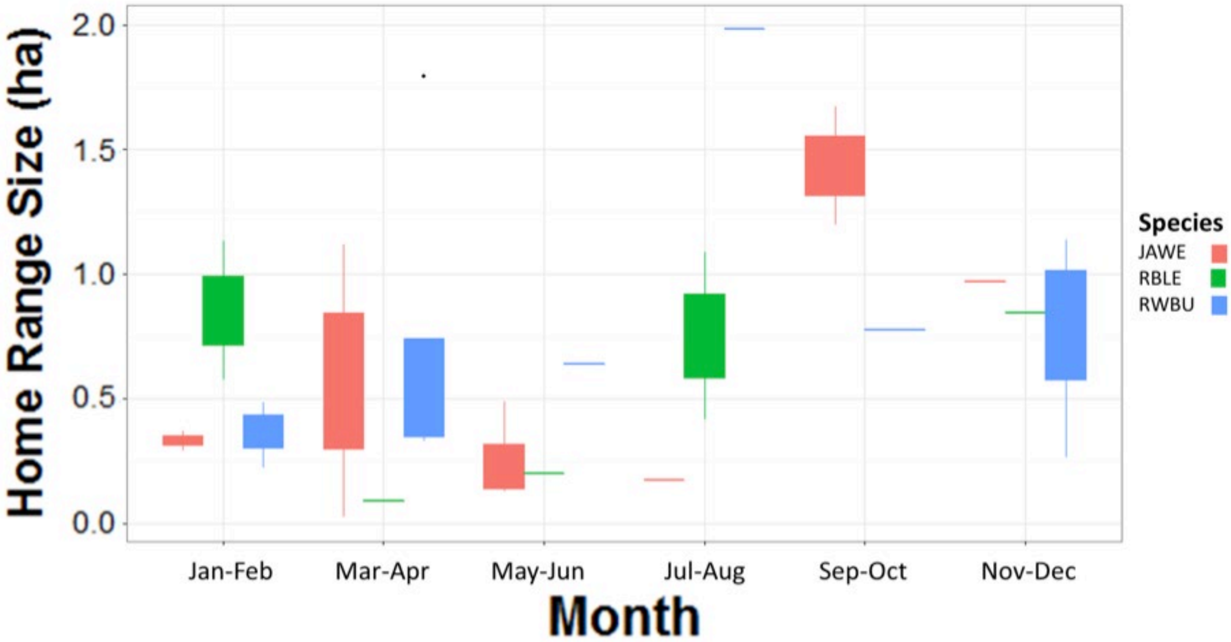


Fig. 6. Home range size per month by species as determined by hand tracking.

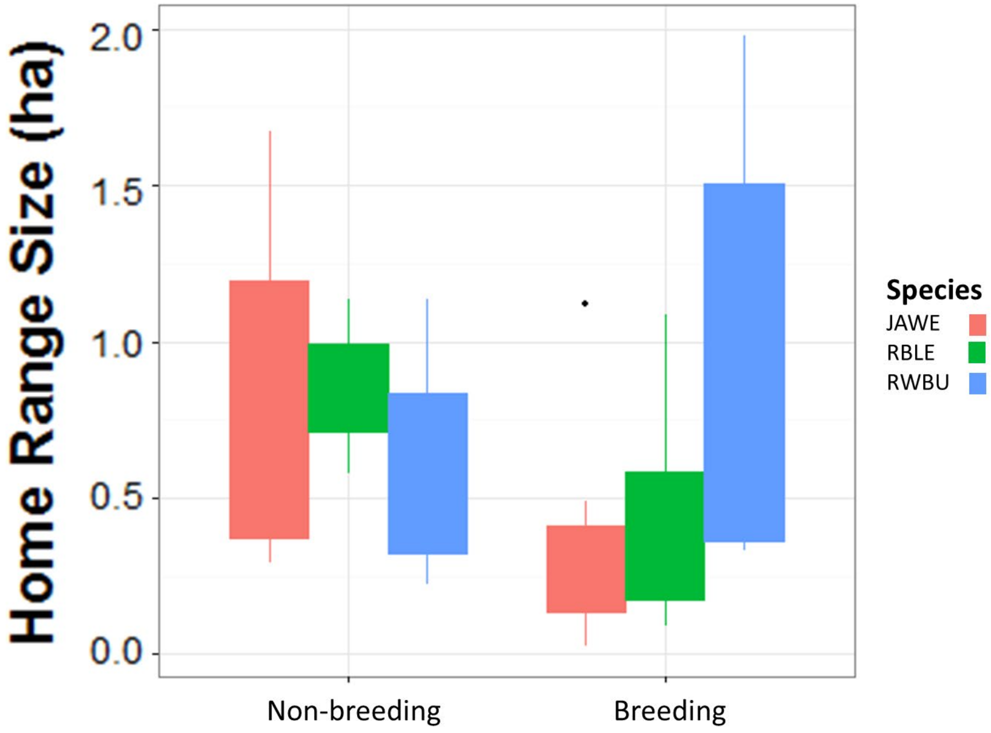


Fig. 7. Home range size comparison between breeding and non-breeding season.

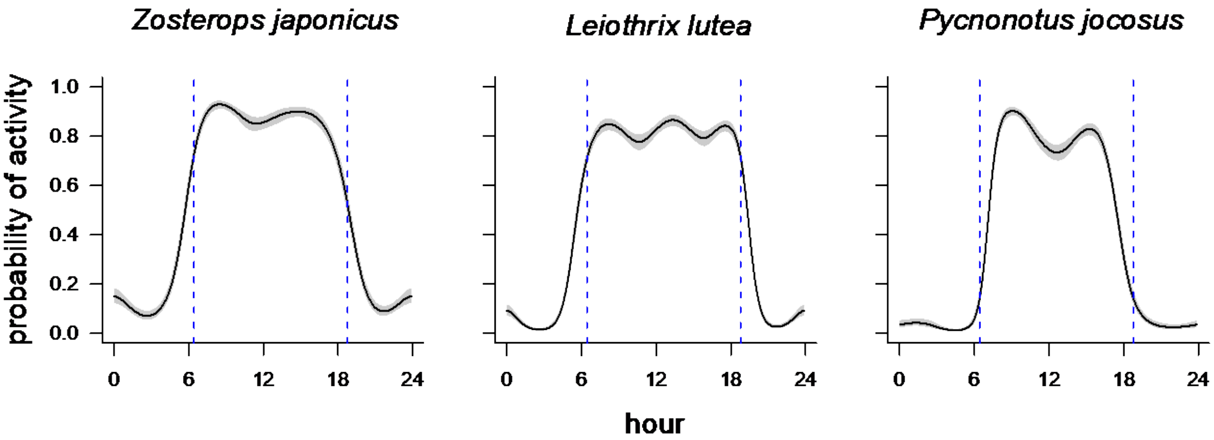


Fig. 8. Modeled activity profile for each of three common bird species.

We also modeled the activity profile of a red-vented bulbul (*Pycnonotus cafer*), a dominant seed disperser in our study (Fig. 9). Data indicate inactivity or activity—based on a calibrated threshold of transmitter signal strength—over a consecutive 15-day period. Data were modeled using a generalized additive mixed model with day as a random factor and a binomial error distribution. Data used in the model were obtained using our three-tower automated radiotelemetry system.

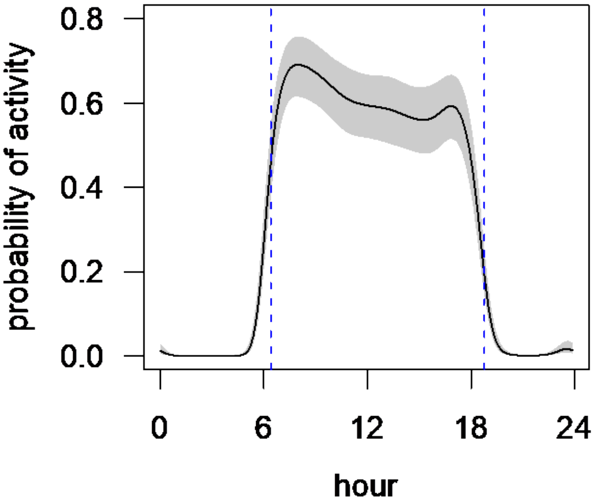


Fig. 9. Modeled activity profile of a red-vented bulbul.

Rodent Abundance

We live trapped animals using Sherman and Tomahawk traps for determining the abundance of rodents as dispersers. We generated a summary of the number of individuals of each species by site as well as the grand totals by species and by site (Table 4). Also included are the number of traps established at each site and the total number of trap nights at each site. House mouse dominated the captures at most sites and were surprisingly common. Abundance data suggest a potential inverse relationship between rat and mouse abundance.

Table 4. Small mammal capture summaries by site.

	site code							
species	**EKA**	**KAH**	**MOA**	**MTK**	**PAH**	**TAN**	**WAI**	**Total**
black rat	14	15	31	5	25	16	24	130
house mouse	19	116	42	23	45	117	29	391
Asian mongoose			11			1	2	14
Pacific rat	4	3	9	7	4	5	1	33
number of traps	50	50	50	50	50	50	50	350
total trap nights	1450	1300	1449	1000	1250	1395	1150	8994
total number of captures	**37**	**134**	**93**	**35**	**74**	**139**	**56**	**568**

Captures of mongoose were unintentional and were not desirable so we modified our trapping protocols to reduce their captures. Trap openings switched to late in the day greatly reduced mongoose captures of this diurnal species. We then used these capture data to assess seasonal variation in apparent abundance (individuals per trap night) of rats at each of the seven study areas (Fig. 10). Data are total numbers of both rat species in our study, Pacific rat and black rat. Data were modeled using a generalized additive model for each site, using a Gamma error distribution. Shaded areas show 95% confidence intervals. Vertical, dotted blue lines indicate the start of a new calendar year. Tick marks indicate months, starting in October 2014 and running until October 2016.

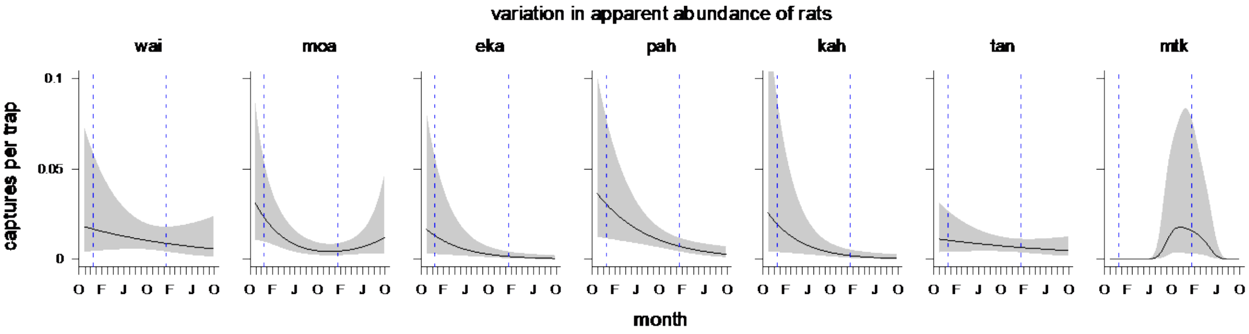


Fig. 10. Rat abundance at seven sites over a two-year period.

Rodent capture data were also used to assess seasonal variation in apparent abundance (individuals per trap night) of mice at each of the seven study areas (Fig. 11). Data are total numbers of house mice (*Mus musculus*). Data were modeled using a generalized additive model for each site, using a Gamma error distribution. Shaded areas show 95% confidence intervals. Vertical, dotted blue lines indicate the start of a new calendar year. Tick marks indicate months, starting in October 2014 and running until October 2016.

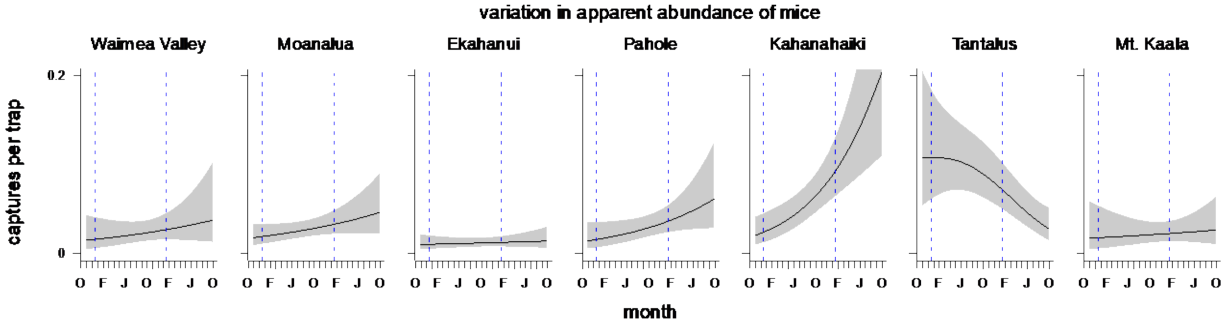


Fig. 11. Mice abundance at seven sites over a two-year period.

Task 3. Quantify structure of seed dispersal networks

As we predicted based on studies on other Hawaiian Islands (Medeiros 2004, Foster and Robinson 2007), two bird species, Japanese white-eye and red-billed leiothrix are hyper-abundant based on mist-net captures and point-counts and appear to form a major component of bird communities on Oahu as well. Each of these species forms substantial links to a variety of plants (via seeds) in all of our study sites. These are dynamic avian communities, as recent as 20 years ago red-billed leiothrix were uncommon throughout most of Oahu and their populations have only recently exploded. A surprising finding was the potential importance of red-whiskered bulbuls as seed dispersers on Oahu. Perhaps this should not have been unexpected, red-whiskered bulbuls are effective dispersers on other islands where they have been introduced (Mandon-Dalger et al. 2004, Linnebjerg et al. 2010). Yet, one rarely encounters this species in these forests and rather sees their abundant congener, the red-vented bulbul.

Also surprising was the relatively low number of captures of rats at our sites. Rodent populations are highly cyclical based largely on environmental conditions, so it is possible that we simply sampled these species during a period of low populations. Interestingly, there appears to be an inverse relationship between rat populations and mouse populations at many of our sites. This is also consistent with previous research showing that mouse populations can respond with rapid growth when rat populations are low. Rodent diets remain to be fully quantified by data thus far suggest that they are not major dispersers of intact seeds.

<u>Study species—plants:</u> We initially focused on seven non-native invasive plant species that were believed to be important plants on Oahu including strawberry guava (*Psidium cattleyanum*), firetree (*Morella faya*), miconia (*Miconia calvescens*), kahili ginger (*Hedychium gardnerianum*), Florida blackberry and/or other blackberry/raspberry species (*Rubus* spp.), Koster's curse (*Clidemia hirta*) and Christmasberry (*Schinus terebinthifolius*), and eight ecologically important native species including olapa (*Cheirodendron trigynum*), kanawao (*Broussaisia arguta*), alani (*Melicope clusiifolia*), kolea (*Myrsine lessertiana*), kawau (*Ilex anomala*), ohelo (*Vaccinium* spp.), pilo (*Coprosma* spp.), and pukiawe (*Leptecophylla tameiameiae*). As we did with the vertebrate dispersers, this list was only a starting point for the species we studied, and several additional species were commonly encountered at the different sites and were added to these lists (e.g. māmaki, *Pipturus albidus*). All native and non-native plant species are understory shrubs and subcanopy trees, except for the herb *Hedychium gardnerianum*. The following trees become

canopy trees under some conditions, *Psidium cattleyanum*, *Morella faya*, and *Cheirodendron trigynum*. All species have vertebrate-dispersed seeds.

Vegetation Sampling

Surveys, data compilation, and analyses were completed for the primary vegetation surveys. Our approach was as follows. Vegetation was sampled using a combination of point intercept (pole intercept) and belt transects. These methods yielded data that were used to determine percent cover for all plant species, while also providing density and dominance estimates for woody species.

Point intercept: Approximately 10, 50-m-long, point intercept transects were established in a stratified random pattern within an area of focus. Plant cover was recorded every meter (50 points/transect x 10 transects = 500 points). At each point, each species that touched a vertical line was recorded as present (a hit). For vegetation ≤4 m tall the line was a pole (0.5-inch-diameter tent pole with four, 50-cm segments joined by shock cord). For vegetation >4 m tall, a densiometer was used to record "hits". The sampling was stratified vertically, such that each species may be recorded as present in multiple strata at each sampling point (e.g., at least 0-2 m and >2 m) but was recorded as present only once within a stratum. Data for each point must be recorded together and identified by transect, point, and stratum, so each point can be reconstructed. All fleshy-fruited plant species were identified to species. Other plants were identified to species if they are important components of the vegetation (i.e., either abundant or structurally significant). Minor, non-fleshy-fruited components of the vegetation were recorded in growth form categories (grass, forb, woody seedling, etc.).

Belt transects: Along the point-intercept transects, woody plants were sampled in belt transects using the following categories:

-Individuals with stems 1-2.4 cm dbh counted in 2-m-wide transects.
-Individuals with stems 2.5-4.9 cm dbh counted, and dbh measured, in 2-m-wide transects.
-Individuals with stems ≥ 5 cm dbh counted, and dbh measured, in 4-m-wide transects.

Fruiting phenology

To determine fruit availability and seasonality we conducted phenology surveys and counted fruits on previously marked plants along vegetation sampling transects (Table 5). Phenology data can provide information about when species are flowering or fruiting as well as the relative abundance of different species during a bioblitz (our term for a focused but short-term survey effort at a site). Across a site, a representative sample of at least 10 individuals (or patches) of every fleshy-fruited plant species was mapped, numbered, and flagged for monitoring. For each species, plants from a range of sizes were chosen. For dioecious species, only female plants are chosen. For woody species, all stems ≥ 1 cm dbh were counted. For woody species with stems ≥ 2.5 cm dbh, a subset of 10 were measured and recorded. For herbaceous species, lianas, and other growth forms not suited to dbh size classes, representative patches are chosen. At chosen intervals, the numbers of fruits on the flagged individuals were estimated by scanning plants and assigning fruit numbers to the following categories, in which each order of magnitude is divided into three equal intervals: 1-3, 4-7, 8-10, 11-39, 40-69, 70-99, 100-399, 400-699, 700-999, 1000-3999, 4000-6999, 7000-9999. For woody plants with diameters ≥ 1 cm dbh, the entire plant was assessed. For all other plants, the number of fruits in a representative 1 m^2 patch are assessed and the percent cover of that plant in the 1 m^2 patch was estimated, as follows:

1) A fixed-area quadrat in a random point in the patch,
2) estimate % cover of the fruiting plant species within the quadrat,
3) count the number of fruits within the quadrat.
4) Flipping quadrat over to do four, contiguous 0.5 m x 0.5 m quadrats.

Fruits available per unit area can be calculated two ways: 1) for species with dbh measurements, using the relationship between dbh and fruit numbers, and 2) for species with cover measurements, the relationship between cover and fruit measurements. Each of the seven sites was visited eight times, once every two months over 2 years.

Table 5. Phenology survey summary data.

		site code							
Scientific Name	**native status**	**EKA**	**KAH**	**MOA**	**MTK**	**PAH**	**TAN**	**WAI**	**Total**
Aleurites moluccana	N					45			45
Alyxia stellata	Y		88			117			205
Antidesma platyphyllum	Y		32			47	70		149
Ardisia crenata	Y						81		81
Ardisia elliptica	N			36			81	78	195
Bischofia javanica	N						77		77
Bobea elatior	Y		16				8		24
Broussaisia arguta	Y				53				53
Cecropia obtusifolia	N						36		36
Cestrum nocturnum	N						93		93
Charpentiera obovata	Y					13	39		52
Cheirodendron platyphyllum	Y				56				56
Cheirodendron trigynum	Y				46		24		70
Cinnamomum burmannii	N						88		88
Citharexylum caudatum	Y						80		80
Clermontia kakeana	Y						48		48
Clidemia hirta	N	89	92	91		108	96	80	556
Coffea arabica	N	100							100
Coprosma foliosa	Y		80			39			119
Coprosma ochracea	Y				52				52
Cyanea angustifolia	Y						11		11
Cyrtandra cordifolia	Y						91		91
Cyrtandra spp.	Y				21	18			39
Diospyros hillebrandii	Y					86			86
Elaeocarpus angustifolius	N						18		18
Elaeocarpus bifidus	Y		3			71	31		105
Ficus spp.	N			50			81	5	136
Freycinetia arborea	Y						57		57
Hedychium spp.	N						50		50
Gynochthodes trimera	Y						14		14

Ilex anomola	Y		16		83	14	20		133
Kadua affinis	Y		76			86	80		242
Labordia waiolani	Y				46				46
Lantana camara	N	62	79	70		73		68	352
Leptecophylla tameiameiae	Y		61		62			29	152
Melicope spp.	Y				20				20
Myrsine lanaiensis	Y					55			55
Myrsine lessertiana	Y					14			14
Myrsine spp.	Y		61		67				128
Nertera granadensis	Y				51				51
Nestegis sandwicensis	Y		71			53			124
Paederia foetida	N			70			39		109
Passiflora edulis	N							18	18
Passiflora suberosa	N	88	60	16		32		71	267
Pimenta racemosa	N			61					61
Pipturus albidus	Y		1			15	79		95
Pittosporum glabrum	Y		47			74	55		176
Planchonella sandwicensis	Y		82			88	1		171
Psidium cattleianum	N	100	80	91		99	74	80	524
Psidium guajava	N	98		56		88	86		328
Psychotria hathawayi	Y		9			55			64
Psychotria kaduana	Y						2		2
Psychotria mariniana	Y		99			59	158		316
Psydrax odorata	Y	34	80			44		80	238
Pteralyxia macrocarpa	Y					12			12
Rivina humulis	N	100							100
Rubus argutus	N				59				59
Rubus rosifolius	N	22	80	22		78	77		279
Santalum freycinetium	Y		12			4		17	33
Scaevola gaudichaudii	Y		88				16	42	146
Schefflera actinophylla	N	66		80			61	16	223
Schinus terebinthifolius	N	98	80	69		56		48	351
Smilax melastomifolia	Y				66				66
Streblus pendulinus	Y					9			9
Syzygium cumini	N	88		77				80	245
Syzygium sandwicensis	Y				27				27
Touchardia latifolia	Y						49		49
Trema orientalis	N			70					70
Urera glabra	Y						23		23
Vaccinium calycinum	Y				52				52
Wikstroemia oahuensis	Y		82			41		79	202
Xylosma hawaiiense	Y		65			57	37		159
Dianella sandwicensis	Y		75		66			4	145
Diospyros sandwicensis	Y		92			42	10	24	168
		945	**1707**	**859**	**827**	**1692**	**2041**	**819**	**8890**

We determined the seasonal fruiting phenology for all common plant species in our sites. Our initial analyses that are representative of our approach are for *Clidemia hirta*, a highly invasive, non-native fruiting species on Oahu (Fig. 12). Plots show the probability of having ripe fruit for populations of *Clidemia* at six of our study sites (the species does not inhabit the Mount Kaala site). Data were modeled using a generalized additive model for each site, using a binomial error distribution. Shaded areas show 95% confidence intervals. Vertical, dotted blue lines indicate the start of a new calendar year. Tick marks indicate months.

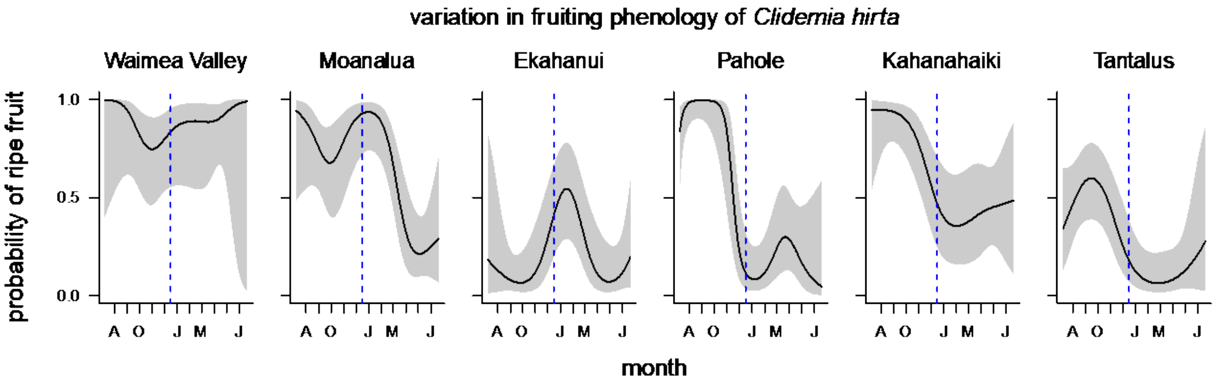


Fig. 12. Variation in fruiting phenology of Clidemia hirta.

Task 4. Assess the impact of competition on diet

These Tasks work with each other largely hand-in-hand, with some aspects of Task 5 dependent on results from Task 4 (e.g. seeds have to be digested in Task 4 to see how they germinate in Task 5). The 14 birds from four species that we have brought into captivity this year has allowed to rapidly generate the necessary data. We have collected gut-passage timing data as well as fruit preference trials on nearly all of these birds. Initial results suggest that seed passage time through the digestive tract of these birds may be far shorter than reported in other studies (Medeiros 2004).

Methods–Competition

To determine the foraging behavior of these species, we conducted observations twice monthly at four sites from January through July in 2016 and 2017. The four sites were Ekahanui Valley (21°26'36.98"N, 158°04'52.11"W; hereafter EKA), Pahole Natural Area Reserve (21°31'56.24"N, 158°10'42.97"W; hereafter PAH), Waimea Valley (21°37'49.97"N, 158° 01'49.59"W; hereafter WAI), and Moanalua Valley (21°22'37.77"N, 157°52'16.62"W; hereafter MOA). The sites ranged in elevation (108–594 m above sea level) and mean annual rainfall (1107–1884 mm). In addition, the sites varied in their plant and bird communities (Vizentin-Bugoni et al. 2019). The sites were visited every other week with 13–15 days between visits. Visits started approximately at sunrise and concluded before 1300. Depending on weather, four observations were conducted during each visit at four randomly selected points from 9–13 (proportional to size of site) previously established points at least 150 m apart. Observations were not conducted in heavy rain due to altered behaviors and lack of foraging activity. After the same four points were visited twice, a new set of four points were randomly chosen (with replacement).

At each point the observation period would last one hour with a five-minute point count at the beginning and the end. For the point counts during the observation period, all birds seen and/or heard were recorded keeping track of individuals as much as possible to avoid double counting.

During the one-hour observation, all observations of the five focal species were recorded. The bird's maximum and minimum height in the tree, location (interior or periphery) in the tree, foraging behaviors (gleaning, flycatching, fruit consumption, and nectar consumption), foraging posture (upright or hanging), mode of movement (hop, walk, flight), and any other behaviors were recorded. In addition, the plant species the bird was interacting with was recorded using an intensity of interaction score (0 = no interaction, 1 = quickly move through, 2 = perching/singing, 3 = foraging in the plant on arthropods, 4 = consumption of plant produced resource). If the bird was in a flock, the flock size was noted and the height range for the flock was recorded. Competitive interactions were also recorded. In order to be able to capture the most behaviors, the observations were dictated into a voice recorder and then later transcribed. All observations were conducted and transcribed by J. Gleditsch.

We ran a principal component analysis (PCA) on the morphological data with the individual bird as the experimental unit. From this analysis we then calculated the Euclidean distance (hereafter D_E) between each of the species' centroids at each site to determine the similarity of their morphologies. The similarity between the species' foraging niche at each site was determined by calculating the proportional similarity index (hereafter PS)(Feinsinger et al. 1981)between the frequency distributions of the various observed foraging behaviors (i.e. gleaning, flycatching, nectar feeding, frugivory) of between each species pair at each site. The proportional similarity index ranges from 0, which correspond to no difference in the distributions to the minimum frequency a behavior is observed meaning the distributions are the most different at 1. We used the DE and PS to determine if there was a relationship between the species' similarity in foraging niche and the similarity in their morphologies by running a generalized linear model with PS as the dependent variable and the DE as the independent variable with a quasibinomial error distribution and only used species with at least 5 observations.

Results–Competition

The morphological dissimilarity (DE) between the bird species had an insignificant negative relationship with the foraging niche similarity (PS) between the bird species (t = -2.019; DF = 16; P = 0.0606; McFadden's $R^2 = 0.20$) indicating that the foraging niches of these species are more similar when their morphology is more similar (Fig. 13)..

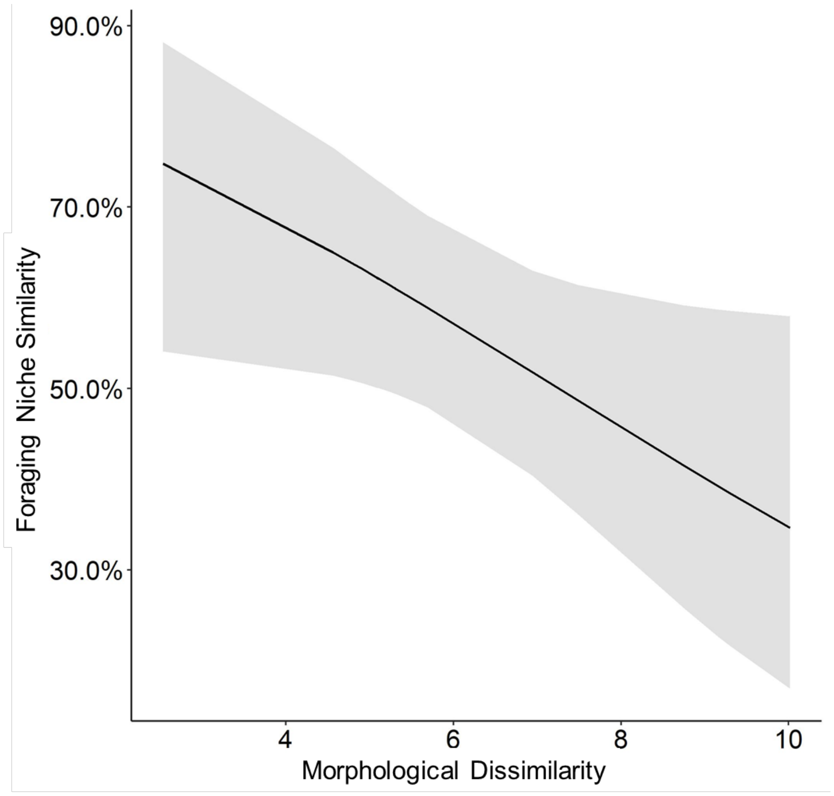


Fig. 13. Foraging niche. The predicted relationship between foraging niche similarity and morphological dissimilarity of the four main frugivore species as predicted by the linear model (See text for details). Error ribbon represents the 95% confidence interval.

Methods–Aviary Experiments

We determined if pairs of frugivore species negatively influenced the foraging of one another through competitive interactions by conducting aviary experiments. Two individuals of two different species were placed in separate cages that were adjacent to one another. The cages were separated by a curtain so that the individuals would not become acclimated to the presence of the other. Fruit displays were hung on the side of the cage so that the center of each array was approximately 6cm from the one in the adjacent cage with 5 fruits of the same species on each display. At the start of the trial the curtain was removed allowing for the presence of the other species to influence foraging behaviors. The trials lasted 30 minutes and recorded for later analysis.

From each video the start and end times each foraging event on the display was recorded. We then determined if the species were avoiding the other by determining if foraging times overlapped between the individuals below levels predicted by chance. To do this we adapted analysis used in song overlap studies (i.e. SONG, Masco et al. 2015). We also compared the amount of fruit removed during the trials for each species using generalized linear mixed models with bird species and a fixed effect, trial as a random effect, and a Poisson error distribution. The results were then compared to the same comparison during fruit choice experiments but with fruit size as another random effect.

Results–Aviary Experiments

We ran a total of 66 competition trials (JAWE = 28, RBLE = 41, RVBU = 35, RWBU = 22, ZEBD = 6). During these trials three of the species removed a similar amount of fruit from the display (JAWE, RBLE, RVBU) and RWBU removed the most and ZEBD removed the least (Fig. 14A). When these results are compared to the amount of fruit removed during fruit choice experiments conducted in the same aviaries (N=208 trials; Fig. 14B), some interesting patterns emerge. When a heterospecific is not present (i.e. the fruit choice experiments), RVBU and RWBU are predicted to remove a similar amount of fruit (Fig. 14B). However, when a heterospecific is present (i.e. the competition trials) RVBU remove less fruit than RWBU. This suggests that potential competition with heterospecific may cause less frugivory in RVBU and have little effect on RWBU. (RVBU and RWBU have similar morphologies). We are currently going through the videos of the trial to determine the causal relationships that may explain the variation in fruit removal in the present of heterospecific. The preliminary results may suggest that RWBU may be heterospecifically dominant to the other species or that they do not perceive competition in the same way as the other species. The little fruit removal we observed by ZEBD is likely due to their lower frugivory rates and not due to heterospecific interactions.

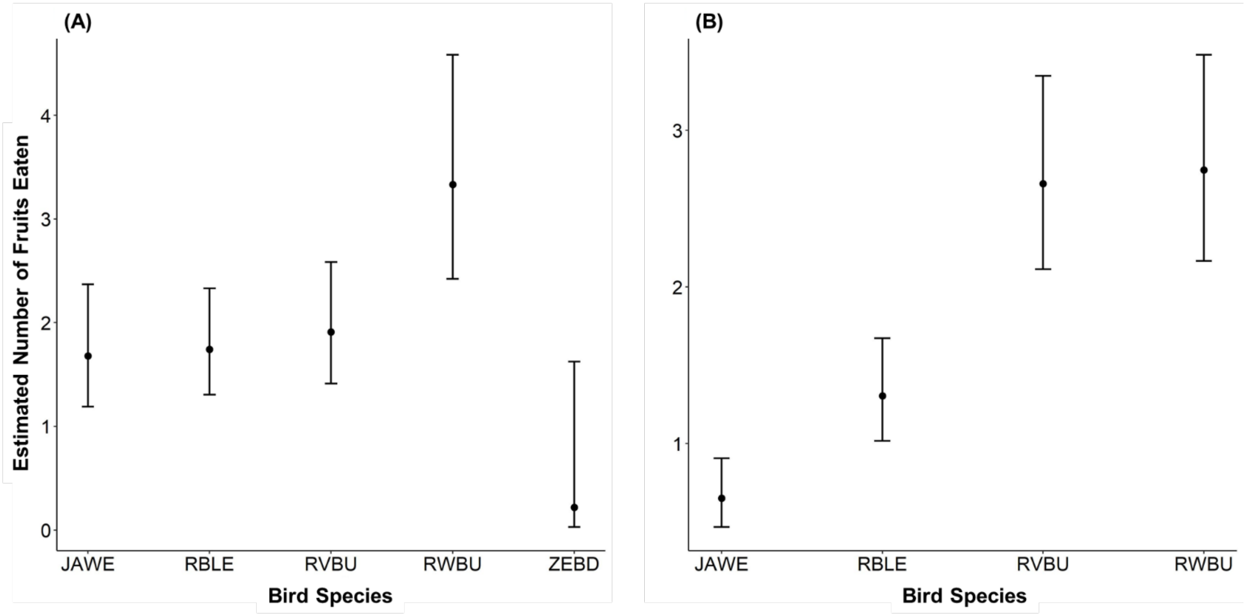


Fig. 14. Aviary feeding trials. The average amount of fruit removed during the (A) competition trials and (B) fruit choice experiments for each bird species as predicted by the generalized linear mixed models. Error bars represent 95% confidence intervals.

Methods–Fruit Preference

In order to determine the fruit color and size preferences of the four main frugivores, we conducted a series of fruit choice experiments on captive birds. Birds were captured in the wild at five of the seven study sites (EKA, KAH, MOA, TAN, and WAI). They were housed in a 16.5 x 15.25 x 30.5 cm cage during transportation to the aviary. In the aviary the birds were housed in a 1 x 1 x 1.5 m cage with a removable divider transecting the cage in the middle. In one half of the cage we place fake vegetation and many perches. This side of the cage was also were they were fed their daily diet of papaya, egg, and ground up kibble. The other side of the cage just had a single "T" shaped perched which we used to display the two fruit types the birds had to choose from during experiments. After a two-day acclimation period, food was withheld from the bird for two hours starting at sunrise. After the two-hour starvation period the divider was place in the cage so that the bird was on the opposite side of the cage as the "T" perch and could not see through the divider. This was done to limit the disturbance caused by the set-up of the experiment. Eight fruits of each type were placed on displays that had spokes extending out from a central ring. This allowed us to control for the accessibility of the fruit which may influence the bird's choice. The displays were made from a ¼ inch PVC coupling and sharpened zip ties. The position the that ran along the perch towards the center was the most accessible and the position that ran in line with the perch away from the center was the least accessible. This is because the bird was able to access the fruit in the most assessable position from the perch but had to hop onto the display to access the fruit in the least accessible. Each position got an accessibility score from one to five with one being the most accessible. While the bird was sequestered to the opposite side of the cage from the "T" perch, we placed the displays on each end of the "T" perch. We then started the trial by removing the divider allowing the bird to make a choice between the two types of fruit. Each experiment lasted 30 min and were video recorded so that there was no disturbance from the presence of an observer. We ran a total of four experiments a day with 45 min starvation period between each trial and day between each day we ran the experiment. Shade cloth and a tarp were used to control the lighting conditions within each cage. Each bird was kept in captivity for no longer than 30 days. Each experiment was set up to test the bird's preference between fruit functional traits (i.e. color – red, blue, white; and size – total mass of fruit on the display).

From the recording of the experiments the following data was collected: the side of the cage each type of fruit was on, the time of each interaction with each individual fruit, the order in which the bird interacted with the fruit, and the intensity of interactions (scored: 0=no interaction, 1=inspection, 2=quick peck, 3=multiple pecks or attempted ingestion, 4=ingestion of fruit material). We then ran mixed models with trial and bird individual as random effects and color (only red and blue since we have not finished watching the videos), size, and accessibility score as fixed effects. In total we ran three different models for each bird species to determine if size and colored influence the bird's probability of ingestion (binomial error distribution), the order in which the bird interacted with the fruit (cumulative link), and the intensity of interaction (cumulative link).

Results–Fruit Preference

Overall accessibility did influence the choices the birds made during the experiments. The more accessible fruit had a higher probability of being eaten, chosen first, interacted with more intensely (Tables 6-8, and Figs. 15,16). Additionally, across the species smaller, blue fruits had a higher probability of being eaten, chosen first, interacted with more intensely. When compared to the networks, the majority of the species in the network have small blue fruits (15/44). Furthermore, both of the species that account for 50% of the seed dispersal events observed had small blue fruits (*Clidemia hirta*, *Trema orientalis*).

- 11/27 invasives in the network have blue fruits
- 7/15 natives in the network have blue fruits

Table 6. Fruit ingestion probabilities. Results from generalized linear mixed models.

Bird Species	Factor	Estimate	SE	z-value	p-value
JAWE	**Intercept**	**-1.90**	**0.62**	**-3.05**	**0.002**
	Accessibility	**-0.59**	**0.14**	**-4.13**	**<0.001**
	Color (red)	0.08	0.44	0.17	0.863
	Mass	0.01	0.02	0.61	0.545
	Color:Mass	**-0.06**	**0.03**	**-2.08**	**0.037**
RBLE	Intercept	0.55	0.45	1.22	0.222
	Accessibility	**-0.34**	**0.08**	**-4.19**	**<0.001**
	Color (red)	**-1.85**	**0.30**	**-6.08**	**<0.001**
	Mass	**-0.13**	**0.03**	**-3.71**	**<0.001**
	Color:Mass	**0.11**	**0.04**	**3.10**	**0.002**
RVBU	**Intercept**	**0.93**	**0.29**	**3.18**	**0.001**
	Accessibility	**-0.13**	**0.07**	**-1.98**	**0.048**
	Color (red)	**-2.22**	**0.25**	**-8.76**	**<0.001**
	Mass	**-0.02**	**0.01**	**-4.20**	**<0.001**
	Color:Mass	**0.03**	**0.01**	**3.17**	**0.002**
RWBU	**Intercept**	**0.72**	**0.33**	**2.20**	**0.028**
	Accessibility	**-0.17**	**0.07**	**-2.41**	**0.016**
	Color (red)	**-2.06**	**0.23**	**-8.87**	**<0.001**
	Mass	**0.01**	**0.00**	**2.75**	**0.006**

Table 7. Results from cumulative link mixed models testing the intensity of interaction.

Bird Species	Factor	Estimate	SE	z-value	p-value
JAWE	**Accessibility**	**-0.60**	**0.08**	**-7.57**	**<0.001**
	Color (red)	**-1.45**	**0.26**	**-5.59**	**<0.001**
	Mass	0.01	0.01	0.82	0.410
	Color:Mass	-0.03	0.02	-1.81	0.070
RBLE	**Accessibility**	**-0.43**	**0.07**	**-5.99**	**<0.001**

	Color (red)	**-1.77**	**0.26**	**-6.71**	**<0.001**
	Mass	**-0.09**	**0.02**	**-3.69**	**<0.001**
	Color:Mass	**0.09**	**0.03**	**3.44**	**0.001**
RVBU	Accessibility	-0.11	0.06	-1.81	0.071
	Color (red)	**-2.29**	**0.22**	**-10.43**	**<0.001**
	Mass	**-0.03**	**0.00**	**-5.37**	**<0.001**
	Color:Mass	**0.04**	**0.01**	**4.67**	**<0.001**
RWBU	**Accessibility**	**-0.26**	**0.06**	**-4.23**	**<0.001**
	Color (red)	**-1.79**	**0.22**	**-8.05**	**<0.001**
	Mass	**0.02**	**0.01**	**2.94**	**0.003**
	Color:Mass	-0.01	0.01	-1.79	0.074

Table 8. Results from cumulative link mixed models testing the intensity of interaction.

Bird Species	Factor	Estimate	SE	z-value	p-value
JAWE	**Accessibility**	**1.00**	**0.11**	**8.933**	**<0.001**
	Color (red)	0.47	0.37	1.276	0.202
	Mass	**-0.05**	**0.02**	**-2.581**	**0.010**
	Color:Mass	0.04	0.03	1.509	0.131
RBLE	**Accessibility**	**0.62**	**0.10**	**6.219**	**<0.001**
	Color (red)	-0.57	0.40	-1.401	0.161
	Mass	-0.01	0.03	-0.232	0.817
	Color:Mass	0.02	0.03	0.508	0.611
RVBU	**Accessibility**	**0.30**	**0.06**	**4.67**	**<0.001**
	Color (red)	**1.05**	**0.24**	**4.32**	**<0.001**
	Mass	0.00	0.01	0.47	0.642
	Color:Mass	**-0.04**	**0.01**	**-3.32**	**0.001**
RWBU	**Accessibility**	**0.68**	**0.07**	**9.77**	**<0.001**
	Color (red)	**1.54**	**0.25**	**6.05**	**<0.001**
	Mass	**-0.01**	**0.01**	**-2.29**	**0.022**
	Color:Mass	-0.01	0.01	-0.65	0.513

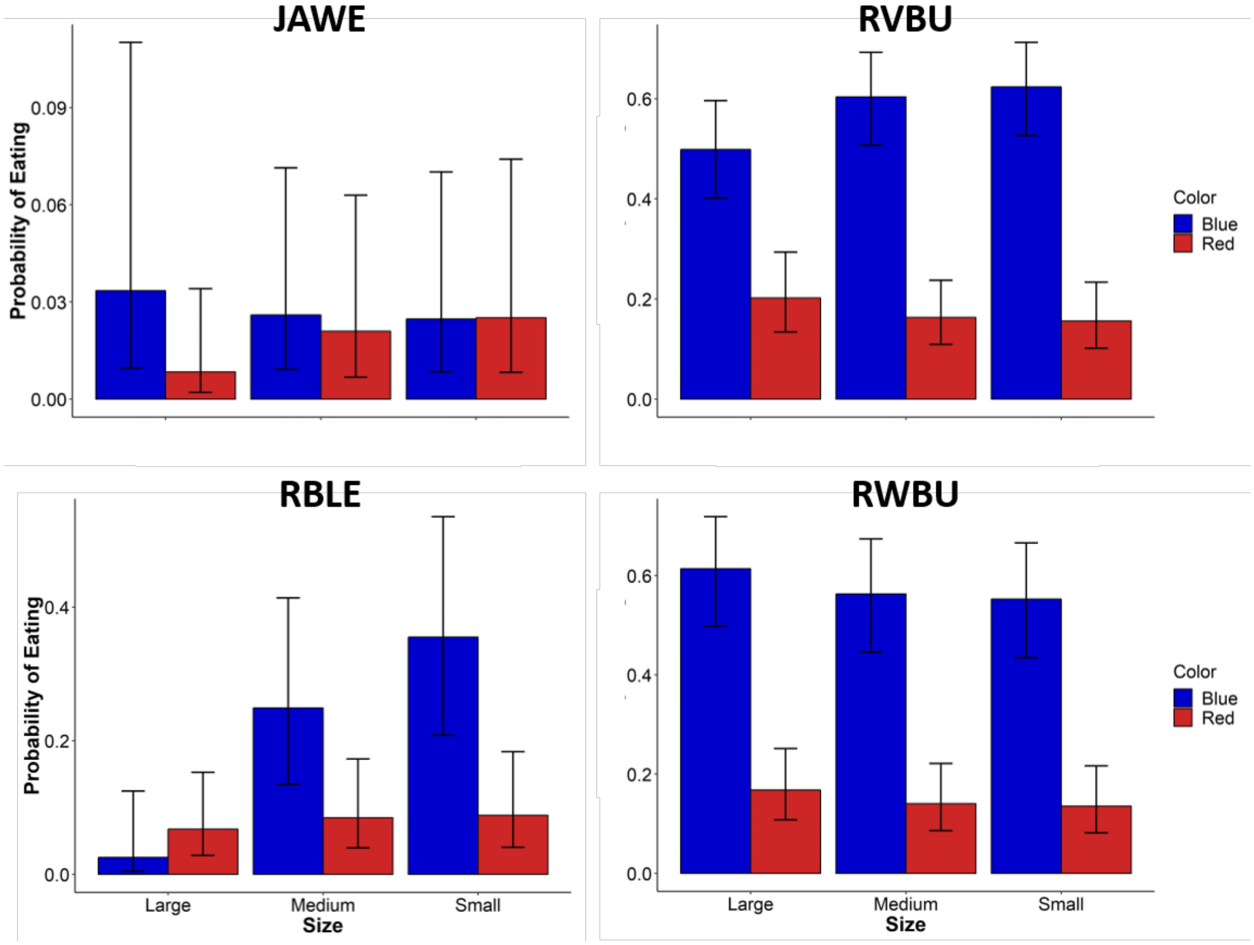


Fig. 15. Probability of ingestion based on fruit color.

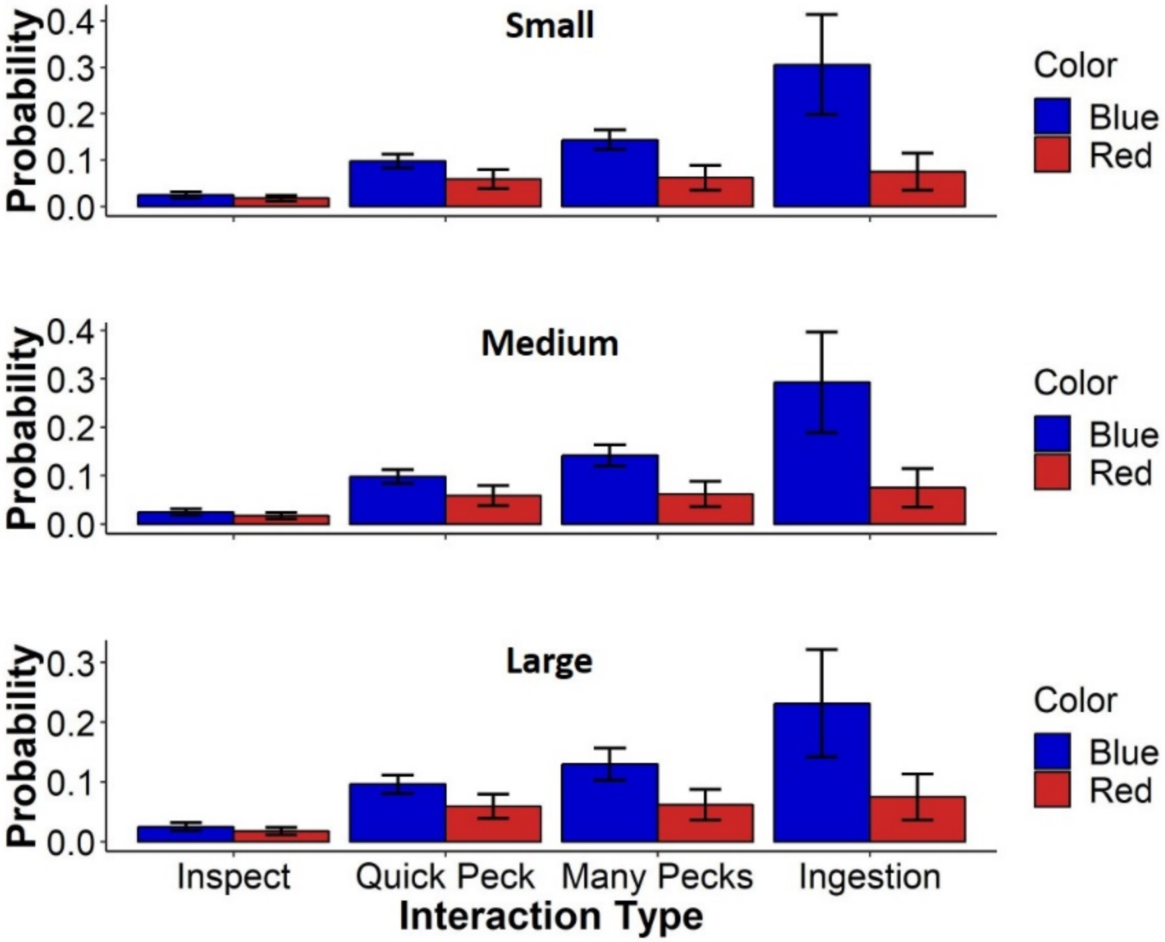


Fig. 16. Interaction intensity for fruits of different colors.

Methods–Gut Passage
In order to determine how long it takes for the frugivorous species to pass seeds, we fed fruit to captive birds at sunrise and then again two hours after the completion of the previous gut passage trial. The birds were then recorded on video or two hours after the fruit was given to them in order to determine the time the bird ingested fruit and the time the bird defecated.

Results–Gut Passage
We conducted a total of 658 trials on 39 fruit species (16 native, 23 non-native) of which the birds ate fruit in at least 344 trials (35 fruit species: 15 native, 20 non-native). The total number of trials where the bird ate fruit per species was as follows: JAWE = 129, RBLE = 80, RVBU = 65, RWBU = 69, and ZEBD = 3 (out of 31 for ZEBD). From the 50 trials that we have already analyzed, RBLE had the longest gut passage (22.64 min ±6.09) and JAWE had the shortest (9.67 min ±2.23SE) (Table 9). We cannot determine gut passage time for individual plant species at this time.

Table 9. Mean gut passage time for 4 bird species.

Species	Number of Trials	Mean Passage Time (min)	SE
JAWE	5	8.67	2.23
RBLE	17	22.64	6.09
RVBU	7	17.53	6.73
RWBU	9	14.74	4.48
ZEBD	3	13.30	7.33

Task 5. Quantify disperser influences on seeds and plant communities

Our aims here were two-fold. First, we sought to assess the overall structure of seed dispersal networks, in a section titled Network Structure, and compare them to other communities worldwide. Second, we sought to identify the role played by each bird and plant species in the seed dispersal network on the novel ecosystems of the island of Oahu, titled Species Roles.

Methods–Network Structure

Study sites

This study was carried out on Oahu, which is the most populated island in the Hawaiian Archipelago and is one of the islands most affected by extinction and biological invasions within the archipelago, and likely in the world (Conry et al. 2010). We collected data in seven sites that encompass significant regional variation in elevation, rainfall, and plant invasion (Fig. S1). Across these sites, mean annual rainfall varies from 1107.8 mm to 3386.1 mm, elevation varies from 108 to 1206 m a.s.l. (Table S1), and 50.0–100% of the plant species consumed by the bird assemblage are non-native (Table S4). Owing to rain shadow effects, rainfall and elevation are not tightly linked in our sites. The introduced Red-billed leiothrix (*Leiothrix lutea*), Japanese white-eye (*Zosterops japonicus*) and two bulbul species (*Pycnonotus jocosus* and *P. cafer*) are the most common and widespread frugivorous birds on the island (Table S2). The most often consumed non-native bird-dispersed plants, such as *Clidemia hirta, Trema orientalis*, *Psidium* spp. and *Rubus* spp. are widespread across sites (Table S3). The less invaded sites have a ubiquitous presence of native plants, such as the bird-dispersed māmaki (*Pipturus albidus*) (Table S3).

Data collection and processing

From November 2014 to December 2017, we carried out standardized mist-netting (140 net-hours over two days per site with ten 12m understory nets) at the seven sites once every seven weeks (minimum total of 980 net-hours per site). During the intervals between the standardized sampling, additional mist-netting was carried out at least once a week in each site, focusing on underrepresented bird species or areas with underrepresented fruiting plant species. In these cases, we used between 4–10 mist nets open for at least 4h, set speakers with playback of songs of all target species near the nets, and often placed nets in the midstory and/or canopy of the forest. For all netting, each bird captured was left inside a paper bag for no more than 20 minutes, to collect a fecal sample. In total, 3,278 fecal samples were collected from 21 bird species (Table S2) and sorted under stereoscope. Seeds were identified by either comparing with reference seeds collected from fruiting plants from field sites or from other local reference collections, by consulting local experts, or via molecular analysis. Two out of 44 plant species were identified as morphotypes (Table S3). These seeds likely represent introduced species in early stages of invasion because they were neither recognized by local experts familiar with seeds of native plants nor were they present in reference collections. We calculated the proportion of introduced plants based on the species present in the networks, and both morphotypes were considered non-native. Proportion of non-native plants was calculated based on network data rather than the overall vegetation cover because we were interested in the origins (native *vs.* introduced) of the resources (fruits) and the overall vegetation cover encompassed introduced species dispersed by other means than birds. However, the proportion of introduced plants found in the diet is correlated with the proportion of introduced species found in independent vegetation surveys, which includes non-bird-dispersed species (Table S14; Spearman r=0.85, p=0.03; d.f. = 6). Six bird species lacked seeds in their fecal samples and were excluded from further analysis (Table S2). Seeds were found in 1,379 samples, representing 1,792 seed dispersal events (414 samples had seeds of multiple species). A dispersal event was defined as the presence of viable seeds (e.g., no signs of damage on seed coat and embryo) of a given plant species in a sample. Following this criterion, potential accidental ingestion of viable seeds by species that occasionally consume fruits (e.g., predominantly insectivorous, nectarivorous, or granivorous birds) were also considered here.

Interaction matrices

For each of the seven sites we created a *local* network, which included all interactions recorded in a site over the entire sampling period. In addition, we created a *regional* (island-wide) network by pooling all sites. A network is an interaction matrix where each row *i* is a plant species and each column *j* is a bird species. The intersection a_{ij} is a measure of interaction intensity, defined as the proportion of samples of bird species *j* containing seeds of plant species *i*. Thus, this measure of interaction intensity accounts for differences in the number of samples collected among bird species and across sites (Table S2). To avoid overestimation of interaction intensity for bird species with few samples in a given site (n<4 samples; 6 cases), we estimated the interaction frequency of the local network based on the total number of samples across the island for these cases (Table S2). To quantify the role of birds as seed dispersers across sites, we calculated the proportion of samples containing seeds for the main frugivorous birds. For that we used a subset of samples sorted for the four bird species with mainly frugivorous diets, corresponding to 69.2% of all the samples (n=2,268) (Table S2, S4). Higher proportions would indicate higher potential for seed dispersal. We also estimated sampling coverage for the number of links to evaluate sampling completeness across sites. We detected minimal differences among sites in the proportion of detected links and sampling was sufficient to detect at least 75% of links in each site, indicating that sampling had a negligible influence on network metrics and sampling was similar or greater than in other studies (see Fig. S5 for details)(Jordano 2016). These estimations considered only endozoochorous events (i.e. when seeds are swallowed and therefore transported inside the animals body) which represents a direct evidence of seed dispersal, while does not include seed regurgitation or seeds transported attached to the animals body (i.e. epizoochory), which can also sometimes lead to seed dispersal.

Network metrics examined across spatial scales

To describe and compare network structure at both the regional and local scales, we calculated a set of complementary network-level metrics for each of the seven local networks and for the regional network. Specifically, we quantified number of birds, number of plants, number of links, number of interactions (i.e., total number of samples in which at least a viable seeds was found; if seeds of two species were found it counted as two interactions), connectance, complementary specialization, nestedness, and modularity. Connectance is the proportion of possible links that were actually observed in a network. Complementary specialization was measured by the H_2' index; this index measures the degree of resource partitioning among all species in a quantitative network (Blüthgen et al. 2006). H_2' varies from zero (minimum specialization) to 1 (maximum specialization possible). Nestedness was quantified with the metric wNODF, which measures the non-overlap and decreasing fill of weighted matrices (Almeida-Neto et al. 2008, Almeida-Neto and Ulrich 2011). This metric varies from zero (non-nested) to 100 (perfectly nested). Modularity was quantified with Newman's metric (Qw) using the DIRTLPAwb+ algorithm, which outperforms other algorithms in detecting subsets of species interacting disproportionally among them than with other members of a bipartite weighted matrix (Beckett 2016). We set this algorithm to 10^7 steps to search for the highest modularity (Dormann et al. 2009). As it is an optimization algorithm, the highest values found may vary among runs, so we repeated the analysis five times for each network and accepted the highest modularity obtained (Vizentin-Bugoni et al. 2015). The modularity ranges from zero (minimum modularity) to 1 (maximum possible modularity). The module composition presented in the Figure S3 represents the module conformation from runs where the highest modularity (Q) was obtained.

To test the significance of specialization (H_2'), weighted nestedness (wNODF), and weighted modularity (Qw), we compared metric values from observed matrices with metric values obtained from random matrices created using the *vaznull* null model from the R package *bipartite* (Dormann et al. 2009). This null model reshuffles interactions in a matrix of the same size, connectance, and marginal totals of the observed matrix. We created 1000 null matrices to test for H_2' and wNODF and 100 null matrices for Qw, as the latter is a time-consuming optimization algorithm. For consistency, for each of the 100 null matrices we calculated Qw five times and kept the highest values, as we did for the observed network. We considered a metric of network structure to deviate significantly from a random structural pattern when the observed value was higher than the confidence interval (95%) obtained from null matrices. All analyses were performed using the R package *bipartite* (Dormann et al. 2009).

Interaction dissimilarity across sites and importance of environmental factors
To examine interaction dissimilarity across sites and test its association with environmental variation, we used the function *network_betadiversity* of the R package *betapart* (Poisot et al. 2012) to calculate the interaction turnover between pairs of networks. Here we calculated interaction dissimilarity using Whittaker's equation (Whittaker 1960):

$$\beta_{WN} = \frac{a+b+c}{(2a+b+c)/2} - 1$$

where *a* is the count of shared interactions between networks B and C, *b* is the count of interactions unique to B, and *c* is the count of interactions unique to C. β_{WN} (total interaction dissimilarity) ranges from zero when all interactions are shared to 1 when no interaction is shared. β_{WN} was decomposed into its two components: 1) species turnover (β_{ST}) - the proportion of interactions that are not shared due to differences in species composition between two networks, and 2) turnover in linkage among shared species ($\beta_{OS,}$ i.e., rewiring) - the proportion of interactions that are unique to a single network despite the occurrence of both partners in both networks (Traveset et al. 2015).

We used a generalized linear model (GLM) to test whether interaction dissimilarity between pairwise sites (B_{WN}; response variable, n=21) was related to differences between sites in elevation, mean annual rainfall, and proportion of invasive plants (predictor variables). All predictor variables were center-scaled prior to analysis. Predictor variables had low collinearity (variance inflation factors <3) and were therefore retained. Even though distance between sites can influence interaction dissimilarity, we excluded it from our analyses because it had an insignificant effect on dissimilarity in our system (β=0.14, SE=0.10, z-value =1.47, p=0.14). Model fitting was performed using the function *glmmadmb* of R package *glmmADMB* (Skaug 2018) and using a Beta error distribution and logit link function. We used the function *dredge* of the R package *MuMIn* (Barton 2018) to compare models including all possible combination of predictor variables, plus an intercept only model. We then performed model selection based on Akaike Information Criterion corrected for small sample sizes (AICc). Finally, as there was not a single model with >95% of the model weight, we conducted model averaging. We repeated these analyses for both components of interaction dissimilarity (i.e., B_{ST} and B_{OS}) to test whether differences in elevation, rainfall, and proportion of invasive plants have distinct effects on the dissimilarity originated from species turnover or rewiring.

Comparing Oahu networks to a global dataset of networks
To test whether network structure and stability in the seven novel networks from Oahu deviates from other communities around the world, we assembled and analyzed a dataset including 42 avian seed dispersal networks. The dataset encompassed a wide array of bird-plant seed dispersal networks from islands (17 networks) and continents (25) in both tropical (18) and non-tropical (24) areas (Table S12). Because our focus was on local networks, we did not include networks that merged multiple communities (e.g., several islands from an archipelago). We focused on birds because (i) they are widespread and particularly important seed dispersers in most ecosystems (Kissling et al. 2009), (ii) most network studies have focused on birds rather than other organisms, even when other animals disperse seeds within the community, and (iii) they dominate seed dispersal networks in Hawaii. We treated these networks as 'native-dominated' because the networks with highest proportion of invasive species in the dataset (e.g. 50% in Azores and 13% in Galápagos; were still lower than Oahu, and none of the compiled networks had all typical frugivore species (i.e., species that consume fruit to a high degree) extinct. Both of these factors make Oahu an extreme case of 'introduced-dominated' communities. For each network we calculated the metrics described above (*i.e.* H_2', wNODF and Qw). In order to include networks that present only the presence or absence of interactions (i.e. binary data: n=16 networks), we also calculated binary nestedness (NODF; *55*) and modularity (Qb). For these analyses, we also convert the remaining 26 weighted networks into binary networks, in order to increase sampling size. Both metrics (binary nestedness and modularity) follow the same logic as their weighted versions (see section above). We also estimated the stability of each networks using Attack Tolerance Curves (ATC)(Memmott et al. 2004, Burgos et al. 2007), which is implemented as the function *robustness* in the R package *bipartite*. This metric calculates the area under a curve which represents the rates of secondary extinction expected under the loss (simulated extinctions) of partners in a matrix. In this case, a species goes extinct when all

partners to which it is connected are lost (Burgos et al. 2007). The metric ranges from 0 to 1 and values closer to 1 indicate lower rates of co-extinctions (i.e., higher stability). We estimated robustness of animals (A) to the extirpation of plants and the robustness of plants (P) to the extirpation of animals. The order of extirpation was done by randomly excluding animal (ranA) and plant (ranP) species and by excluding species based on specialization (degA and degP), from the most generalist to the most specialist species. These additional metrics based on binary data (NODF, Qb, ranA, ranP, degA and degB) were also calculated for the seven networks from Oahu for comparison with the global dataset.

To compare structure and stability of Oahu and the global dataset, we applied a Δ-correction on all metrics. This correction consists of the subtraction of an observed value of a metric and the mean value of a metric obtained from null matrices. Thus, negative values occur when the observed value is lower than the mean expected value. This procedure is recommended to account for variation in sampling intensity and network dimensions across studies, which are likely to bias metrics and hamper direct comparisons of network metrics. To calculate Δ, each metric was calculated for each observed network from the global dataset and from Oahu. For each of these communities, we generated 1000 null matrices using *vaznull* (described above), except for modularity to which we used 100 null matrices because the algorithm is time-consuming. Using the Δ of each metric, we calculated 95% confidence intervals for the Oahu networks and the global dataset. We considered the two groups of networks (Oahu *vs.* global dataset) to differ significantly when there was no overlap between both 95% confidence intervals. In order to test the consistency of our results, we also calculated the confidence intervals for subsets of networks in the dataset, which included all combinations of the categories ‘islands’ or ‘continents’ and ‘tropical’ or ‘non-tropical’ regions (Table S13).

Results and Discussion–Network Structure

High rates of human-caused species invasions and extinctions are a ubiquitous feature of the Anthropocene (Hui and Richardson 2017, Vizentin-Bugoni et al. 2019). As a result, ‘novel communities’ have emerged, characterized by a reshuffling of species, changes in species interactions, and, in some cases, alteration or disruption of ecosystem services maintained by these interactions (Brodie et al. 2014, Traveset and Richardson 2014). Mutualistic plant-animal networks are particularly susceptible to species loss (Pocock et al. 2012) and invasions (Mitchell et al. 2006, Heleno et al. 2012, Traveset and Richardson 2014), increasing the vulnerability of species and communities to further perturbations (Traveset and Richardson 2014). Previous studies have focused on native-dominated communities where few or no invasive species occur and mutualistic partners have interacted for prolonged periods of time, developing complex and often coevolved interactions (Thompson 2005, Bascompte et al. 2006). Contrastingly, the architecture and stability of novel interaction networks across spatial scales and how they compare to native-dominated communities remains virtually unknown. This knowledge gap hampers our ability to forecast and mitigate the impacts of extinctions and invasions on ecosystem functions.

Here, we address these gaps by examining the structure, dynamics, and stability to perturbations of multiple spatially-explicit novel communities in the Hawaiian archipelago and compare our results to networks from communities worldwide. Hawai‘i provides an opportunity to investigate the consequences of an extreme scenario of loss of native species and their replacement by non-native species. Most native Hawaiian forest plants are bird-dispersed, yet no native dispersers remain in most ecosystems (Foster and Robinson 2007, Chimera and Drake 2010). Thus, seed dispersal is almost entirely dependent on a handful of introduced vertebrate dispersers, nearly all of which are birds (Foster and Robinson 2007, Chimera and Drake 2010). O‘ahu, in particular, is among the areas most affected by extinctions and biological invasions in the world (Conry et al. 2010): all its native frugivores are extinct.

To what extent are introduced species integrated into seed dispersal networks (SDNs) and do introduced dispersers replace extinct native animals? To investigate these questions, we examined interactions based on 3,278 fecal samples from 21 bird species (Tables S1-S3) collected over three years at seven sites encompassing broad environmental variation across O‘ahu (Fig. S1, Table S1). We identified 109,424 viable seeds, representing 1,792 seed dispersal events (presence of viable seeds in a sample). O‘ahu's SDN included 15 bird and 44 plant species connected by 112 distinct links (Fig. 17). Most birds (86.7%) and plants (65.9%) are not native to Hawai‘i; introduced plants accounted for 93.3% of dispersal events, and there was no interaction between a native bird and a native plant. Proportions of introduced species varied from 60.0–100.0% for birds and 50.0–100% for plants, two local networks consisted entirely of introduced species, and the number of species and links was highly variable across sites (Table S4). We found that 59.0% of fecal samples contained seeds (Table S4), but only 0.22% of interactions (n=4 events) involved native birds (two species not specialized for fruit consumption). Thus, although introduced birds are critical for seed dispersal in the ecosystem, they are primarily dispersing introduced plants (only 6.7% of interactions involved native plants).

We assessed species interaction patterns via complex network analyses and used four complementary metrics known to vary geographically and reflect community level responses to major drivers of biodiversity patterns, such as productivity, climatic seasonality, and historical climatic stability (Schleuning et al. 2012, Sebastián-González et al. 2014, Dalsgaard et al. 2017). A network is an interaction matrix where each row *i* is a plant species and each column *j* is a bird species, with intersections a_{ij} describing interaction intensity. The significance of the observed topological patterns is assessed by contrasting observed values for each metric with the confidence interval from null models. Like other mutualistic networks, SDNs in native-dominated communities typically have consistent structures: (i) low connectance – not all possible interactions are realized, (ii) high specialization – few supergeneralist species exist and most species interact with a few partners in a complementary way, (iii) nested topology – specialist species tend to interact with subsets of partners of the most generalist species, and (iv) modular structure – subsets of species interacting preferentially with each other, forming modules of highly-connected species (Bascompte and Jordano 2007, Vázquez et al. 2009, Almeida and Mikich 2017).

Novel insular communities are predicted to have low specialization because of niche broadening (MacArthur et al. 1972) and interaction release (Traveset et al. 2015). For example, both fleshy-fruited plants and frugivores on islands tend to have wide niches due to resource limitation (Traveset and Richardson 2014). Consequently, high connectance and non-modular structures are expected, as both are linked to low specialization (Martín González et al. 2015, Dalsgaard et al. 2017). For nestedness, contrasting predictions exist because low specialization can either lead to non-nested topology, owing to random partners associating, or to nested topology, driven by species' relative abundances, which defines probabilities of species encountering one another (Krishna et al. 2008, Vizentin-Bugoni et al. 2018). In contrast to theoretical predictions, we found that Oahu networks were non-random and had highly complex structures at local (site-specific) and regional (island-wide) scales. The regional network had low connectance, moderate specialization, and nested and modular topologies, with three distinct modules (Fig. 17, Fig. S2, Table S4). At the local scale, networks had low to intermediate connectance and, unlike the regional network, were not nested. Similar to the regional network, 6 of 7 local networks were specialized and modular, presenting 3 or 4 modules (Fig. 18, Fig. S3, Table S4). We found that despite all interactions being novel and primarily involving introduced species, networks were

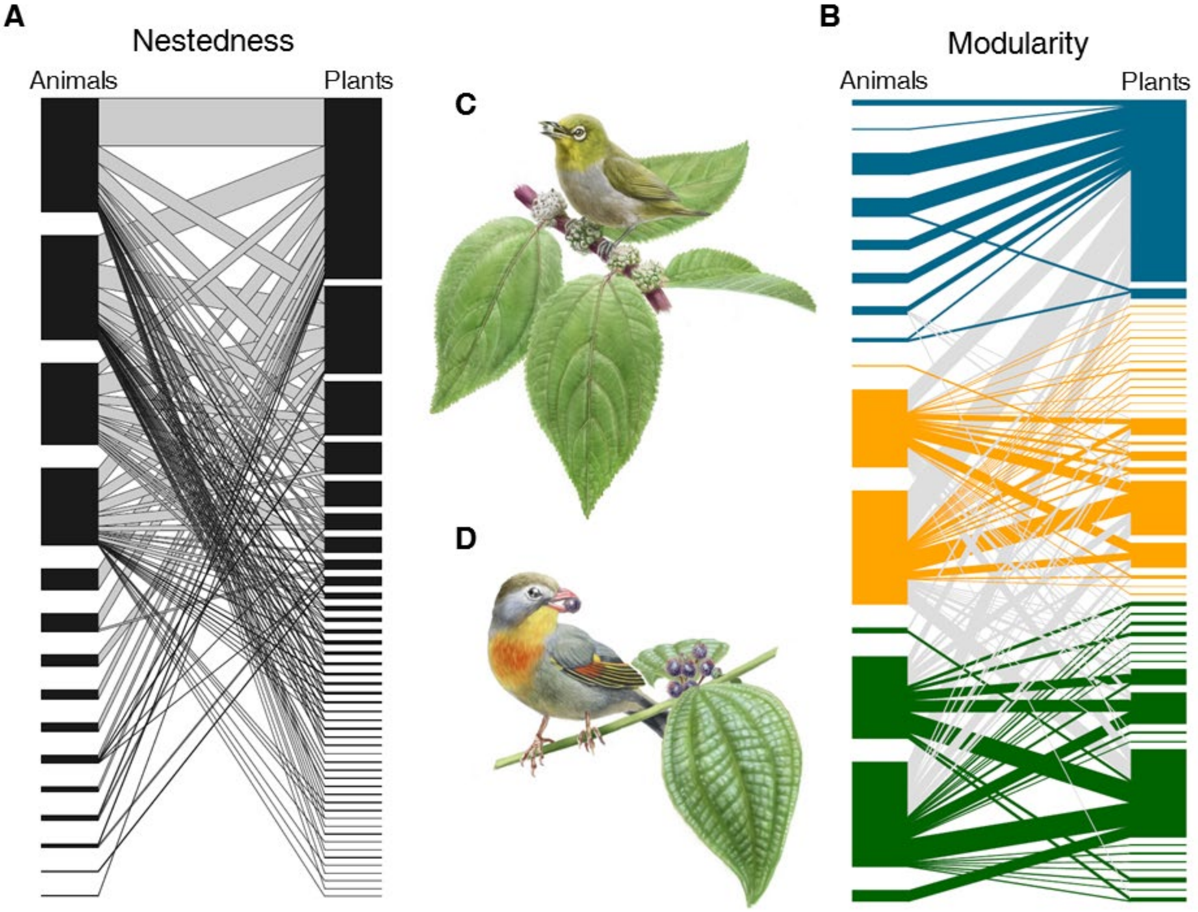


Fig. 17. Structure of the island-wide seed dispersal network on Oahu and illustration of two emblematic interactions. The novel network was **(A)** nested (wNODF = 48.67; 95% CI = 34.24 - 46.66) and **(B)** modular (Q_W = 0.24; 95% CI = 0.07 - 0.09). Species and links from distinct modules are depicted by distinct colors (blue, orange and green) and gray links are interactions connecting modules. For list of interacting species see **fig. S2**. **(C)** Japanese white-eye feeding on *Pipturus albidus*, the most commonly consumed native plant and **(D)** a red-billed leiothrix feeding on *Clidemia hirta*, the most widely consumed and widespread introduced plant. Illustration credit: P. Lorenzo.

structurally complex and notably similar between scales (local *vs.* regional) and across sites. Furthermore, partner sharing (how distinct species share resources) in SDNs on Oahu is structured in a complementary way among bird and plant species, giving rise to distinct modules in which certain birds and plants interact preferentially. The emergence of such structures indicates that these novel SDNs largely reproduce the well-known patterns exhibited in mutualistic networks (Vázquez et al. 2009), and that SDN structure is highly conserved, regardless of variation in plant and bird communities. Given the low generalization in our novel insular networks, interaction release (Traveset et al. 2015) is either not occurring, or may occur in the form of consumption of more food types (e.g., insects, fruits, nectar), rather than increased diversity within a specific resource type (e.g., greater number of species of fruits).

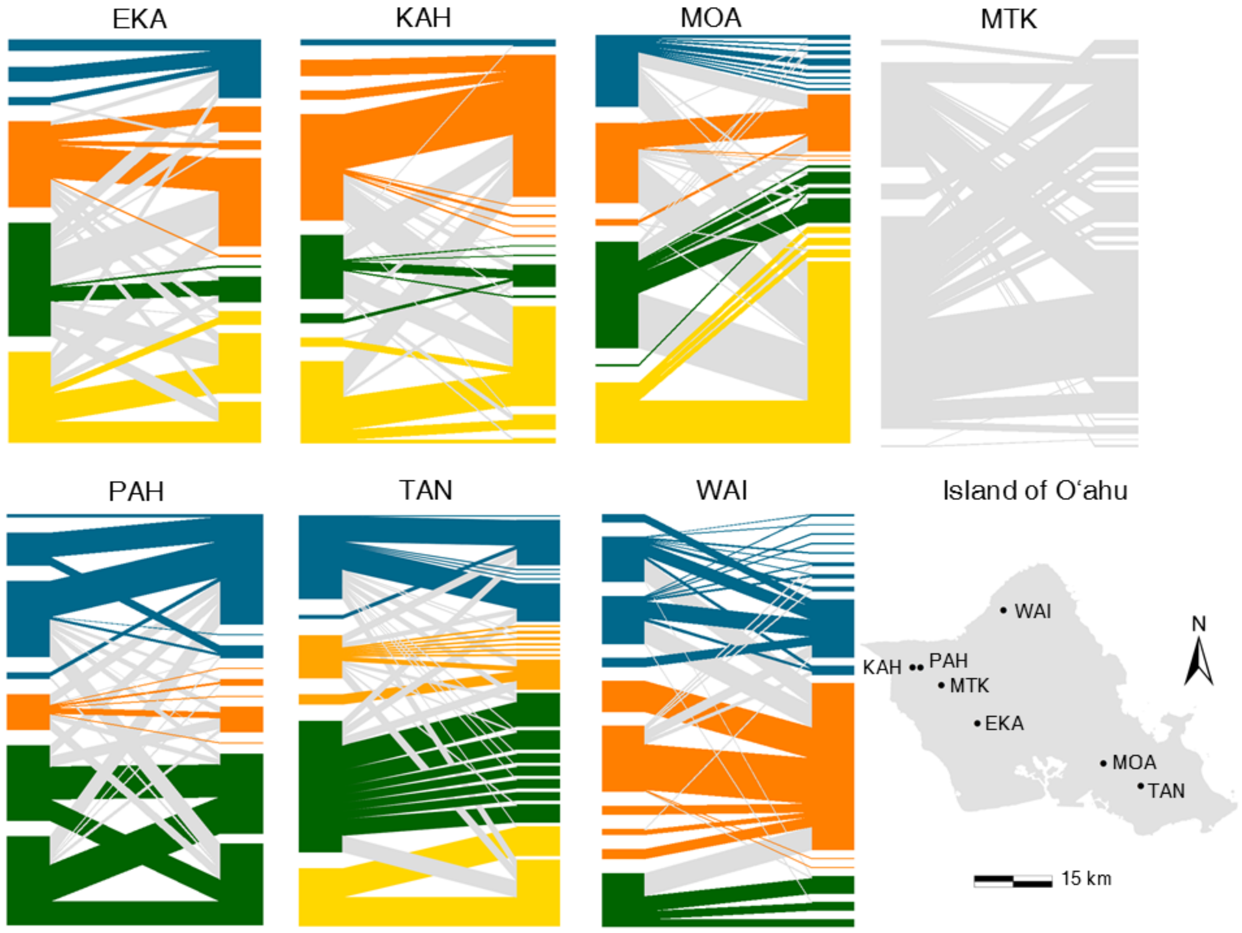


Fig. 18. Local seed dispersal networks on Oahu. Each network includes all birds (left) and plants (right) consumed in a specific site. Blue, orange, green and yellow depict modules with species interacting more among themselves than with other species, as identified by Beckett's algorithm (*33*). All local networks but MTK were modular, presenting three or four modules. Line thickness indicates frequency of interactions. For list of interacting species see Fig. S3.

Several studies suggest that the phylogenetic relationships of species contribute to structuring mutualistic networks (Rezende et al. 2007, Vitória et al. 2017), which is an expected consequence of coevolved interactions among species interacting for prolonged (evolutionary) periods of time (Thompson 2005). Here we show that the interaction patterns recurrently identified in native-dominated networks also emerge in novel mutualistic networks composed of species with little or no shared evolutionary history. This result indicates that prolonged shared evolutionary history is not necessary for the emergence of complex network structure. We should note, however, that pre-existing adaptations of introduced birds for frugivory and fruits for bird dispersal are necessary for their integration into novel networks. Furthermore, the presence of nested structure at regional, but not local scale, indicates the critical importance of spatial scale to understanding network patterns and their underlying processes. The wider variety of partners used at the larger scale (regional network) corresponds to the 'fundamental niche', while the subset of partners found at local scales indicates that local populations have much more restricted 'realized niches' (Blüthgen et al. 2006, Devictor et al. 2010). Therefore, not all species use available resources in the same way across all sites. By sampling across large spatial scales, researchers may be evaluating species fundamental niches and not population-level realized niches. Therefore, processes operating at different spatial scales may be overlooked or confounded.

Most networks have been studied primarily as static entities at single sites, despite the importance of multi-scale studies for understanding the processes underlying network structure and for evaluating the generalizability of network patterns (Dáttilo and Rico-Gray 2018). To examine interaction dynamics across sites and to test their association with environmental variables, we calculated the dissimilarity (interaction turnover) between pairs of networks, using data limited to species present in the networks. Highest dissimilarity occurs when two sites share no interactions. We decomposed this metric into two components: species turnover (β_{ST} – proportion of interactions that are not shared due to differences in species composition between two networks), and linkage turnover (β_{OS}, also called rewiring – proportion of interactions unique to a single network despite the occurrence of both partners in both networks)(Poisot et al. 2012).

We found high interaction dissimilarity among sites due to both changes in species composition and rewiring. This suggests high flexibility of birds and plants to switch partners, which is a major characteristic of highly successful invasive species (Mooney and Cleland 2001). Interaction turnover across sites was high ($\beta_{WN} = 0.57 \pm 0.11$, mean ± SE; n=21 pairwise sites; Fig. 19, Table S5), indicating that, on average, only 43% of interactions were shared between sites despite the most common bird and plant species occurring at all sites (Tables S2, S3). Surprisingly, only 53% of the interaction dissimilarity was due to differences in species composition among sites ($\beta_{ST} = 0.30 \pm 0.09$), while 47% was because pairs of species that interacted in one site did not interact in another site where they co-occurred ($\beta_{OS} = 0.27 \pm 0.07$; Fig. S4). This indicates that, in addition to its influence on the structure of mutualistic networks (i.e. nestedness)(Zhang et al. 2011), partner switching is a major component of the spatial dynamics of novel networks. High interaction dissimilarity has also been reported in specialized, native-dominated pollination networks, even between spatially close networks (Carstensen et al. 2014). Thus, plant-animal networks appear to have distinct links (high interaction rewiring) even when the same species are present in both sites, irrespective of whether networks are dominated by native or introduced species.

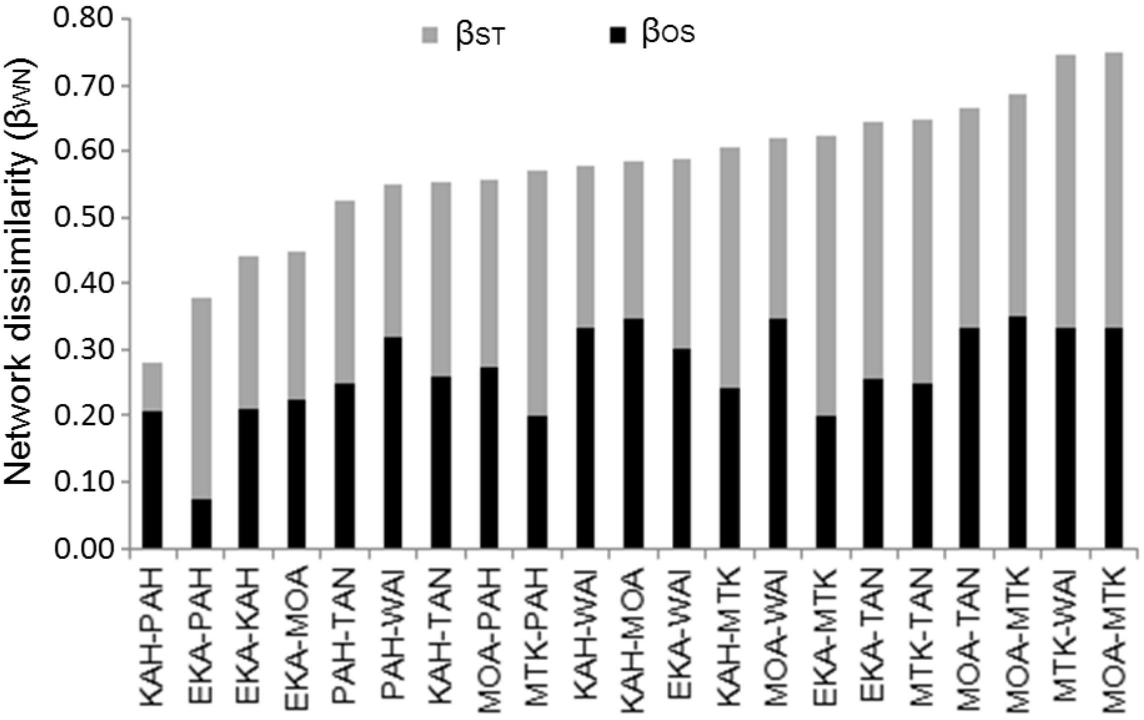


Fig. 19. Interaction dissimilarity between each pair of sites on Oahu. Interaction dissimilarity (β_{WN}) was decomposed into its two components - species turnover (β_{ST}) and linkage turnover among species shared by pairwise sites (i.e., rewiring, β_{OS}).

Abiotic factors had a greater effect than biotic factors on the overall interaction dissimilarity and the dissimilarity caused by species turnover between sites, while interaction rewiring was not influenced by any factor examined (Tables S6-S11). Specifically, interaction dissimilarity and the dissimilarity caused by species turnover were influenced by elevation and rainfall, but not by percent of introduced plant species (Tables S6-S9). This suggests that the environment indirectly influences interactions via effects on species distributions, including the distribution of introduced species. However, the lack of association between rewiring and examined factors indicates that birds and plants in the system are highly flexible and can switch partners, irrespective of abiotic conditions and the identity of species in the community.

Lastly, we compared Oahu SDNs to native-dominated SDNs around the world and found that Oahu's novel networks resemble the structure and stability of native-dominated networks. We assembled and analyzed a dataset of 42 avian SDNs encompassing a broad geographical range, with data from islands (n=17) and continents (n=25) in tropical (n=18) and non-tropical (n=24) areas (Table S12). Although some of the other SDNs in the analyses included introduced species, SDNs on Oahu present an extreme case of dominance by introduced species (>50%), coupled with extinction of all native frugivorous birds. For these 42 networks and the seven on Oahu, we calculated a set of weighted (for 26 networks where frequency of interaction was reported) and binary (for all 42 networks) descriptors of network structure. We also estimated robustness (stability to species loss) of each network as the rate of secondary extinction expected under the simulated loss of network partners, assuming a species goes extinct when all connected partners are lost (Memmott et al. 2004, Burgos et al. 2007). We estimated robustness of animals to the extirpation of plants (assuming bottom-up control) and robustness of plants to the extirpation of animals (top-down control). We simulated two scenarios, one in which order of extirpation was random and another – more extreme – where order was from the most generalist to the most specialist species. After using a null model correction on each metric to account for variation in sampling intensity and network dimensions across studies (Dalsgaard et al. 2017), we compared the 95% confidence intervals for the Oahu networks to the global dataset. We found that specialization, modularity, nestedness, and the simulated robustness in all scenarios to species loss of the Oʻahu networks overlapped with the range of values observed in other networks. These results held true for both weighted and binary data and when Oahu's networks were compared to subsets of networks from tropical and non-tropical islands and continents. The only exceptions were that the specialization and weighted modularity observed in Oʻahu networks were lower than in networks from non-tropical continental areas (Fig. 20, Table S13).

Most SDNs from communities around the world have been described as specialized, nested, and modular (Almeida and Mikich 2017) and the variation in such structures reveals the responses of species interactions to biotic and abiotic factors at both small (Kaiser-Bunbury et al. 2017)and large scales (Schleuning et al. 2012, Nogales et al. 2015, Dalsgaard et al. 2017). Here we show that Oahu's novel networks strikingly resemble the structure and stability of native-dominated networks elsewhere. This high degree of similarity between novel and native-dominated networks suggests that the processes structuring interactions in such communities are largely independent of species identity and that ecological filtering occurs over relatively short (ecological) time, leading to functionally similar sets of players as compared to systems having long evolutionary histories. Yet, because filtering depends on the pool of species introduced, novel networks may have an incomplete set of roles fulfilled. For example, in Hawaiʻi, large frugivorous birds are absent, resulting in a lack of dispersal of large native fruits (Culliney et al. 2012). Therefore, functional characteristics (e.g., beak and seed/fruit sizes) and species abundance (Gonzalez-Castro et al. 2015) may be more important in the structure of mutualistic networks than species identity, supporting the role of ecological fitting (Janzen 1985). Thus, further investigation on the influence of functional traits and abundances on novel networks may shed light on the ultimate mechanisms driving network structure and species roles.By studying novel networks across scales and comparing them to native-dominated networks worldwide, we identify several key considerations. First, sampling across scales is critical for testing generalizability of patterns and identifying the underlying processes (e.g., abiotic or biotic) structuring networks. Thus, explicitly examining multiple spatial scales is an essential next step towards advancing the understanding of processes that define specialization and shape ecological networks (Dormann et al. 2017). We also predict the patterns described here are more likely to be found in other isolated ecosystems, such as oceanic islands or isolated habitat patches, which are more prone to species invasions than less isolated ecosystems. Second, our results show that introduced dispersers incompletely fulfill species roles lost by Oahu's extreme scenario of plant and bird loss and introductions. Although these introduced birds on Oahu are the only dispersers of native plants, they disperse a much higher proportion of seeds from invasive plants; therefore, their presence is a 'double-edged sword' for conservation. The flexibility of birds and plants for partner switching and the fact that novel networks may be highly robust to species removal should be considered in restoration efforts. These efforts would benefit from initiatives that increase use of restoration sites by targeted frugivores and their consumption of native fruits. This would include outplanting commonly consumed native plants (e.g., *Pipturus albidus*) within plant restoration areas, removing commonly consumed introduced plants in sites with high densities of native fruits, and attracting (e.g., via playback) specific frugivores to restoration sites. The dramatic changes that have occurred in Hawaiian ecosystems provide a unique opportunity to better understand, anticipate, and mitigate the impacts of widespread and increasing biological invasions and species extinction, while also determining how network complexity develops.

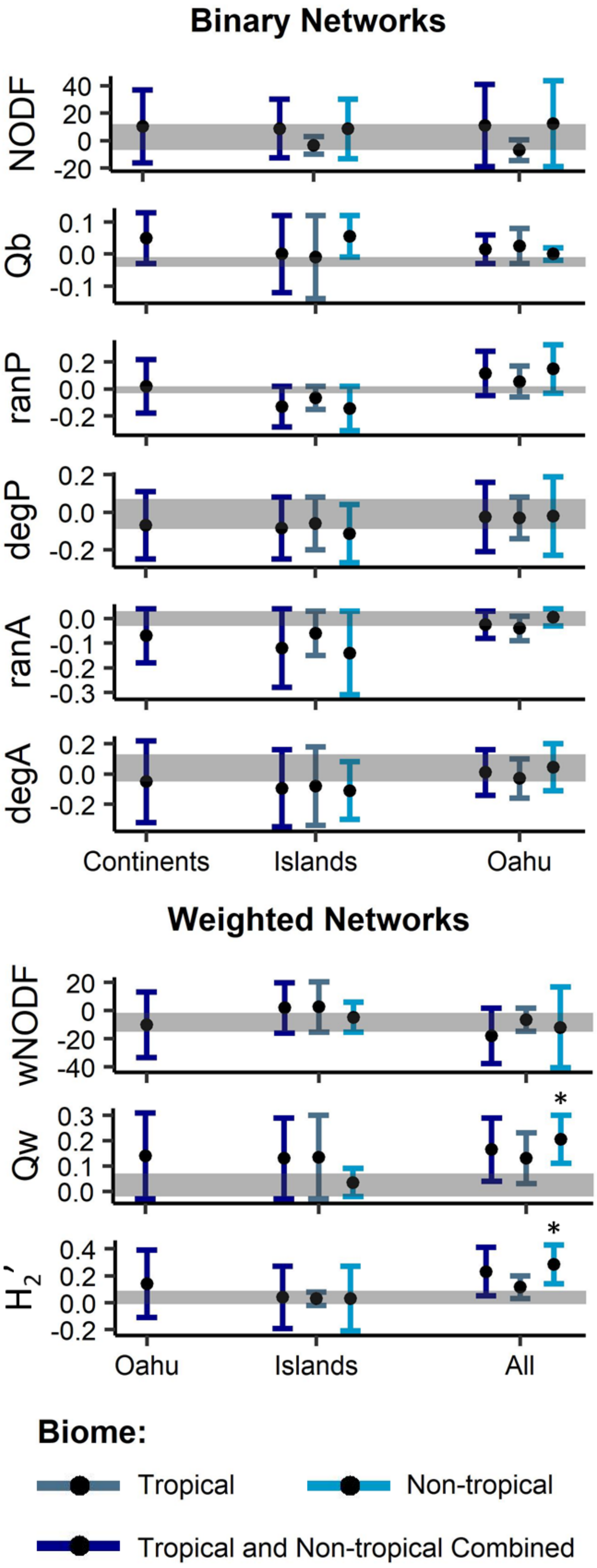


Fig. 20. Structure and stability of 42 seed dispersal networks from islands and continents in tropical and non-tropical communities worldwide in comparison to novel networks on Oahu. Significant difference (*) occurs when the 95% confidence interval of a metric for the seven sites in O‘ahu (grey shade) do not overlap the intervals for non-O‘ahu networks (color bars). H_2’= complementary specialization; wNODF and NODF= nestedness; Qw and Qb=modularity; ranP, ranA, degP and degA= network robustness to the sequential extinction of animals (A) and plants (P) by random (ran) or from the most generalist to the most specialist species (deg). The latter is calculated only for binary data.

In addition to our approach of investigating overall network structure, we evaluated species roles in networks. Although this species roles approach is not currently as well developed as our overall network structure work, we have as an extensive seed dispersal dataset as we have encountered in the scientific literature.

Methods–Species Roles

Data were collected by carrying out standardized mist-netting (140 net-hours over two days per site with ten 12m understory nets) at the seven sites once every seven weeks (minimum total of 980 net-hours per site) from November 2014 to December 2017. We obtained 3,278 fecal samples collected from 21 bird species and sorted under a dissecting scope. Seeds were identified and this data was used to create a *regional* (island-wide) network. The network is an interaction matrix where each row *i* is a plant species and each column *j* is a bird species. The intersection a_{ij} is a measure of interaction intensity, defined as the proportion of samples of bird species *j* containing seeds of plant species *i*. Thus, this measure of interaction intensity accounts for differences in the number of samples collected among bird species and across sites. For more details on sampling refer to Vizentin-Bugoni et al. (2019). For this interaction matrix, we described the role of each species in the seed dispersal network, as the normalized degree (ND). This metric describes the proportion of the available partners and species interact with. This metric is linearly correlated to more sophisticated metrics of species roles such as betweenness and closeness centrality (Martín González et al. 2010), thus, to avoid redundancy we opt for presenting only ND.

Results and Discussion–Species Roles

We detected 1793 interactions, constituting 112 distinct links among 15 bird species and 44 plant species. Three introduced bird species (RBLE, JAWE and RWBU) presented higher importance as each of them interacts with over 50% of the plant species. Only two native bird species dispersed disperse seeds (APAP and OAAM) and both present low ND as they disperse seeds of only one plant species, the introduced CLIHIR (Fig. 21).

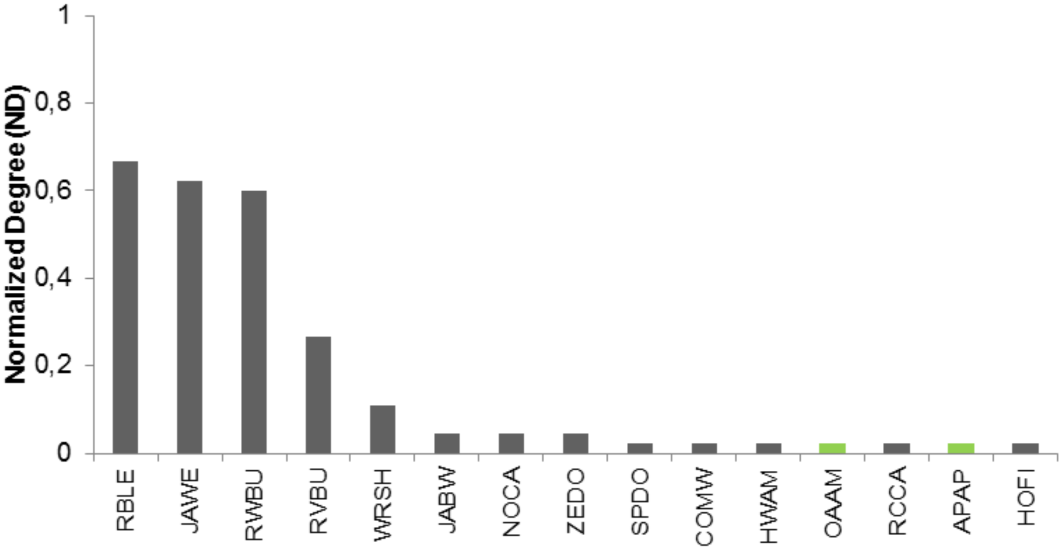


Fig. 21. Normalized degree of the 15 bird species dispersing seeds on the Oahu Island, Hawaii. Green represents native species and grey are introduced species.

Similarly, the five most important plants were introduced. These species are dispersed by over 30% of the bird species. Most of the native plants play secondary roles in the network, as most of them interact with less than 20% of the bird species. The most important native plants species was PIPALB, which interact with the four main seed dispersers, i.e. ND = 0.27 (Fig. 22).

The seed dispersal network in the novel ecosystem of Oahu are dominated by introduced species (Vizentin-Bugoni et al. 2019). In fact, these results indicate that introduced bids and plants play core roles in the network, occupying central positions as they are highly connected to other partners. On the other hand, native species play secondary roles, as they are connected to few other species, which are always other introduced species.

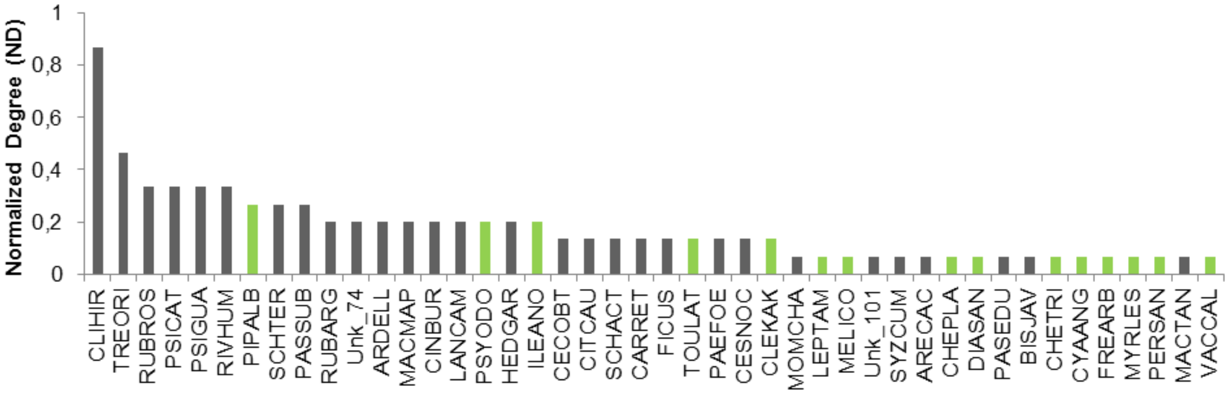


Fig. 22. Normalized degree of the 44 plant species dispersed by birds on Oahu, Hawaii. Green represents native species and gray are introduced species.

Steps forwards in this study include the investigation of which variables define the role each species perform in the community. Abundances, traits and phenologies are some of the most important defining interspecific mutualist interactions (Vázquez et al. 2009, Sebastián-González 2017), thus, we recommend these variables be considered first. By knowing the processes driving interactions and species roles in the system, it may be possible to define more effective restoration initiatives aiming to increase dispersals of native plants (Vizentin-Bugoni et al. 2019).

Task 6. Construct movement ecology models of seed dispersal

This task comprises project steps V and VI, which apply data generated in steps I-IV (corresponding with SEMS Tasks 1-5). We have taken two approaches to movement ecology modeling and describe them in two separate sections.

Methods–Movement Ecology Models

Study species and site

We examined the four most important frugivores on Oahu, with over 50% of their fecal samples containing fruit (Tarwater et al. unpublished., Vizentin-Bugoni et al. 2019). They include; Japanese white-eye, red-billed leiothrix, red-whiskered bulbul, and red-vented bulbul. These species range in body size, gape size, diet, and local abundances (Table S1, Vizentin-Bugoni et al. 2019). Birds were captured at two different sites on Oahu, Hawaii; Waimea Valley Conservation Area and Pahole Natural Area Reserve. These two sites range in plant composition (percent native vs. invasive vegetation), elevation, and rainfall (Table S2, Vizentin-Bugoni et al. 2019).

Radio-telemetry and evaluating space use

We evaluated space use using data from individuals tagged with radio-transmitters. Radio transmitters were acquired from Sparrow Systems (JDJC Corp, Fisher, IL), Lotek (Lotek Wireless Inc, Ontario, Canada), and Holohil Systems (Holohil Systems Ltd, Ontario, Canada) and weighed less than 3% of the bird's body mass. Birds were captured with mist nets and banded with unique combinations of color-bands and one U.S. Fish and Wildlife band. Radio transmitters were placed using the leg-harness method (Rappole and Tipton 1991) from August 2015 to December 2017.

Tagged focal individual birds were tracked and observed twice a week. Upon relocation of the birds, observation periods lasted approximately one hour and locations were taken whenever an individual moved more than 5 meters. If the bird left the general area, a point was taken whenever the bird was relocated. Due to uneven temporal sampling of locations during field data collection, we used a correlated random walk model (CRAWL package in Program R, version 3.5.1)(Johnson et al. 2008, R Core Team 2013, Durner et al. 2017) to estimate locations every 10 minutes within each sampling period. By using this method, we sought to minimize bias associated with the variation in observation times between observation periods. Focal individuals were followed for the duration of their transmitter's life (Table S1) or until the individual left the study area or died. We only included individuals that had 40+ generated locations, to ensure adequate spatial coverage (Farnsworth et al. 2015). This included 12 *Z. japonicus*, 12 *L. lutea*, nine *P. jocosus*, and two *P. cafer*. The minimum number of locations used for an individual was 45 and the maximum was 295 (Table 10).

Table 10. Study species tracked with radio telemetry. The number of individuals tagged, hours tracked, and average number of locations per individual refers to data used to create utilization distributions. Percent fruit in diet was derived from data in Tarwater et al. unpublished.

Species	Mass grams (SE)	Gape Width mm (SE)	% fruit in diet	Transmitter Life (months)	# Tagged	# of Obs Hours	Ave # locs/ind (SE)
Japanese White-eye *Zosterops japonicus*	10.8 (0.06)	7.71 (0.07)	51	3-4	12	204	122 (22)
Red-billed leiothrix *Leiothrix lutea*	21.2 (0.07)	9.36 (0.03)	67	4-6	12	200	116 (18)
Red-whiskered bulbul *Pycnonotus jocosus*	26.1 (0.18)	11.04 (0.08)	61	7-9	9	195	144 (29)
Red-vented bulbul *Pycnonotus cafer*	37.69 (0.85)	12.67 (0.21)	54	7-9	2	31	140 (25)

To examine space use, we created utilization distributions (UD) for each individual. UD's use a kernel density method to create a probability distribution that estimates the probability of an animal being within a 1 m^2 area. After the UD is created, the result is a map with areas of higher and lower probabilities of space use within the area that an animal was observed (Van Winkle 1975). We used a fixed kernel home range estimator, a CVh smoothing parameter, and a 1-meter resolution grid cell size (Hoglander et al. 2014, Farnsworth et al. 2015)}. We created UDs for 35 individual birds using the adehabitat package in Program R Version 3.5.1 (R Core Team 2013). We then used these individually-specific probability of use landscapes to extract values for the response variables in both analyses (see below). For the landscape scale analysis, we extracted probability of use values for points associated with our 10-minute intervals. For the understory scale, we extracted probability of use values for points where we conducted understory vegetation surveys (see below).

Landscape scale covariates

To evaluate space use at the landscape scale we selected variables that we hypothesized would influence bird space use, and have been previously shown to influence plant performance and distributions in Hawaii and elsewhere (Seoane et al. 2004, Dobrowski 2011, Fortini et al. 2013, Vorsino et al. 2014). Previous studies, using non-radio-tagged birds and a limited spatial and temporal scale, suggest that the invasive bird species associate with different habitats on Oahu. Habitat segregation has been observed between *P. jocosus* and *P. cafer* (Williams and Giddings 1984), where *P. jocosus* were more abundant in wetter habitats and *P. cafer* were more abundant in open drier habitats. *L. lutea* are commonly observed in areas with high canopy cover, close to streams, and not on ridges (Fisher and Baldwin 1947). Lastly, *Z. japonicus* are more common along forest edges than in forest interiors (Scott et al. 1986). On Oahu, many native plant species tend to prefer higher light environments, and exist on ridges and gullies (Wagner et al. 1999). Invasive plants perform well across habitats, and can perform well in darker light environments (Pattison et al. 1998).

Based on these previous studies, we decided to select landscape variables that characterize the light availability, topography, and dominant vegetation type (Table 1A). Slope, aspect, and Topographic Position Index (TPI) were generated from a 10-meter digital elevation model acquired from the United States Geological Survey National Elevation Dataset and the raster package in Program R (lta.cr.usgs.gov/NED; R Core Team 2013). Distance from stream was derived from stream data acquired from the Hawaii Department of Land and Natural Resources (DLNR planning.hawaii.gov), canopy cover came from the National Landcover Dataset, and we categorized general vegetation type using the Hawaii Carbon landcover data set (Jacobi et al. 2017).

Understory scale covariates

Few studies have described space use of the invasive birds in relation to understory habitat selection. However, birds in other systems have been shown to respond to variation in understory habitat structure (MacArthur and MacArthur 1961), and composition (Mac Nally et al. 2002). For example, frugivorous birds will cue into and track the presence of fruiting plants (Jordano 1994). Two studies using abundance data on non-radio-tagged birds in Hawaii found *Z. japonicus* were found across habitat types (Mountainspring and Scott 1985) and *L. lutea* were common in dense, exotic dominated habitats (Fisher and Baldwin 1947). Light availability at this scale can greatly influence recruitment success for plants (Schupp 1995, Muller-Landau and Hardesty 2005). Habitat complexity structures the microhabitat (light availability, humidity, etc.), which can influence plant recruitment (Schupp 1995). While plant community composition (native vs. exotic) has also been shown to influence competitive dynamics, which can affect germination and seedling success (Vitousek et al. 1987b).

Based on these previous studies, we selected understory vegetation characteristics that we hypothesized would influence daily avian space use requirements and plant recruitment. We measured variables to characterize the understory local light availability, habitat complexity, and plant community composition (Table 1B). We performed rapid vegetation surveys at locations where the focal bird was observed during tracking, on the same day of tracking. We established a 2-meter diameter quadrat at each point and all metrics recorded below were taken within the quadrat.

Table 11. Description of sampling sites on Oahu. Mean annual rainfall (2017) calculated from Rainfall Atlas of Hawaii (http://rainfall.geography.hawaii.edu/rainfall.html), number of fruiting plants came from vegetation surveys conducted at each site.

Study Site Name	Elevation (m)	Mean Annual Rainfall (mm)	Approx. Size of Site (ha)	Number of Fruiting Plants	
				Native	Exotic
Pahole Natural Area Reserve	643	1,425	30	23	8
Waimea Valley Conservation Area	237	2,000	36	11	6

Analysis

All models were run in Program R version 3.5.1 (R Core Team 2013). For both the understory and landscape scale analyses we constructed a global model for each bird species. Bird species were analyzed separately owing to the additional model complexity that would occur if we included interactions between all covariates and each species. Therefore, results in figures (Figs. 2&3) represent relative intensity of space use transformed (divided by maximum estimated probability of use values for each species) to represent a visual comparison between species (e.g. where probabilities of space use were at the maximum or minimum per species). For both the landscape and understory scale analyses we checked for collinearity between fixed effects and found none (VIF<3.4)(Zuur et al. 2009); therefore, all terms were retained. We ran models using a Generalized Linear Mixed Model (GLMM) with a Gamma error distribution and a log link function. In both analyses, we included a hierarchical random effect of observation period nested within individual to account for any temporal autocorrelation associated with location points taken during the observation period and variation attributed to different individuals. We conducted model selection by taking the global model and running all possible combinations of models against each other, including an intercept only model. Year, site (only in understory analysis), and random effects were retained in all models. No single top model was found for any of the models we ran (with >90% of model weight) and, therefore, we model averaged models that contained 95% of the model weight to estimate beta parameters and 95% confidence intervals (Burnham and Anderson 2004, Zuur et al. 2009).

Landscape scale analysis – We included the following fixed effects in the global model: slope, aspect, TPI, distance from stream, canopy cover, landcover type, and year. Site was not included in the model due to its high correlation with distance from stream. To detect any non-linear patterns in space use, quadratic terms were included for all continuous terms above. We included year as a fixed effect because space use may differ between years. Twelve *Z. japonicus* (188 observations), 12 *L. lutea* (189 observations), nine *P. jocosus* (185 observations), and two *P. cafer* (30 observations) were used to determine space use of the species at the landscape scale. *P. cafer* was tracked in 2017 only and therefore year was not included in that analysis.

Understory scale analysis – The global model included the following fixed effects: canopy cover, canopy height, stem density, vertical structure, plot species diversity, percent fruiting plant species, percent native plant species, presence/absence of a currently fruiting plant, site, and year. We included quadratic terms to detect non-linear relationships for terms that we had sufficient spread of the data, including stem density, canopy height, canopy cover, species diversity, and percent fruiting plant species. We conducted understory vegetation sampling between January 2016 and December 2017. In this analysis we included 11 *Z. japonicus* (234 locations), ten *L. lutea* (137 locations), and eight *P. jocosus* (224 locations). We did not have sufficient sample size to include *P. cafer* in this analysis.

Landscape scale covariates – Light availability – To represent space use in relation to light environment we included canopy cover (0-100% closed, National Landcover Dataset) at the 10-meter scale.

Topography – We selected the following topographic features – slope (percent), aspect (radians), distance from stream (meters), and topographic position index. Topographic position index (TPI) is a measure of topographic shape and identifies ridges, valleys, and flat areas on the landscape. TPI values greater than zero indicate ridges, less than zero indicate valleys, and values close to zero indicate middle slope. Slope, aspect, and TPI were generated from a 10-meter digital elevation model acquired from the United States Geological Survey National Elevation Dataset (lta.cr.usgs.gov/NED) using the terrain function in the Raster package in program R, version 3.5.1 (R Core Team 2013). Distance from stream was derived using the distance function in the Raster package and stream data acquired from the Hawaii Department of Land and Natural Resources (DLNR planning.hawaii.gov).

Vegetation type – To evaluate general vegetation type we used the Hawaii Carbon landcover data set (Jacobi et al. 2017). This dataset was created for Hawaii based on land-use maps, land-cover maps, and updated with high resolution imagery to create 27 general vegetation classes. Based on the Hawaii Carbon landcover dataset, seven vegetation types exist at the study sites, including the following: alien mesic, grassland, alien mesic forest, alien mesic shrub, alien tree plantation, mixed mesic forest, native mesic forest, and native wet forest.

Understory scale covariates
Local light availability – We evaluated local light environment using percent canopy closure (1-100%). To measure canopy cover we took a measurement at the center of the plot using a spherical densiometer.

Habitat complexity –We selected characteristics that would describe the habitat structure and complexity of the understory including the following: canopy height (meters), stem density (count of stems), and vertical structure (estimated percent open space from ground to 24 meters high). We evaluated canopy height using a range finder to estimate the height of the tallest canopy tree in the quadrat. For stem density, we counted all of the stems with a diameter at breast height greater than 6.35 cm. We assessed vertical habitat structure by visually making the quadrat into a column that extended into the canopy (maximum 24 meters) and breaking up the column into roughly 2-meter sections. We used 24 meters because ~95% of sample locations had canopies that did not extend above this height. We then deemed a section "closed" if a 2-meter section was more than half filled with vegetation. We then calculated the proportion of closed sections compared to open to represent vertical structure.

Plant community composition – We measured plant species diversity, percent of plant species that produce fleshy fruit, percent of plant species that are native, and the presence/absence of a currently fruiting plant. For species diversity, we recorded all vine, shrub, and tree species that fell within the quadrat. Percent of fruiting and native plants were calculated as the number of plants (vine, shrub, and tree) that produce fleshy fruits or are native, respectively. If there was a plant in the quadrat that had a ripe fruit, then the quadrat was considered to be "actively fruiting".

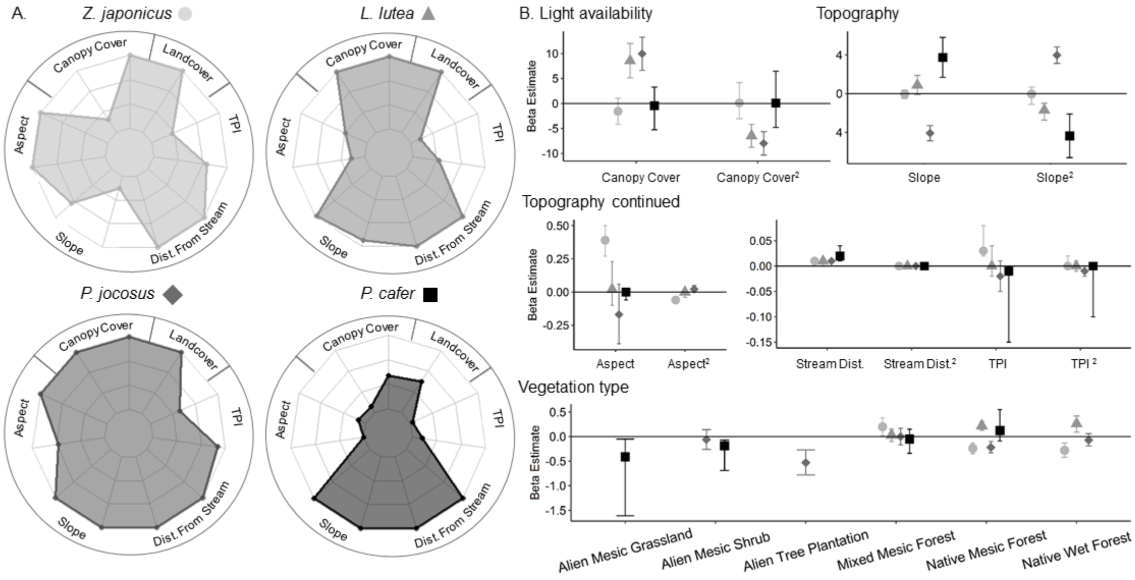
Results–Movement ecology models

Landscape scale

In contrast to our prediction, landscape variables strongly influenced space use of all bird species, but the relationships differed among the four bird species (Fig. 23). *Z. japonicus*, *L. lutea*, and *P. cafer* were the least influenced by different landscape scale factors, with three of the six factors examined influencing their probability of use (Fig. 23). *P. jocosus* was the most influenced by landscape scale factors, with all six factors influencing their use (Fig. 23). All species were influenced by topography but varied in what topographic factors were important and in what direction, except for distance from stream (Figs. 23&24). All species had a positive quadratic relationship between distance from stream and space use (Fig. 23). *P. jocosus* and *L. lutea* were positively influenced by light availability (Fig. 23). Vegetation type influenced all species, with each species being found in 2–3 of the seven potential vegetation types (Figs. 23&25). Three of the bird species were found in unique vegetation types not used by other species; *P. cafer* was the only species found in mesic grassland and alien mesic shrubland, *P. jocosus* was the only species found in alien tree plantation, and *Z. japonicus* was the only species found in mixed mesic forest (Figs. 23&25). Three vegetation types – alien mesic forest, native mesic forest, and native wet forest – were often used by multiple species (Figs. 23&25).

For *Z. japonicus* the global model explained 22% of the variation in space use patterns (marginal adjusted R^2=0.22), the top model explained 18% of AICc weight, and 16 models made up 95% of AICc weight (Table S3A, standard deviation of individual random effect=0.48). *Z. japonicus* space use patterns were influenced by three topographic features and vegetation type (Fig. 23). *Z. japonicus* were more likely to be found on south facing slopes (Fig. 24C), on average ~220m from streams, and spend less time closer or farther from streams (Fig. 24D). They were also found along ridges (Fig. 2E) and most often in mixed mesic forest, followed by alien mesic forest, then native mesic and native wet forest (Fig. 25). They were never observed in the other three vegetation types.

Fig. 23. (A) Radial plots show importance of each landscape factor in species-specific model sets. Importance is based on cumulative AICc weight from all models in which that specific parameter occurred. (B) Beta estimates and 95% confidence intervals based on the model averaged results for factors that characterize light availability, topography, and vegetation type for each species (colors and shapes correspond to species radial plot colors). Any factor followed by “^{2}” represents the quadratic form of the term.



For *L. lutea*, the global model explained 19% of variation in space use (marginal adjusted R^2=0.19), the top model explained 37% of AICc weight, and 12 models made up 95% of the AICc weight (standard deviation of individual random effect=0.38). *L. lutea* space use patterns were influenced by light availability, two topographic features, and vegetation type (Fig. 23). *L. lutea* were more likely to spend time in habitats with an average canopy cover of ~70% and to spend less time under darker or lighter conditions (Fig. 24A). They spend more time at slightly closer distances from streams compared to the other species (average ~160m) and avoid going too close or too far from streams (Fig. 24D). *L. lutea* spend more time in regions with shallow slopes and less time near steep slopes (Fig. 24B) and most often in native wet forest, followed by native mesic forest, and then alien mesic forest (Fig. 25). They were not observed in the other four vegetation types.

The global model for *P. jocosus* explained 31% variation in space use (marginal adjusted R^2=0.31), the top model had 33% of the AICc weight, and five models made up 95% of the AICc weight (standard deviation of individual random effect=0.57). *P. jocosus* space use patterns were influenced by light availability, all four topographic features, and vegetation type (Fig. 23). Similar to *L. lutea*, *P. jocosus* were more likely to spend time in habitats with an average canopy cover of ~70% and to avoid lighter or darker habitats (Fig. 24A). They also spend more time in north-facing slopes (Fig. 24C) and were on average ~260m from streams (Fig. 24D). *P. jocosus* were more likely to spend time either in very shallow or very steep slopes (Fig. 24B), in valleys

(Fig. 24E), and mostly in alien mesic forests, followed by native mesic forest, and then alien tree plantation (Fig. 25). They were not observed in the other four vegetation types.

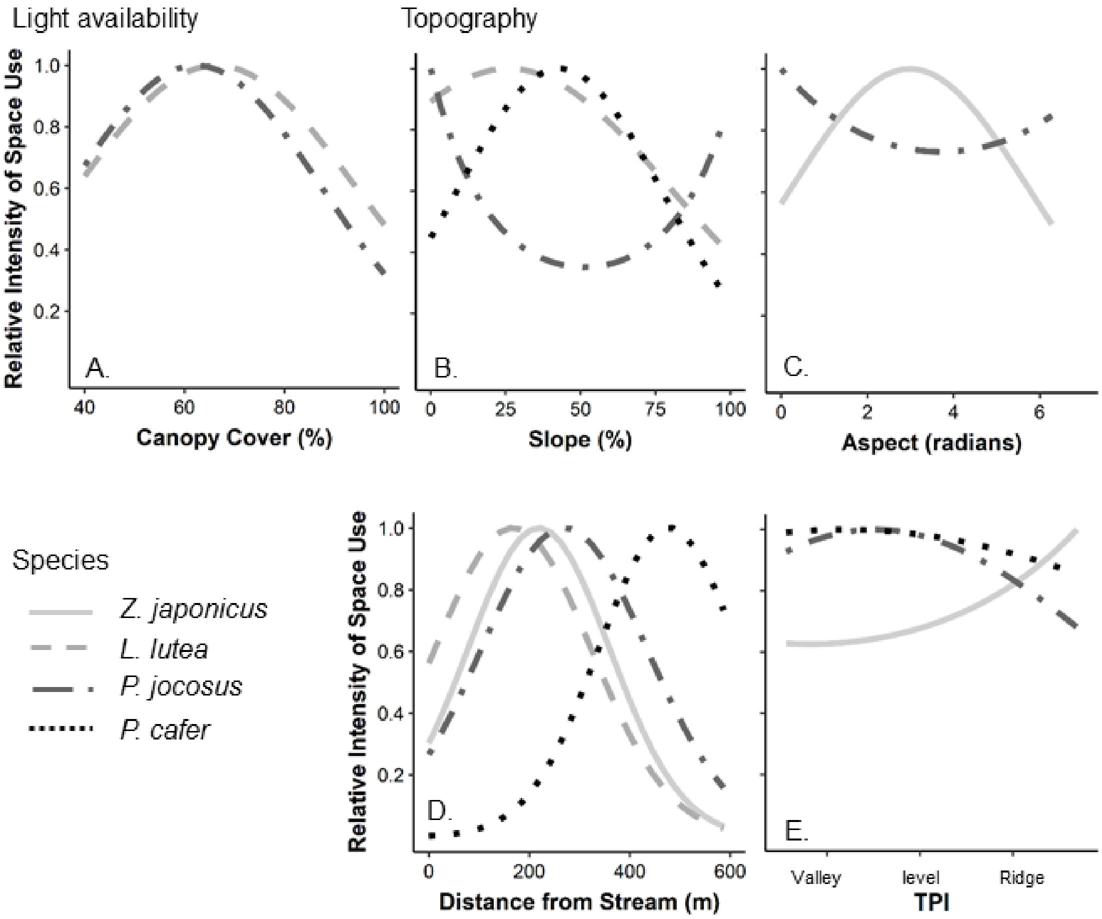


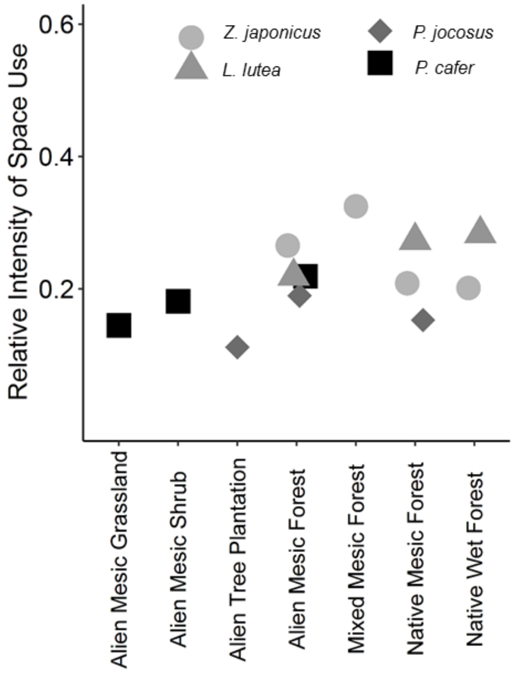
Fig. 24. Model predicted estimates of relative intensity of space use at the landscape scale for (A) canopy cover, (B) slope, (C) aspect, (D) distance from stream, and (E) TPI. Lines are only drawn for a given metric and for an individual disperser species when 95% CIs around beta estimates do not cross zero.

The global model for *P. cafer* explained only 3% variation in space use (marginal adjusted R^2=0.03), the top model had 27% of AICc weight, and 22 models made up 95% of AICc model weight (standard deviation of individual random effect=0.24). *P. cafer* space use patterns were influenced by three topographic features and vegetation type (Fig. 23). *P. cafer* was observed farther away from streams compared to the other species, with an average distance of ~480m away from streams (Fig. 24D). They were also found more often on moderate slopes then on shallow or steep slopes (Fig. 24B) and in gulches (Fig. 24E). They spend the most time in alien mesic forests, followed by alien mesic shrub and alien mesic grassland (Fig. 25). They did not spend time in the other vegetation types (Fig. 25).

Understory scale

In contrast to our prediction that birds would be more responsive to understory rather than landscape level habitat features, the bird species responded to fewer understory factors and these models explained less of the variation in space use compared to the landscape scale analyses. Furthermore, factors that were measured at both scales did not show consistent patterns across scales. The three species varied in their space use depending upon habitat complexity and plant community composition (Fig. 26). *Z. japonicus* was the most influenced by understory scale factors, with three factors influencing their space use. *P. jocosus* was influenced by two factors, and *L. lutea* was influenced by one factor. *Z. japonicus* was the only species influenced by a habitat complexity factor; stem density (Fig. 26) and was most likely to be found in moderately dense habitats (Fig. 27B). *P. jocosus* was the only species influenced by local light availability (Figs. 26&27A) and light environment at the landscape scale (Fig. 1). This is compared to *L. lutea* which was influenced by light availability at the landscape scale but not at the understory scale (Figs. 23&26). Plant community composition influenced all of the species, but in different ways. *Z. japonicus* was the only species influenced by the percent of native vegetation (in a negative direction, Fig. 27C), even though at the landscape scale, *Z. japonicus* was often observed in mixed (alien/native) forest, *P. jocosus* was most often found in alien forest, and *L. lutea* was most often found in native forest (Fig. 25). *P. jocosus* and *L. lutea* were also more likely to be found in habitats that had actively fruiting plants (Figs. 26&27E).

Fig. 25. Model predicted estimates of relative intensity of space use by vegetation type for all species. Plot only includes model estimates for vegetation types where 95% CIs do not cross zero.



The global model for *Z. japonicus* did a poor job of explaining variation in understory space use (marginal adjusted R^2=0.05), the top model explained 2% of the AICc weight, and 1018 models made up 95% of the AICc model weight (standard deviation of individual random effect=0.63).

Z. japonicus space use patterns were influenced by one habitat complexity feature and two plant community composition variables (Fig. 26). *Z. japonicus* were more likely to use habitats that had moderate stem densities (Fig. 27B), lower percentages of native vegetation (Fig. 27C), and more fruiting plant species (Fig. 27D).

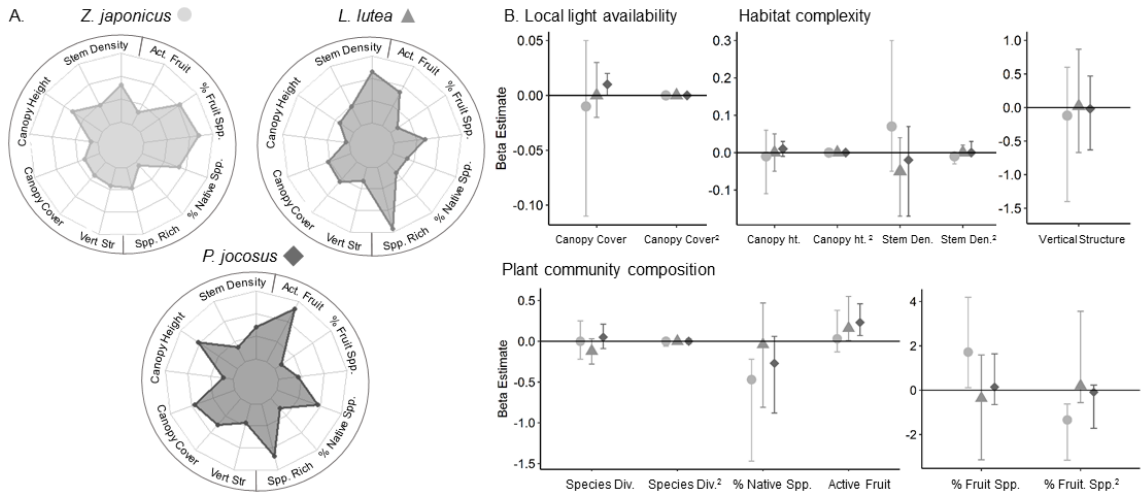


Fig. 26. (A) Radial plots show importance of each understory habitat factor in species- specific model sets. Importance is based on cumulative AICc weight from all models in which that specific parameter occurred. (B) Beta estimates and 95% confidence intervals based on the model averaged results for factors that characterize local light availability, habitat complexity, and plant community composition for each species (colors and shapes correspond to species radial plot colors). Any factor followed by "^{2}" represents the quadratic form of the term.

The global model for *L. lutea* also performed poorly in describing variation in space use (marginal adjusted R^2=0.02), the top model explained 1% of the AICc weight, and 1134 models made up 95% of the AICc model weight (standard deviation around the random effect=0.31). *L. lutea* space use patterns were influenced by one plant community composition variable (Fig. 26). *L. lutea* was more often found in habitats where there was an actively fruiting plant (Fig. 27E).

For *P. jocosus* the global model described 38% of space use (marginal adjusted R^2=0.38), the top model explained 2% of the AICc weight, and 1138 models made up 95% of the AICc model weight (standard deviation of individual random effect=0.33). *P. jocosus* space use patterns were influenced by local light availability, and one plant community composition variable (Fig. 26). *P. jocosus* would spend more time in habitats with denser canopies (Fig. 27A), and with an actively fruiting plant (Fig. 27E).

Discussion–Movement ecology models

Three key points emerge from our multi-scale and multi-species analyses of space use in avian frugivores on Oahu. First, in contrast to our prediction, landscape scale factors explained more variation in space use, and a greater number of factors were important compared to our understory scale analyses. Thus, although all four disperser species are successful invaders, they are not homogeneously using the landscape. This suggests that future analyses assessing spatial overlap of plants and dispersers of interest should be performed at the landscape scale. Second, disperser species varied in their space use patterns even though they are all abundant and consume many similar fruits (Vizentin-Bugoni, et al., 2019). Therefore, both spatial matches and mismatches are likely occurring within this system, depending on the species pairs. This result is a double-edged sword; in any given landscape there is at least one disperser present, but in most landscapes, the number of dispersers is highly limited. Third, results were inconsistent across scales for variables examined at both spatial scales. Thus, studies should not assume consistency across scales. Identification of similarities and differences between avian dispersers in habitat use will be useful for managers deciding where to add or remove plant species, depending upon whether their goal is to increase or decrease dispersal of a given plant species (Buckley et al. 2006). We argue that incorporating spatial overlap between plants and dispersers in models predicting future distributions of vertebrate-dispersed plant species is critical (Araújo and Luoto 2007).

Given that invasive species are often habitat generalists (Richardson et al. 2000) and niches are generally broader on islands due to reduced competition (MacArthur et al. 1972), we predicted that invasive dispersers would not vary in their space use patterns at the landscape scale. Instead, we observed that the four species strongly varied in their space use at the landscape scale and that understory scale metrics were less important (Figs. 1&4). We may have explained little variation in space use at the understory scale either because we did not measure the variables important to space use at the small scale or because the 2m^2 scale is too fine a scale to describe variation in avian space use in this system. Other studies on songbird foraging habitat selection found differences at similar or smaller scales (MacArthur and MacArthur 1961, Robinson and Holmes 1982), but detecting the scale at which invasive species respond to variation in habitat can be difficult (Thuiller et al. 2006). In our system there are two possible reasons for this. First, there may not be enough variation in understory characteristics for species to separate themselves across (Table 1B). Second, there is an abundance of food for these generalist species, which results in reduced competition for foraging habitat, and potentially results in a lack of niche partitioning at this scale. Instead, niche partitioning may occur primarily in association with larger scale processes, such as in home-range selection, and this may explain, in part, why we found variation at the landscape scale (Johnson 1980). Given that plant distributions are commonly examined at the landscape scale and using existing remote sensing is cheaper and faster than collecting one's own measurements (Müller et al. 2010), our findings increase the feasibility of conducting studies of spatial overlap. Conservation biologists and land managers can use existing landscape scale data to model the spatial overlap between plant species and disperser species, generate predictions for which plant species may be limited by dispersal, and use this information to add or remove plants to increase or decrease the probability of dispersal (Araújo and Luoto 2007, Wisz et al. 2012).

Although a high diversity of habitats was covered by the entire disperser community, results indicate few species of dispersers are present in some landscapes, therefore, spatial matches and mismatches are likely occurring depending on the species pairs. Given that these disperser species may only be opportunistically consuming fruits of given plant species (no co-evolved dependencies on particular plants) and species vary in their abilities to consume some fruits (e.g., based on gape size), the greater the number of disperser species consuming fruit, the higher the probability of seed dispersal (Bascompte and Jordano 2007). Current work indicates that the most invasive plant species at our study sites are dispersed by the greatest number of dispersers, while most native plants are dispersed by only 1–2 dispersers (Vizentin-Bugoni et al. 2019). If native plants are found in smaller geographic areas than invasive plants in Hawaii, as would be predicted (Fortini et al. 2013, Vorsino et al. 2014), then less dispersal is predicted for native plants. For example, many native plants on Oahu exist on ridges or in gulches (Wagner et al. 1999). *Z. japonicus* was the only species commonly found on ridges, while *P. jocosus* and *P. cafer* commonly used gulches (Fig. 2E). Likewise, plants found on very steep slopes are likely to only be dispersed by *P. jocosus*, plants on average slopes are likely to be dispersed by *P. cafer*, and plants on shallower slopes are likely to be dispersed by *L. lutea* and *P. jocosus* (Fig. 2C). In general, we found that *P. cafer* and *P. jocosus* most commonly use alien-dominated landscapes, *L. lutea* more commonly uses native-dominated landscapes, and *Z. japonicus* is mixed in its use and this depends on scale (Figs. 35C). Plants that can occupy all of these habitats will be dispersed by all four species. Thus, plant species with narrower habitat requirements, such as many native species (Fortini et al. 2013), are going to have fewer disperser species, and thus a greater probability of limited dispersal (Bascompte and Jordano 2007).

Predicting space use patterns and niche requirements of invasive species is notoriously difficult given the unique interactions present in each introduction (i.e., novel competition, predation, climate)(Thuiller et al. 2007, Jiménez-Valverde et al. 2011). It can also take a period of time before an invasive species settles in a niche within a given community (Fridley et al. 2007). The observed variation between species in space use patterns in this study suggests that there is some niche partitioning occurring (at the landscape scale) in the forests of Oahu; however, lack of information on their native range makes it difficult to establish if this is an example of niche conservatism or if niche shifting has occurred (Wiens and Graham 2005, Fridley et al. 2007). If niche shifting has occurred that would suggest that niches of these generalist species are malleable, and some habitat relationships might shift through time. However, if niches have been conserved and the fact that some habitat variables are most likely consistent (i.e. those associated with general placement of nests) then we can be confident that this is an accurate representation of community level space use. Thus, we should start to incorporate this information into management to strategically place native out-plantings into areas with high disperser space use, and create a dispersal limitation parameter that can be used for predicting future plant distributions (Wisz et al. 2012). Fixed variation in space use patterns also means that if one species goes extinct then plants that occupied that bird's spatial niche are more likely to lose a disperser and become vulnerable to co-extinction.

Our results were inconsistent for the metrics examined at both spatial scales, suggesting that either different processes may be occurring at each level and cannot simply be scaled up or down, or data retrieved from remote sensing is not comparable to data obtained on the ground (Wiens 1989, Mayor et al. 2009). For example, *L. lutea* was influenced by canopy cover at the landscape scale (Fig. 1), but not the understory scale (Fig. 4). This is compared to *P. jocosus*, which was influenced by canopy cover at both scales but was more likely to be in moderately closed habitats at the landscape scale (Fig. 2A) and highly closed habitats at the understory scale (Fig. 5A). Likewise, at the landscape scale, *L. lutea* was primarily found in native forests, *Z. japonicus* was primarily found in mixed forests, and *P. jocosus* was found in alien forests. However, at the understory scale, only *Z. japonicus* was influenced by percent native vegetation. Our two spatial scales were not orders of magnitude different (2m^2 vs 10m^2), but canopy cover and vegetation type were derived from different methods - our own data collection vs. remote sensing. When comparing canopy cover from densiometers to canopy cover from remote sensing data, the Pearson correlation coefficient was weak (0.08). Likewise, percent of native species based on our small-scale measure compared to native habitats (native mesic and native wet forest) and exotic habitats (alien mesic shrub, alien tree plantation, and alien mesic forest) based on land cover had weak Pearson correlation coefficients (-0.16 and -0.05, respectively). These results are consistent with other studies which suggest that data collected on understory characteristics are poorly correlated with vegetation types generated from remote imagery (Martinuzzi et al. 2009). Because remote sensing data is typically used at the large-scale and on the ground, data collection is typically used at the small-scale (for logistical purposes), disentangling which patterns arise due to scale itself vs. different methods of data collection is challenging (Martinuzzi et al. 2009). To adequately determine this, we suggest studies should collect on the ground data at the same scale as remote sensing data to address this question. Until this is done extensively, we urge caution in making management recommendations or in making generalizations in species-specific patterns when combining studies at different scales.

Biotic interactions are threatened by the introduction of invasive species (Traveset and Richardson 2014) and identifying the mechanisms that degrade or facilitate these interactions, and the scales at which they occur, are important steps toward directing conservation. This is particularly important in seed dispersal systems where mismatches between native and invasive species pairs are likely to occur, and matches between invasive species pairs may be more common and will quickly modify systems (e.g., invasion meltdown)(Simberloff and Von Holle 1999). Future studies that integrate disperser space use patterns into seed shadows and predictive plant species distribution maps will strengthen our ability to predict what plants are most likely to be encountered, what types of habitats seeds are likely to be deposited in, and ultimately what groups of vertebrate-dispersed plants will be limited or facilitated by spatial matches and mismatches into the future (Buckley et al. 2006, Araújo and Luoto 2007, Wisz et al. 2012).

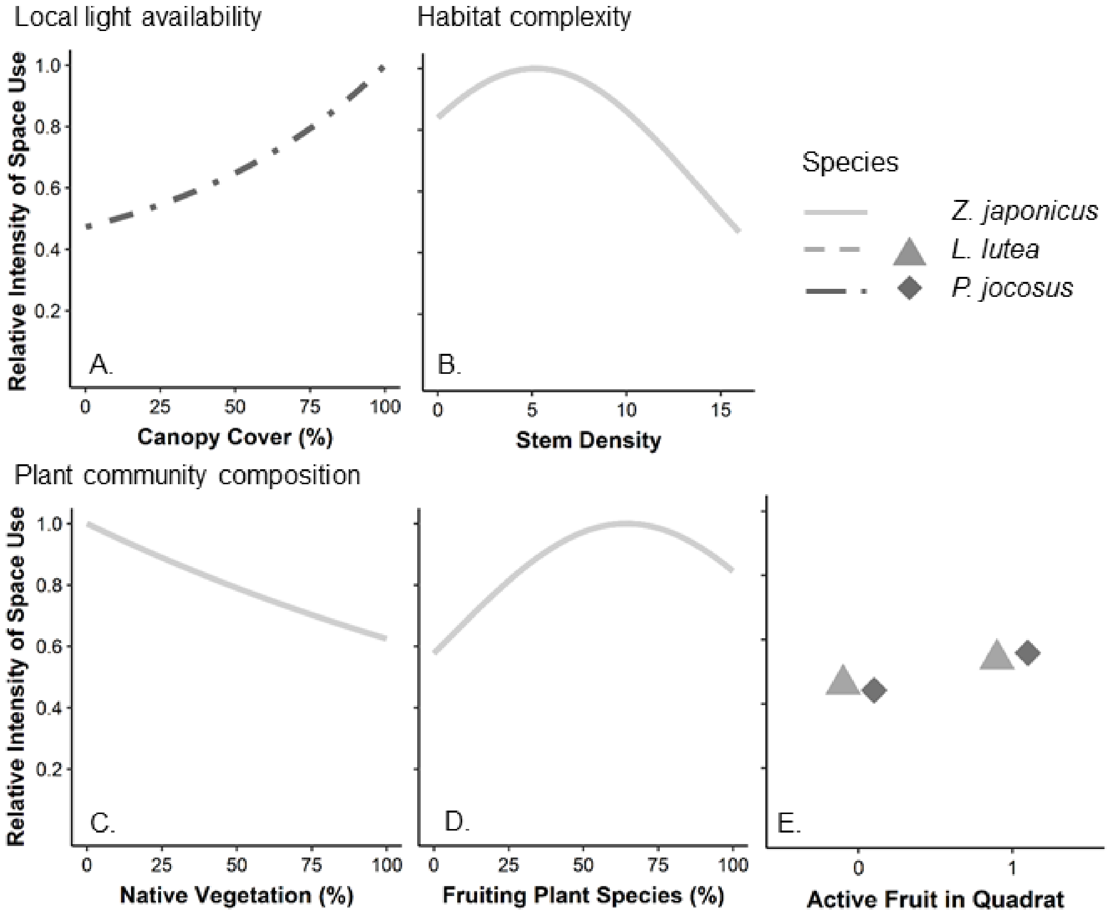


Fig. 27. Model predicted estimates of relative intensity of space use at the understory scale for (A) percent of canopy cover, (B) stem density, (C) percent of native vegetation, (D) percent of fruiting plant species, and (E) presence of an actively fruiting plant. Lines are only drawn for a given metric and for an individual disperser species when 95% CIs around beta estimates do not cross zero.

Table 12. Landscape and understory scale variables. Description of variables included in this study at the (A) landscape and (B) understory scales. Table includes the metric used to describe the variable and the range of the data.

A. Landscape Scale ($10m^2$)	Metric	Minimum	Maximum	Mean	Standard Deviation
Light availability					
Canopy cover	Percent closed	0	100	78.05	12.07
Topography					
Slope	Percent	0	1	0.37	0.2
Aspect	Radians	0	6.28	2.79	1.57
Distance from stream	Meters	0	587	178	150
Topographic position index (TPI)	Index	-5.75	6.75	0.03	1.08
Vegetation type					
Landcover classification	Dominant vegetation type	Alien Mesic Shrub[+]	Alien Mesic Forest[*]		
B. Understory Scale ($2\ m^2$)					
Local light availability					
Canopy cover	Percent closed	0	1	0.87	0.14
Habitat complexity					
Canopy height	Meters	0	57	14.01	6.93
Stem density	Count of stems	0	16	1.74	2.16
Vertical structure	Percent open	0	1	0.58	0.19
Plant community composition					
Species diversity	Count of tree, shrub, vine spp.	0	10	4	2
Fruiting plant species	Percent species that fruit	0	1	0.62	0.26
Native vegetation	Percent species that are native	0	1	0.12	0.2
Actively fruiting plant	Presence of fruit in quadrat	0	1		

[+] Landcover type that had the lowest number of observations.

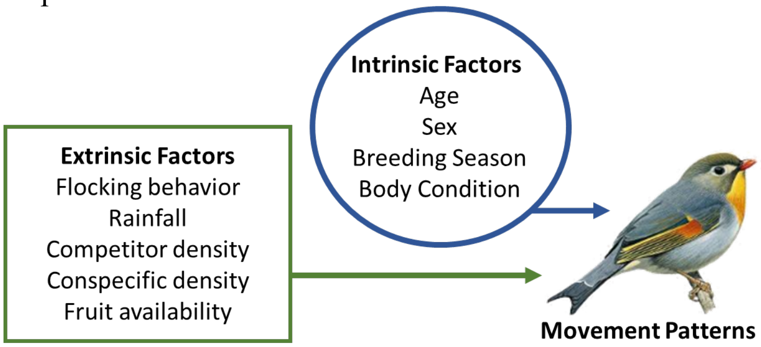
[*] Landcover type that had the highest number of observations.

We took a second approach to assess movement ecology of introduced birds on Oahu. We sought to identify intrinsic and extrinsic factors that influence bird movement.

Introduction–Movement Variation

Identifying intrinsic and extrinsic factors that influence movement is critical for understanding why movement varies across populations, space, and time (Nathan et al. 2008). In particular, temporal and individual variation in animal movement patterns can have implications for critical ecosystem functions such as seed dispersal (Cortes and Uriarte 2013). When introduced species become the dominant dispersers in a system, seed dispersal distance may be drastically altered. Animal movement metrics can influence seed dispersal in different ways. Speed influences the number of fruits an animal encounters, net displacement impacts how far a seed will be deposited from the parent plant, and straightness combines speed and displacement to identify if animals that move faster also have higher net displacement.

Research Questions: We examined movement patterns of three invasive seed dispersing bird species on Oahu, Hawaii, where all of the native frugivores have functionally gone extinct. We asked the following questions: (1) Is there temporal variation in speed, displacement, or straightness? Do these patterns differ between species? (2) What intrinsic and/or extrinsic factors explain variation in speed?



Methods–Movement Variation

We examined the three dominant invasive bird disperses species on Oahu (Vizentin-Bugoni et al. 2019), which range in gape size, body size, and percent frugivory. We examined variation in disperser movement patterns using radio-telemetry at two sites on Oahu, Hawaii between July 2015 and December 2017. To account for bias associated with uneven sampling periods between individuals we used a correlated random walk (Durner et al. 2017) to estimate locations every five minutes for each tracking period. From the estimated points we extracted distance traveled and displacement at the 30-minute scale, which is equivalent to gut passage time for two of these species (Weir and Corlett 2007, Wu et al. 2014).

Q1: We examined temporal variation in speed, displacement, and straightness (displacement/speed) using a generalized additive mixed model with the cyclic cubic regression spline. We included all species in the same model to determine if there was a significant difference in movement between species.

Q2: We conducted species-specific models using Generalized Linear Mixed Models to determine if intrinsic (age, sex, breeding status, and body condition) and/or extrinsic (flocking behavior and rainfall) factors explain variation in speed.

	 **Japanese white-eye** *Zosterops japonicus*	 **red-billed leiothrix** *Leiothrix lutea*	 **red-whiskered bulbul** *Pyconontus jocosus*	 **red-vented bulbul** *Pyconontus cafer*
Mean gape size (mm)	7.71	9.36	11.04	12.67
Mean body size (g)	10.8	21.2	26.1	37.7
Percent fruit in diet[7]	51	67	61	54
Transmitter life (month)	3-4	4-6	7-9	7-9
Number of individuals (n)	24	22	15	5

Results–Movement Variation

Japanese white-eyes and red-billed leiothrix did not show temporal variation in speed, displacement, or straightness (Figs. 28 & 29). This suggests that for a plant, it does not matter what time of year you are consumed by either of these species, the dispersal quality will be similar.

Red-whiskered bulbuls showed temporal variation in their speed and straightness (Fig. 30), suggesting that in the middle of the year individuals are moving fast and circuitously. During this time period they could be encountering more fruit, but not displacing as far as they would at the beginning or end of the year.

Red-vented bulbuls showed temporal variation in their speed (Fig. 31), suggesting that at the beginning of the year they will be moving fast and possibly encountering more fruits ten they would at other times of year. On average red-vented bulbuls moved the fastest in a 30-minute period (164 m), followed by red-whiskered bulbuls (144 m), red-billed leiothrix (120 m), and Japanese white-eye (114 m). On average red-vented bulbuls also displaced the furthest in a 30-minute period (81 m), followed by red-whiskered bulbuls (65 m), red-billed leiothrix (55 m), and Japanese white-eye (51 m).

Japanese white-eyes showed variation in speed in relation to body condition and breeding season. This suggests that individuals in high body condition are able to move faster and potentially encounter and consume more fruits than individuals of lower body condition during the breeding season (Fig. 32).

Red-whiskered bulbuls showed variation in speed in relation to the breeding season (Fig. 33). This suggests that both males and females move faster and are more likely to encounter more fruits during the breeding season than the non-breeding season.

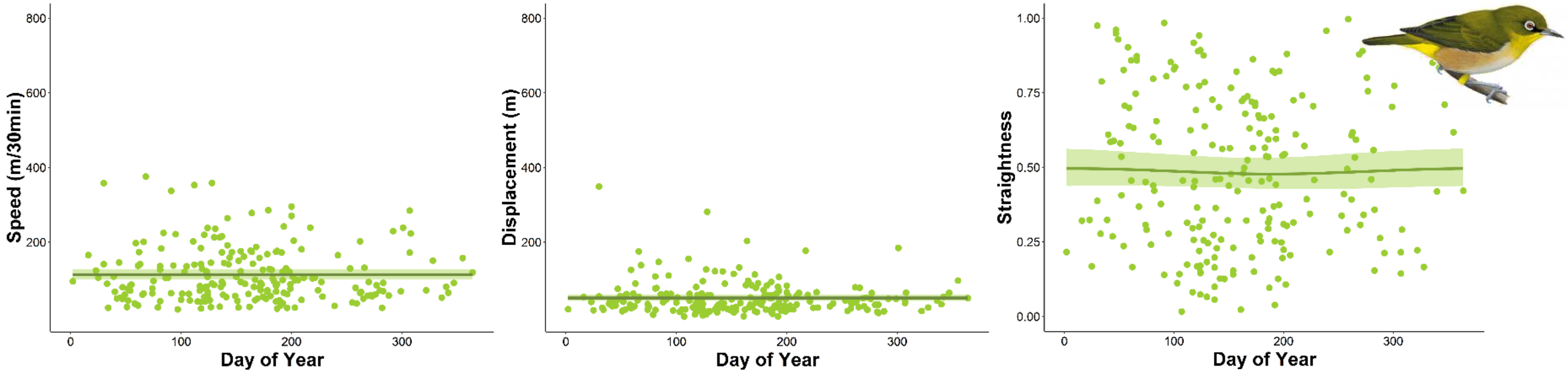


Fig. 28. Japanese white-eyes did not show temporal variation in speed (β=-0.23, 95% CI=-0.42 – 0.05), displacement (β=-0.25, 95% CI=-0.50 – 0.01), or straightness (β=-0.03, 95% CI=-0.18 – 0.11).

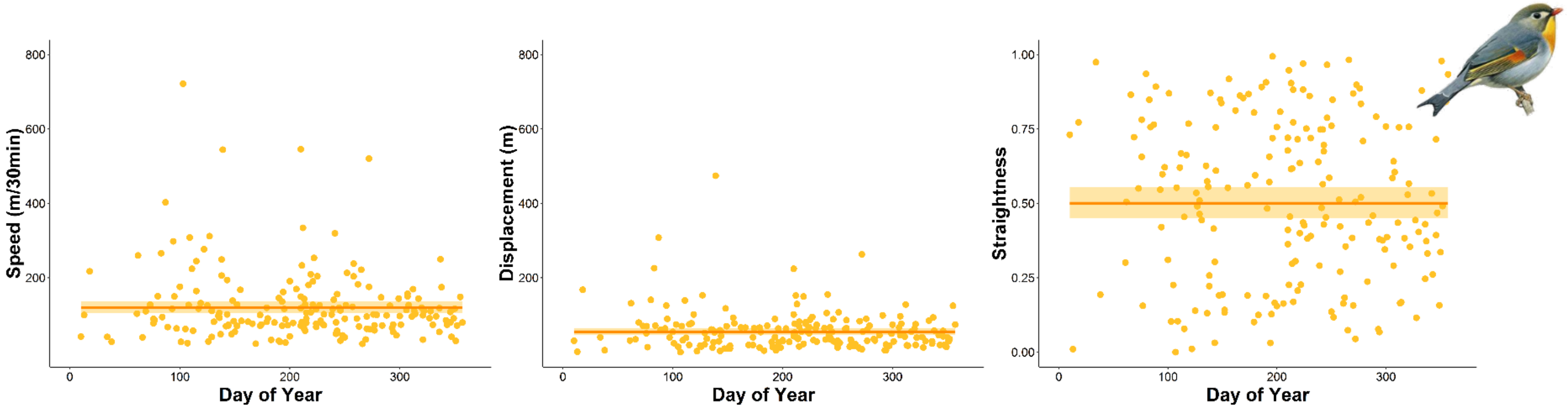


Fig. 29. Red-billed leiothrix did not show temporal variation in speed (β=0.05, 95% CI=-0.12 – 0.23), displacement (β=-0.17, 95% CI=-0.43 – 0.09), or straightness (β=0.03, 95% CI=-0.20 – 0.18).

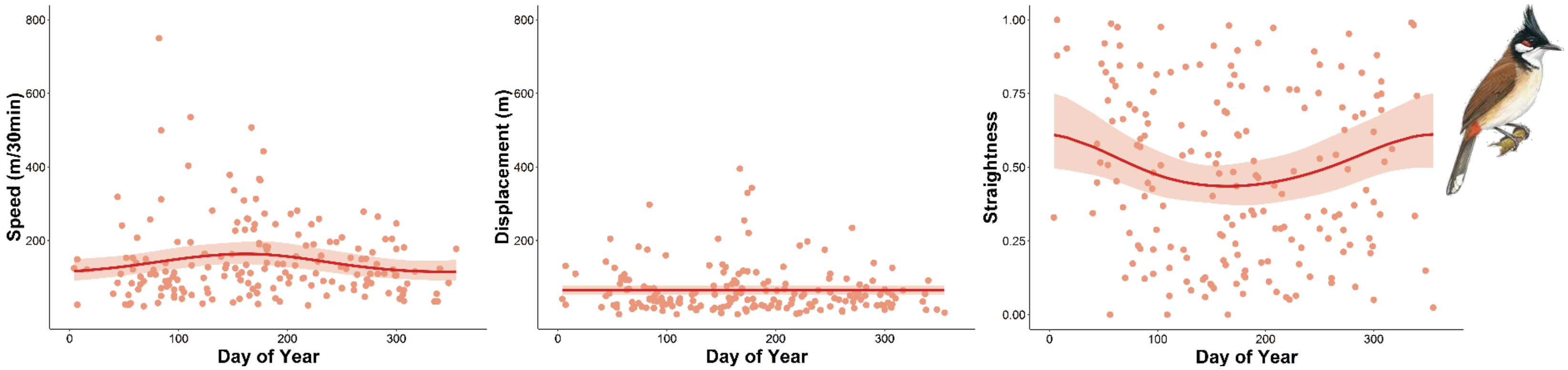


Fig. 30. Red-whiskered bulbuls showed temporal variation in speed (β=0.23, 95% CI=0.04 – 0.42) and straightness (β=0.01, 95% CI=-0.15 – 0.42). They did not show temporal variation in displacement (β=0.25, 95% CI=-0.01 – 0.53).

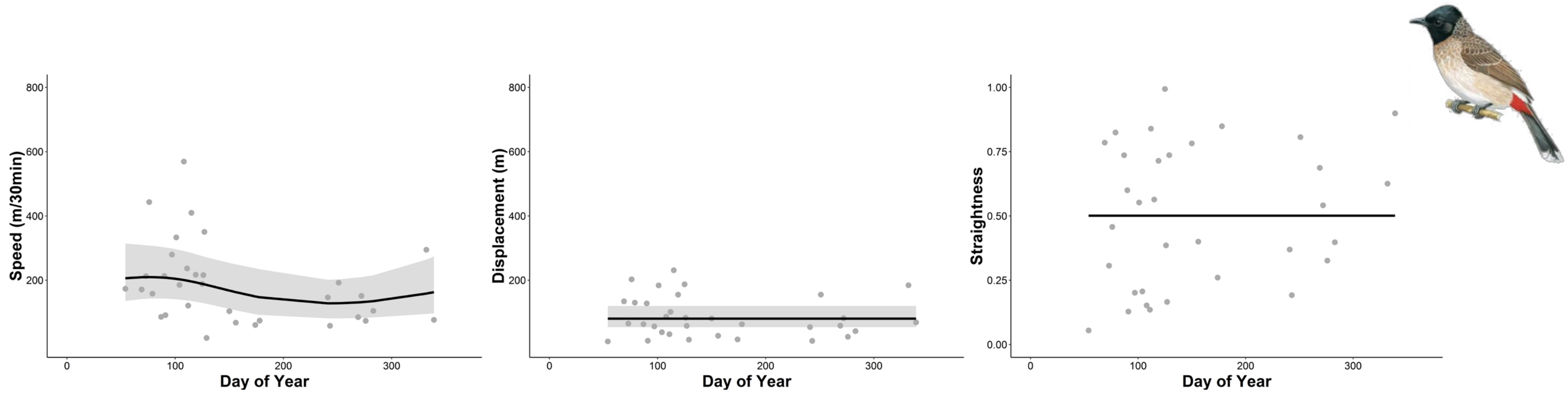


Fig. 31. Red-vented bulbuls showed temporal variation in speed. They did not show temporal variation in displacement or straightness.

Results: Intrinsic and Extrinsic Factors that Explain Variation in Speed

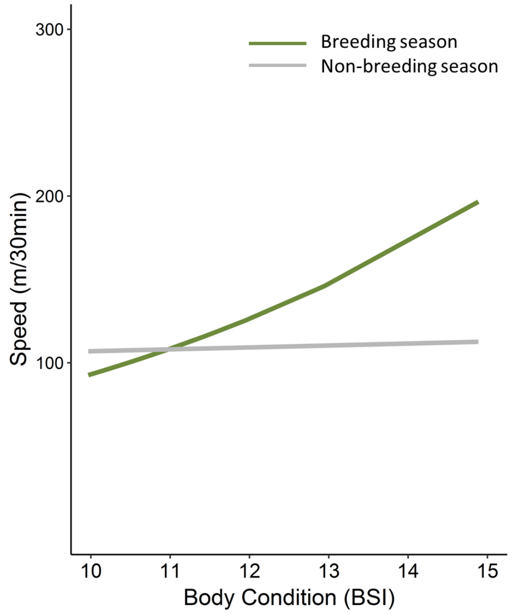


Fig. 32. Body condition effects. During the breeding season, Japanese white-eyes with higher body condition moved faster than individuals with lower body condition or any individual in the non-breeding season ($\beta_{\text{body condition*non-breeding season}}$=-0.14, 95% CI=-0.5-0.0).

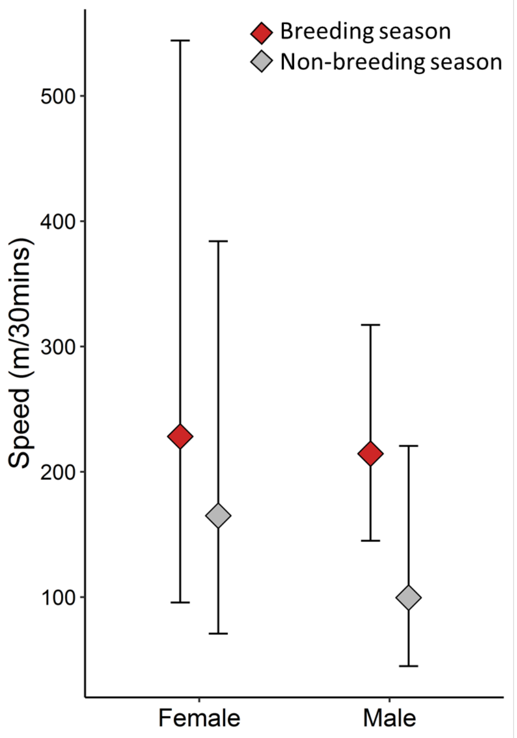


Fig. 33. Breeding season effects. Male and female red-whiskered bulbuls tended to move faster during the breeding season than during the non-breeding season ($\beta_{\text{male*non-breeding season}}$=-0.44, 95% CI=-1.42- -0.06).

Discussion–Movement Variation

Identifying variation in movement and the factors that explain that variation is central to our understanding of why animals move (Nathan and Muller-Landau 2000). Temporal and individual variation in movement patterns can have implications for how we link movement to critical ecosystem services such as seed dispersal. Temporal variation in disperser movement patterns means that there are times of year when seed dispersers are more effective, either consuming more fruits or moving seeds farther away from the parent plant. This means that depending on the phonological patterns of the plant community, some plant species could experience temporal matching or mismatching with disperser quality. Individual variation in movement means that scaling up to population level movement patterns may be difficult and could explain dispersal differences that we observe in different environments. Here we found that while only one species showed temporal variation in movement patterns, intrinsic and extrinsic factors explained variation in speed for all species, suggesting that considering both temporal and population level variation in predictive seed shadow maps of seed dispersal could be important.

Future Directions

1. Assess temporal synchrony between disperser movement, diet, and abundance in relation to local fruiting phenology.
2. Link temporal variation in movement to fruiting phenology to estimate seed shadows for different plant species.

Task 7: Determining climate effects on dispersal competence

The overall aim of this task was to estimate the robustness of seed dispersal network to climate change. Specifically, we estimated and compared the rates of coextinction (i.e. loss of plants following bird extinction) and how they differ between a scenario where birds are randomly lost compared to when most climatically vulnerable birds are lost first. This change in approach to the task was suggested at the Spring 2019 IPR as a way to better leverage our existing network analyses and take them in a novel direction that few groups are working on worldwide.

Methods–Climate effects

In order to estimate species climatic niche, we collected climatic variables throughout the distribution range on each native or introduced seed disperser bird on Oahu (Vizentin-Bugoni et al. 2019). This data was extracted at 1-km scale from WorldClim (Fick and Hijmans 2017) where the species were reported on eBird (Sullivan et al. 2009). For the introduced species, we used all reports including those from their native range and other areas where they are established as we wanted to estimate their potential climatic niches even if their range of tolerance does not occur on Oahu in the present.

We then used dynamic range boxes (Junker et al. 2016) to estimate the vulnerability of each species to climate change. This nonparametric method allows the quantification of the overlap between the species' present range of climates they occupy, and the future climate of Oahu (2080–2099) as predicted by Zhang et al. (2016). The result is the proportional overlap of the n-dimensional hypervolumes representing the current niche and the future available niche on a scale of 0 to 1 where 1 is complete overlap based on the arithmetic mean size and dimensional overlap. Since the proportional overlap is dependent on the size of the hypervolume that is being compared to, which was variable for the bird species, we compared current species climate niche to the future available niche so that the proportion of overlap is the proportion of the future climate that is within the current climate niche. The same variables obtained from WorldClim were determined and averaged across the twenty-year projection and included yearly temperature maximum, mean, minimum, and seasonality (standard deviation x 100) as well as precipitation maximum, mean, minimum, and seasonality (coefficient of variation). The most vulnerable species are the ones whose present climate niche present low overlap with the future climates (i.e. overlap → 0). We were not able to include two species, i.e. NOCA and HOFI, which are however poorly influential on the network as they rarely disperse seeds and interact with only one and two plant species, respectively.

Network robustness to climate chance was modeled by excluding sequentially bird species from the most to the least vulnerable to climate change and quantifying plants coextinction rates. This model is based on the notion that a secondary extinction occurs when all partners this species interact are lost. In our models, a plant goes extinct when all birds dispersing its seeds are lost. The robustness metric ranges from zero to 1, when all animals have to be lost in order to coextinction occur in the network (Memmott et al. 2004). As a benchmark model for comparison we also estimated the robustness of the network assuming bird extinctions occur by random, regardless of species vulnerability to climate change.

Results and Discussion–Climate effects

Vulnerability to climate change was high among bird species, varying from 0.76 to 0.88 (i.e. Vulnerability = 1-overlap; Table 13). This high vulnerability is not surprising as islands are particularly susceptible to climate change (Nurse et al. 2014). Robustness was higher for the

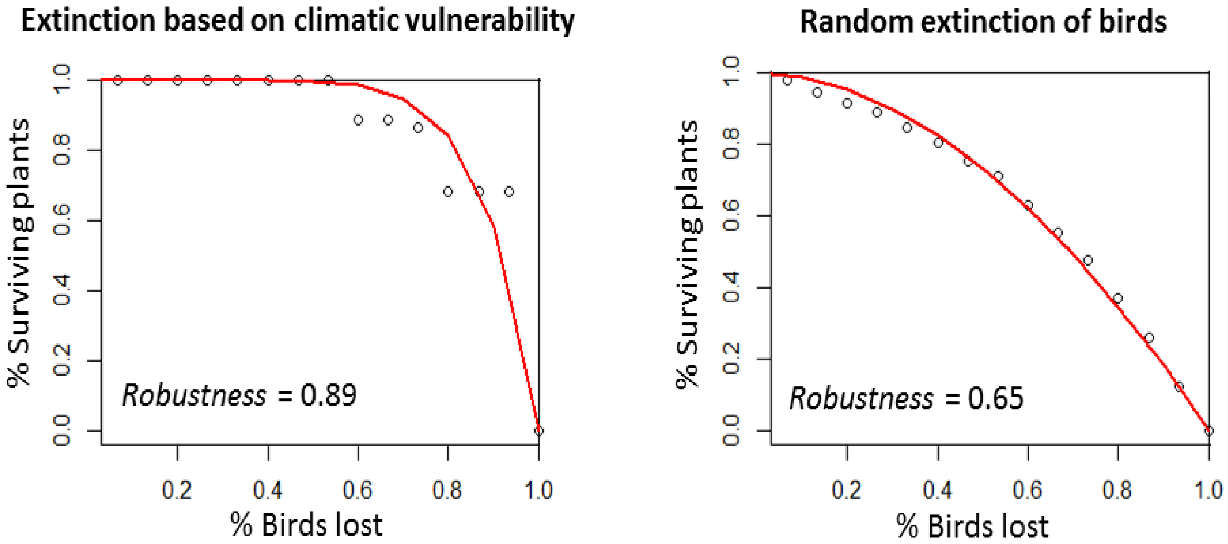


Fig. 33. Robustness of the seed dispersal network to the simulated extinction of climatic venerable species first (left) and to the random extinction of species (right). Note that in the former, half of the species have to be lost in order to cause any coextinction of plants, while in the latter coextinctions may occur much earlier.

scenario where climatic vulnerable species are lost first, in comparison to the random lost (0.89 vs. 0.65; Fig. 33). This means that the seed dispersal network on Oahu is relatively robust to the estimate scenario of climate change.

The high robustness of networks to climate change has two main reasons: First island-wide, there is high overlap on the diets of the four main seed dispersers (RBLE, JAWE, RWBU and RVBU). Because these species vary in their vulnerability to climate change, when a more vulnerable species is lost (such as RBLE), other species that are also important frugivorous can still promote seed dispersal because they are less vulnerable to climate change, such as RWBU. Second, some of the most sensitive species are not important seed dispersers (such as JABW and the native APAP). Thus, the loss of these species may have relatively low influence on the seed dispersal network because the plants they disperse are also disperser by other species at much higher frequencies (Vizentin-Bugoni et al. 2019).

Caveats

Here we estimate network robustness to the extinction of seed dispersers while the estimation of the effects of plant extinction remains unexplored. As the world's capital of invasions and extinctions, Hawaii harbors high diversity of plants, most of which are confined to mountaintops indicating that they may have narrower climatic niches and be more vulnerable to climate change than the bird community.

Table 13. Climatic vulnerability of seed dispersers on Oahu estimated using dynamic range boxes.

Bird Species	Volume	Overlap	Vulnerability	Extinction Order
Oahu Future	0.3736528	-	-	-
RBLE	0.7141271	0.1203239	0.8796761	1
APAP	0.4767312	0.1242664	0.8757336	2
JABW	0.7087479	0.1355833	0.8644167	3
JAWE	0.6844823	0.1411056	0.8588944	4
RVBU	0.7216275	0.1454207	0.8545793	5
SPDO	0.7726795	0.1472674	0.8527326	6
RWBU	0.7278728	0.1518728	0.8481272	7
HWAM	0.6277056	0.1604785	0.8395215	8
COMW	0.5940852	0.1704998	0.8295002	9
WRSH	0.6822666	0.1931522	0.8068478	10
RCCA	0.5329143	0.2084599	0.7915401	11
OAAM	0.4451687	0.2222421	0.7777579	12
ZEDO	0.5479237	0.2459718	0.7540282	13
HOFI	NA	NA	NA	14
NOCA	NA	NA	NA	15

Tech Transfer and Dissemination

At the request of the 2016 SERDP IPR panel, we wrote and subsequently submitted a white paper to more fully describe “the benefits to DoD from your work in terms of products, models, etc.”, with an emphasis on Tech Transfer and the dissemination of our data and findings. We detailed the numerous ways we have been distributing our findings to DoD and other interested parties through one-on-one meetings, annual, conferences, volunteer and outreach activities, websites, social media, and peer-reviewed publications. The primary components of that white paper are detailed below.

Coordination with DOD facilities and projects

In additional to generally broadening our understanding of the role of non-native species in seed dispersal networks on Oahu, this work can be used to address specific rare plant management questions such as optimal placement of outplantings, plant community and structure of restoration sites to maximize seed dispersal. Current rare plant restoration sites, managed by the Oahu Army Natural Resource Program (OANRP), have widely varying levels of recruitment and it is suspected that those restoration sites with characteristics (e.g. specific plant diversity and structure) favorable to frugivores have higher rates of seed dispersal, and germination, than those with less favorable traits. Our work can be used to identify those frugivore species that are more effective seed dispersers and the habitat and environmental characteristics that these species select. This information can then be used to improve the success of rare plant conservation efforts through targeted placement or management of restoration sites that have higher abundances of effective seed dispersers.

Although seed dispersal networks are the focus of the research project, we are also filling critical knowledge gaps on species communities and ecologies on Oahu that will be valuable for Army conservation and management objectives. OANRP has a specific mandate to manage a large number of native plants and animals on its lands as well as has established restoration areas on state of Hawaii lands to mitigate impacts of troop activity on its own lands. Given the dynamic nature of the Hawaiian Island communities, with relatively recent species extinctions and invasions, there are numerous aspects of species and species interactions that are unknown or undocumented. For example, our project provided detailed information on plant (both rare and invasive), bird and rat phenology, distribution and abundance that was previously unknown. Further, our use of numerous study sites, across an elevational and precipitation gradient, allows a detailed examination of how these factors vary over time, space and management and invasion history. We worked and continue to work directly with OANRP at several of its endangered plant outplanting sites to assess methods of increasing fruit visitation by non-native birds, followed by monitoring of subsequent consumption and dispersal.

Coordination with state, federal, and non-profit organizations for weed control

Although non-native frugivores have the potential to aid in conservation of rare plants through seed dispersal, they are also likely facilitating encroachment and spread of non-native invasive plants. Our project identified which non-native invasive plant species are spread via non-native frugivores and our work provides projections for potential dispersal distances that are important for creating management buffers around new weed infestations. We work with OANRP, the state of Hawaii’s Division of Forestry and Wildlife (DOFAW) and its Natural Areas Reserve System (NARS), and the Oahu Invasive Species Committee (OISC). Further, results of the rat portion of the project can be used to understand the role of non-native rats in predation of rare plants, seed dispersal of invasive plant and predation of bird nests, thus providing information valuable for refining or expanding rat removal programs already in place across the island.

Transitioning Findings

The movement ecology and landscape models created in Years 4 and 5 of the project from the bird, rat and plant data have been transitioned to OANRP and other stakeholders for use in conservation and management planning. These models can be used to project and predict impacts of various management strategies as well as climate change. Ongoing efforts, particularly those involving identification of seed species in the diets of non-native birds and rats, frugivory events at rare plants, and distribution/abundance of potential seed dispersers, has already been transitioned to stakeholders through a variety of forums. Our SERDP research group regularly communicates the results of the project with OANRP staff and coordinates all efforts to assure project results match with management questions and objectives. We operate a Facebook page (www.facebook.com/hawaii.vine.project) where we provide regular updates and photos to various stakeholders (as of this writing there are 449 people following the page). We are involved with or conduct a wide variety of outreach and/or volunteer efforts where we engage with the Oahu land management and local community. In addition to our current papers, numerous scientific publications are in progress for each project task. Finally, the animal movement and landscape models will be included in scientific publications where the code will be made available through the publisher or via online data sharing sites. We will additionally assure that our DoD contacts have access to the models, and we will continue to provide assistance on their use. Rather than interacting with stakeholders and end users only at the completion of our project, we are actively engaging them during all phases of our project. This open and full collaboration allows for rapid dissemination of results, the ability to tailor our work to address specific stakeholder needs, and the flexibility to modify our approaches.

Conservation Community Interactions

At the 2016 Project In-Progress Review (IPR), there was some concern about how managers will have access to our results. We are proud of our partners and/or collaborators with whom we work for integrating research with land and resource management: U.S. Army Garrison in Hawaii, Oahu Army Natural Resource Program (OANRP), Manoa Cliffs Native Forest Restoration Project (non-profit), State of Hawaii Department of Land and Natural Resources-Division of Forestry of Wildlife & Natural Areas Reserves System, and Waimea Valley Hiipaka LLC. Our interactions with these partners occur both in the field and in the office. We have also hosted or participated in a broad range of volunteer activities with these and related conservation partners. For broader dissemination, the Hawaiian conservation community is tight knit and holds two large annual meetings each year. The first is the Hawaii Conservation Conference, which rotates annually among the largest of the main islands. We are frequent attendees of this meeting, where we can meet with collaborators, stakeholders, partners, land managers, and other researchers to discuss our respective projects, goals, and plans. These in person meetings are the foundation of field work in Hawaii, fostered by a culture that emphasizes the need to "talk story" and share experiences. The second major annual meeting, the Hawaii Ecosystems Meeting, brings together researchers to exchange findings. Yet, we understand the need to have a lasting record as well.

Data Management and Dissemination
Soon after the conclusion of this project, or sooner if as part of publications, the majority of our data will be freely available online through a variety of sources such as Harvard's Dataverse and Dryad. Relevant scripts for analysis and modeling will also be posted at these or similar programming sites for use by more sufficient programming skills (computer skills that are increasingly being taught at the college and graduate levels). In the meantime, we will be hosting a data portal at hawaiivineproject.org for data access by collaborators, where there will be database integration with the website's CMS (content management system). The data portal will have dynamic data querying and online analyses. All of our software for data management and analysis is open source, allowing unrestricted access once we release our data. We have chosen this route of data management and access based on our experience in working with land managers. Providing raw data allows managers such as DoD to see what's available and data summaries are easily performed. However, more sophisticated graphical interfaces (e.g. well-developed web sites) take large amounts of time to do well. In our conversations with our collaborators these websites focused on such a specific topic are seldom used and typically become outdated soon after project completion. In contrast, the raw data and data summaries we utilize avoid those issues and provide access to the essential information that may not be available in manuscripts, reports, and presentations. When necessary we can provide expert guidance to our data for managers needing additional support.

Project Training
This project provided training and resources to six graduate students (Jason Gleditsch, University of Illinois; Marilou Hircq, University of Montpellier; Amy Hruska, University of Hawaii-Manoa; Sean MacDonald, University of Illinois; Becky Wilcox & Sam Case, University of Wyoming). In addition, we had 12 undergraduate students conducting research in our labs for university credit.

Publications

Vizentin-Bugoni, J., C.E. Tarwater, J.T. Foster, D.R. Drake, J.M. Gleditsch, A.M. Hruska, J.P. Kelley, J.H. Sperry. 2019. Structure, spatial dynamics, and stability of novel mutualistic networks. Science. 364: 78–82. doi: 10.1126/science.aau8751

Gleditsch, J. M., and J. H. Sperry. 2019. Rapid morphological change of nonnative frugivores on the Hawaiian island of Oahu. Evolution 73:1456-1465. doi: 10.1111/evo.13744

Hays, B.R., J. Sperry, D.R. Drake and A.M. Hruska. 2018. Husking stations provide insight into the diet of non-native rodents on O‘ahu, Hawai‘i. Pacific Science 72(3).

Gleditsch, J.M., A.M. Hruska, and J.T. Foster. 2017. Connecting resource tracking by frugivores to temporal variation in seed dispersal networks. Frontiers in Ecology and Evolution 5:98. doi: 10.3389/fevo.2017.00098

Hircq, M. Impact of poor seed dispersal on seed predation by introduced rodents in a Hawaiian wet forest. Master's Thesis in Biodiversity, Ecology & Evolution. University of Montpellier, September 2016.

Publication in review or in preparation (full manuscripts available)
Wilcox, R.C. and C.E. Tarwater. *In review*. Multi-scale approach to evaluating variation in space use in invasive birds; implications for seed dispersal mismatches in a novel ecosystem. Ecology.

Case, S.B. and C.E. Tarwater. *In preparation*. Functional changes in assemblages of avian frugivores following extinction and invasion. Target journal: Ecology.

Gleditsch, J.M., J.P. Kelley, D.R. Drake, J.T. Foster, A.M. Hruska, C.E. Tarwater, R.C. Wilcox, and J.H. Sperry. *In preparation*. Drivers of avian community composition and habitat relationships of native and non-native birds in Hawaiian forests. Target journal: Ecological Applications.

Presentations at National and International Meetings
Gleditsch, J.M. et al. The bird community composition and the factors that influence the distribution of bird species in Oahu forests. Annual Meeting of the Association for Tropical Biology and Conservation. July 2015. Honolulu, HI.

Hruska, A. et al. Frugivory networks of Hawaiian nonnative birds and their role as potential seed dispersers in Oahu forests. Annual Meeting of the Association for Tropical Biology and Conservation. July 2015. Honolulu, HI.

Dittmar, E. et al. Nonnative birds and the maintenance of native plant communities. Hawaii Ecosystems Meeting. 7-8 July 2016. University of Hawaii, Hilo, HI.

Hruska, A. et al. Frugivory networks of nonnative birds across Hawaiian forest communities. Island Biology 2016. International Conference on Island Evolution, Ecology, and Conservation, 18-22 July 2016, University of Azores, Azores, Portugal.

Gleditsch, J.M. et al. Phenotypic variation in introduced bird populations in Hawaii. North American Ornithological Conference, August 16-20, 2016. Washington, DC.

MacDonald, S. et al. Effects of conspecific attraction on native plant recruitment in Hawaii. North American Ornithological Conference, August 16-20, 2016. Washington, DC.

Drake, D.R., J. Vizentin-Bugoni, J. Gleditsch, J. Sperry, J. Foster, A. Hruska, J.P. Kelley, C. Tarwater. Seed dispersal networks in O‘ahu's forests are dominated by novel interactions involving non-native species. Hawai‘i Native Seed Conference. Oahu, HI. May 2018.

Gleditsch, J.M., J.P. Kelley, C.E. Tarwater, J.T. Foster and J.H. Sperry. Ecomorphology of the introduced avian frugivores on the Hawaiian Island of Oahu and how it relates to rapid morphological change. 2018 American Ornithological Society. Tucson, AZ. April 2018.

Case, S.B., and C.E. Tarwater. Functional Changes in Assemblages of Avian Frugivores Following Extinction and Invasion. American Ornithological Society, Anchorage, Alaska, June 24-28, 2019.

Wilcox, R.C., and C.E. Tarwater. Multi-Scale Approach to Evaluating Space Use in Invasive Avian Dispersers and the Implications for Seed Dispersal. American Ornithological Society, Anchorage, Alaska, June 24-28, 2019.

Responses to 2019 IPR Review

1. **In the Final Report please include the following information: - Discuss whether seed size was an influence with the variables tested? - In regard to predictive modeling, whether can you generalize a result and come up with a semi-generic model that would have predictive power and help with management decisions/decision making process?**

As detailed above, we assessed many aspects of fruit traits and their effects on the probability of being dispersed. We did not directly assess seed size in our models, with the primary rationale being limited variation in seed size. All of the bird and rodent-handled species are small-seeded (<9 mm diameter) and most also produce many seeds per fruit. Six of seven alien species and six of eight native species with >50% animal-handled seeds at one or more sites produce fruits with multiple seeds. Across sites, the smallest animal-handled alien seed was *Clidemia hirta* (0.5 mm) and the largest was *Psidium cattleyanum* (5.1 mm). The smallest native animal-handled seeds were *Cyanea angustifolia and Cyrtandra cordifolia* (0.5 mm), and the largest was *Antidesma platyphyllum* (8.9 mm). Despite what we believe will be small effects of seed sizes, we are actively continuing to work on these questions. In particular, we have prepared a manuscript on this topic titled, "Functional changes in assemblages of avian frugivores following extinction and invasion", that demonstrates strong shifts in the seed disperser community.

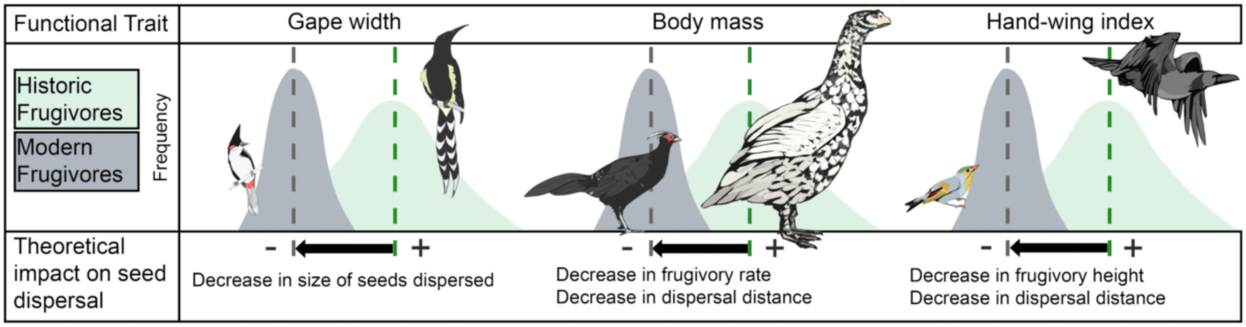


Fig. 34. Conceptual diagram with hypothesized shifting in functional traits between historic and modern frugivore assemblages and with associated theoretical impacts of shifts on seed dispersal. Illustrated birds belong to assemblages and exhibit traits that exemplify hypothesized shifting.

As for predictive modeling, we are currently analyzing our data to make such generalizable results—the primary reason we are investigating species roles in Task 5. Once we have multiple predictors (traits, phenology, abundances), we can then test which variable or set of variables is most influential. When we can define the frequencies and strengths of interactions, managers would then be able to focus their *in situ* efforts towards the most influential variables. For example, if the goal is to have plant communities as 'native' as possible and assuming that abundances and trait matching are the main driver of species interactions, managers could focus on reducing abundances of undesired plants that have close matching to specific bird bills of the key dispersers, while also increasing abundance of the desired plant species that best match the local bird community.

2. **In the Final Report, please provide more clarity on a network science approach taken. [Also], please provide clarification of the overall dispersal network considered most appropriate as a result of this project.**

Despite extensive studies, seed dispersal research has classically considered only a few focal species although coexisting assemblages of plants and their dispersers engage in complex interaction networks encompassing multiple species (Jordano 1987). Studying interactions among plants and seed dispersers as ecological networks allows the investigation of the structure and dynamics of these complex interactive assemblages and facilitates the understanding of system-level phenomena that cannot be inferred by looking at the components of a community in isolation (Memmott 1999, Bascompte 2009). In doing so, a network analysis offers possibilities to explore novel and long-lasting questions in ecology (Bascompte 2009). Importantly, network thinking has been integrated into conservation, restoration and management, offering valuable tools to cope with the urgent challenge to understand and mitigate environmental changes, biological invasions, and species loss on crucial ecological processes such as seed dispersal (Tylianakis et al. 2010).

The starting point of such a network analysis is building an interaction matrix based on field data that describe which species interact with whom in a community and, often, the strength of their relationships. In the context of the work in this project, the network is an interaction matrix where each row i is a plant species and each column j is a bird species. The intersection a_{ij} is a measure of interaction intensity, defined as the proportion of samples of bird species j containing seeds of plant species i. Thus, this measure of interaction intensity accounts for differences in the number of samples collected among bird species and across sites (Vizentin-Bugoni et al. 2019).

Interaction matrices such as this are then suitable for network analysis, allowing investigations at both species and community level. At species level, each network member can be described in terms of its specialization and role played in the community which is estimated taking into account how its interactions are distributed across the potential partners in the community and in comparison to other species within the same trophic level (Sebastián-González 2017). In ecology, such analyses include distinct degree and centrality measures, that are related to the concept of keystone species (Martín González et al. 2010, Sebastián-González 2017). At the community level, the goal is to understand system-level patterns of interactions that may emerge as a consequence of distinct processes and have broad implications for community stability (Thebault and Fontaine 2010). Such patterns are described to the overall level of niche partitioning (i.e. complementary specialization) and topology (i.e. nestedness and modularity). Thus, we consider the overall dispersal network that we chose is the most appropriate network approach for this dataset because it best captures the complexity of the interactions. Note that for some subprojects that required spatially explicit data, the overall (island-wise) network was subset per site. In this case, each site was described as a distinct interaction matrix based on site specific data (see Vizentin-Bugoni et al. 2019 for details).

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Supplemental Materials–Additional Figures and Tables

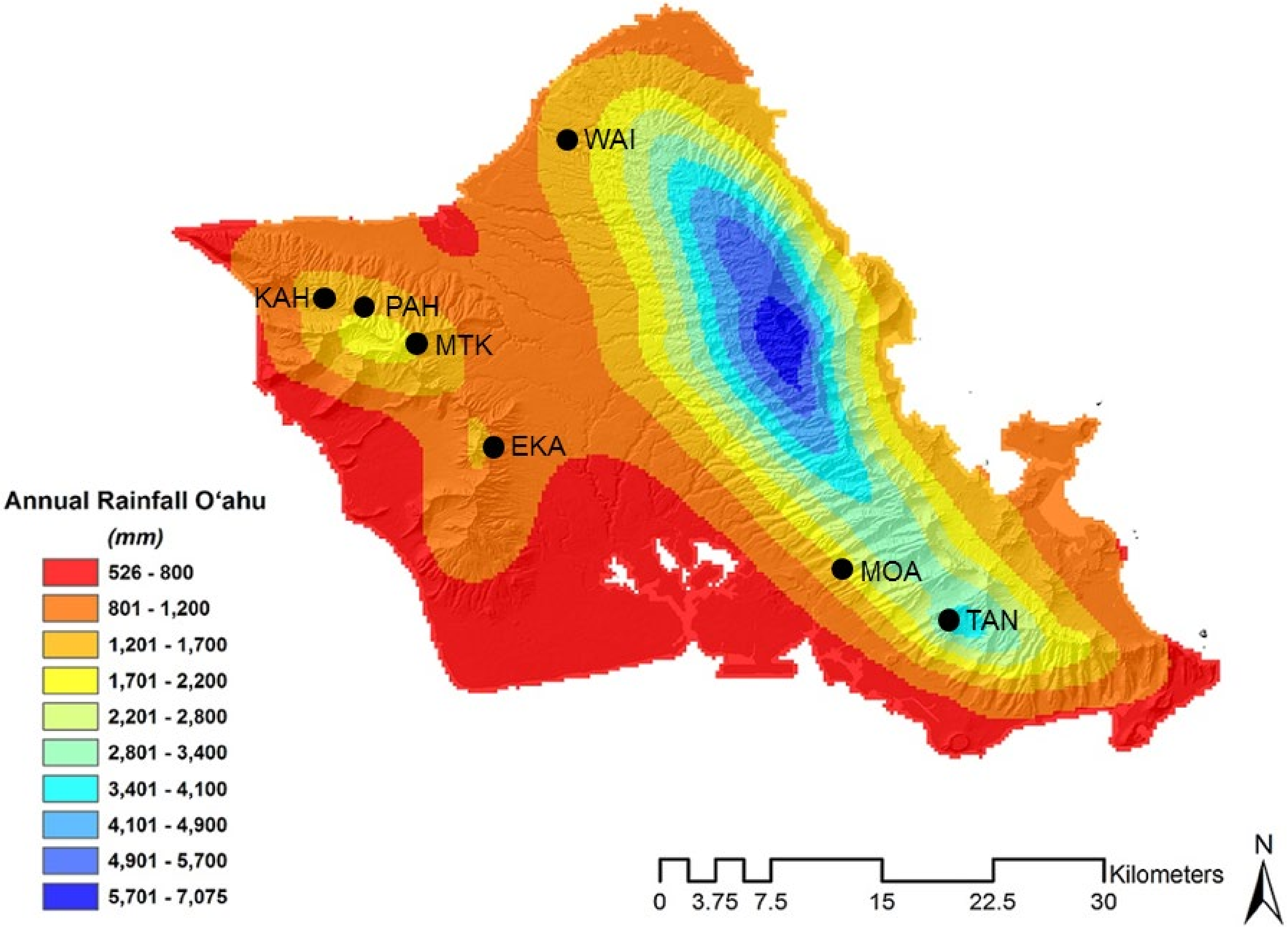

Fig. S1. Seven sampling sites and the distribution of mean annual rainfall from 1978-2017 on Oahu. Modified from 'Rainfall Atlas of Hawai'i'.

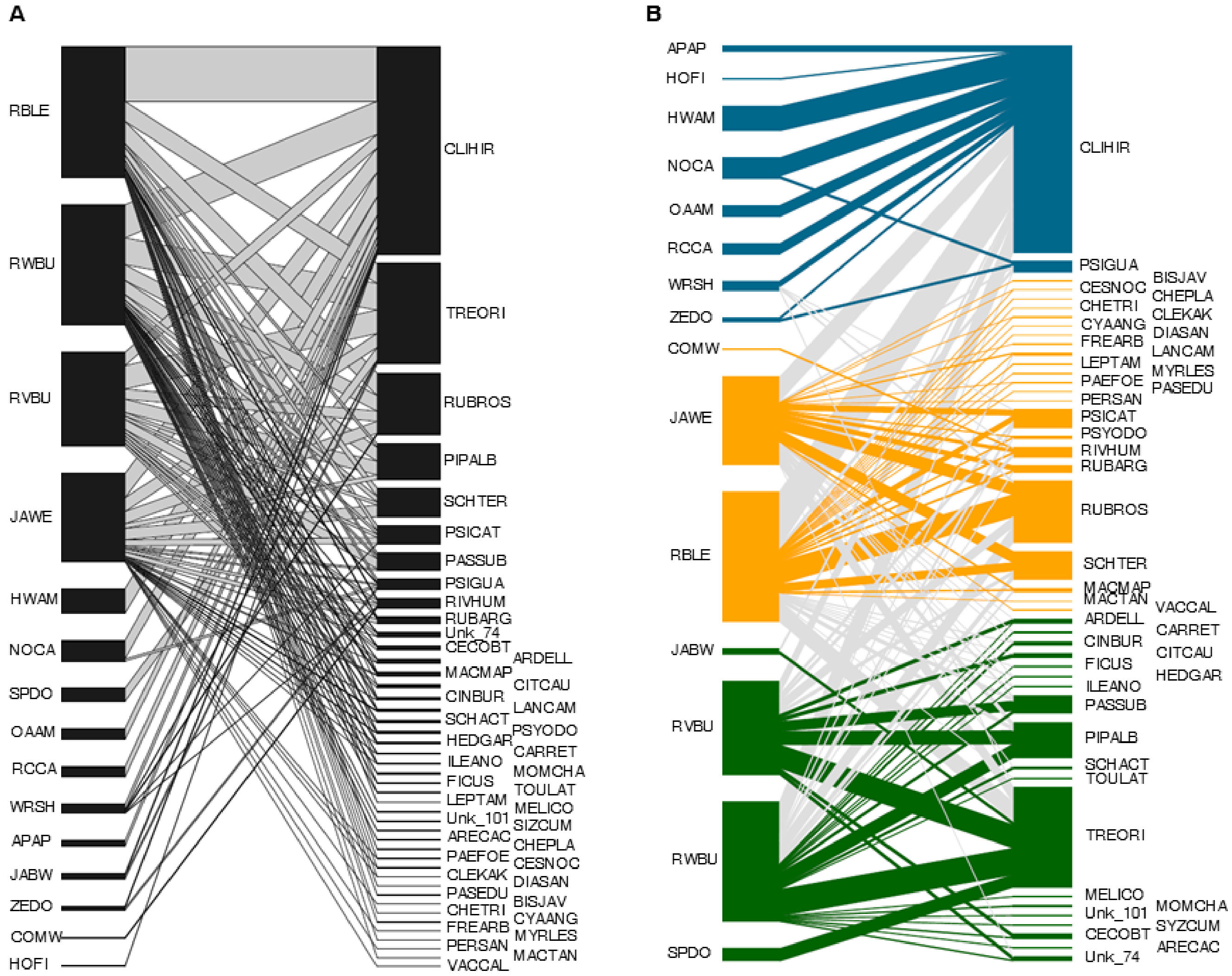

Fig. S2. Structure of the seed dispersal network in Oahu. (A) The novel island-wide seed dispersal network was nested and **(B)** modular. Species and links from distinct modules are depicted by distinct colors (blue, orange and green) and grey links are interactions connecting modules. See Tables S2 and S3 for acronyms.

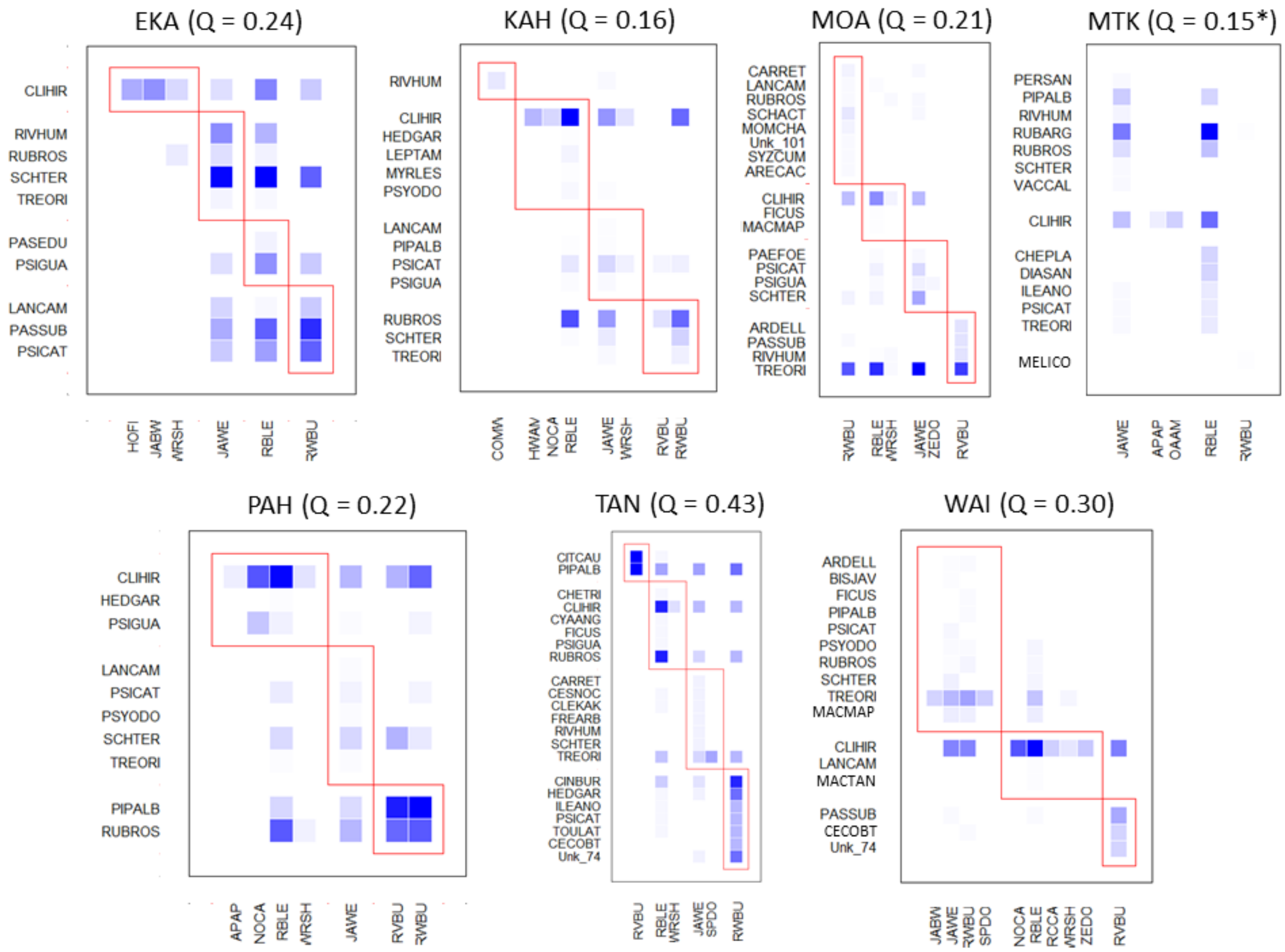

Fig. S3. Modularity in local seed dispersal networks in Oahu. Each figure includes all birds (bottom) and plants (left) consumed in a specific site, and red squares indicate modules of interactions among species interacting more among themselves than with other species, as identified by Beckett's algorithm. The module composition presented in the one from the runs where the highest modularity (Q) was obtained. Note that all local networks but MTK were modular, presenting three or four modules. Shades of blue indicate the frequencies of interactions, where darkest blue occurs when 100% of the fecal samples of a bird species contained seeds of a plant, and white indicates no interaction. For full site and species names see Tables S1-S3.

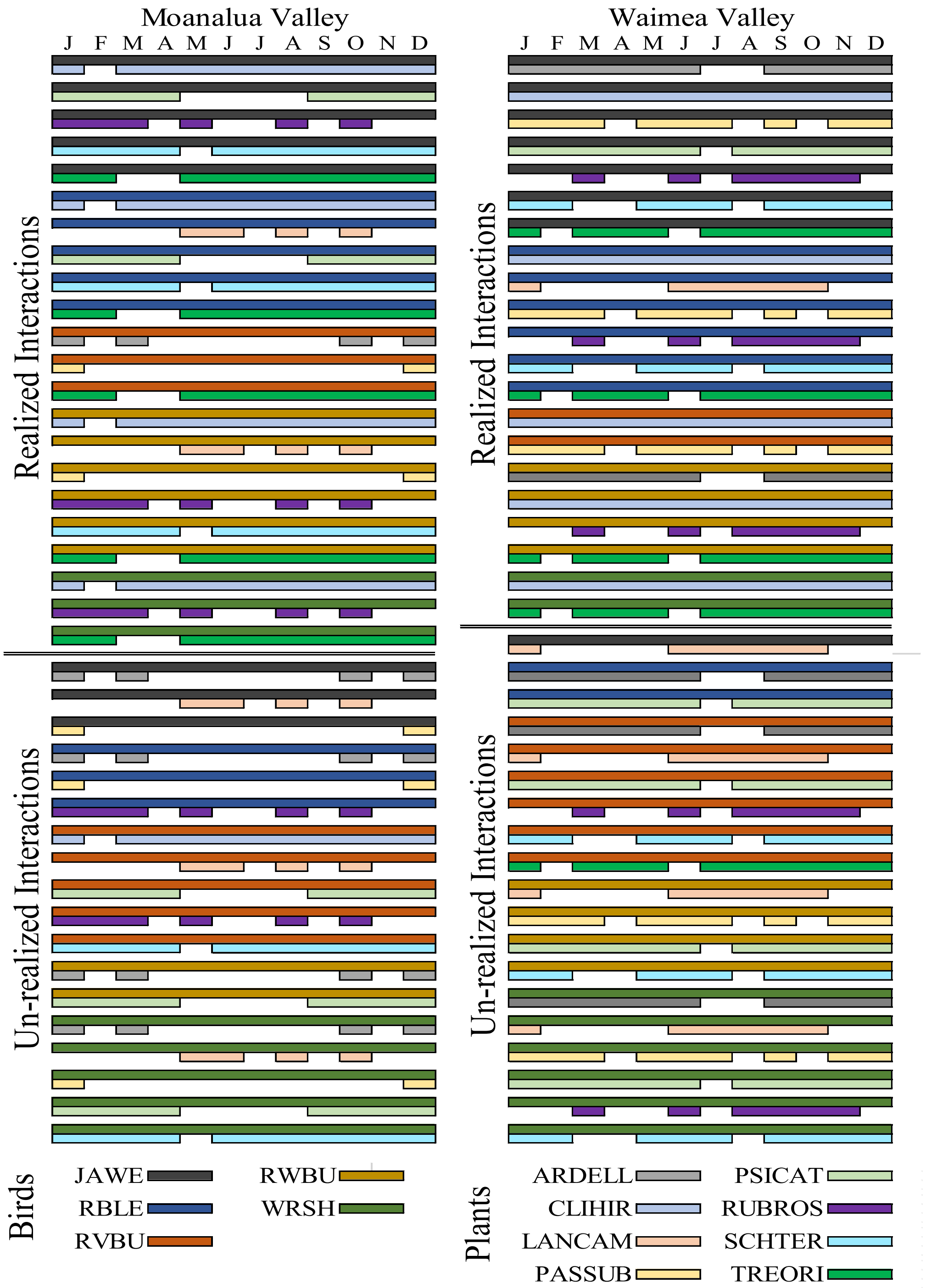

Fig. S4. Monthly occurrence of bird species and fruits of each plant species in Moanalua and Waimea sites. Each pair of bars represents pairwise bird (top) and plant (bottom) species. Note that all birds were present year-round at the sites and only phenology of fruiting for different plant species varied over time. These sites presented higher interaction dissimilarities due to rewiring (β_{OS}=0.35). Note that despite the overlapping bird and fruiting phenologies of all birds and plants shared by each network, only about half of the interactions were realized. Bird presence data obtained from point counts and mist-netting, and fruiting phenological data obtained from fecal samples, fruit counts and seed rain traps.

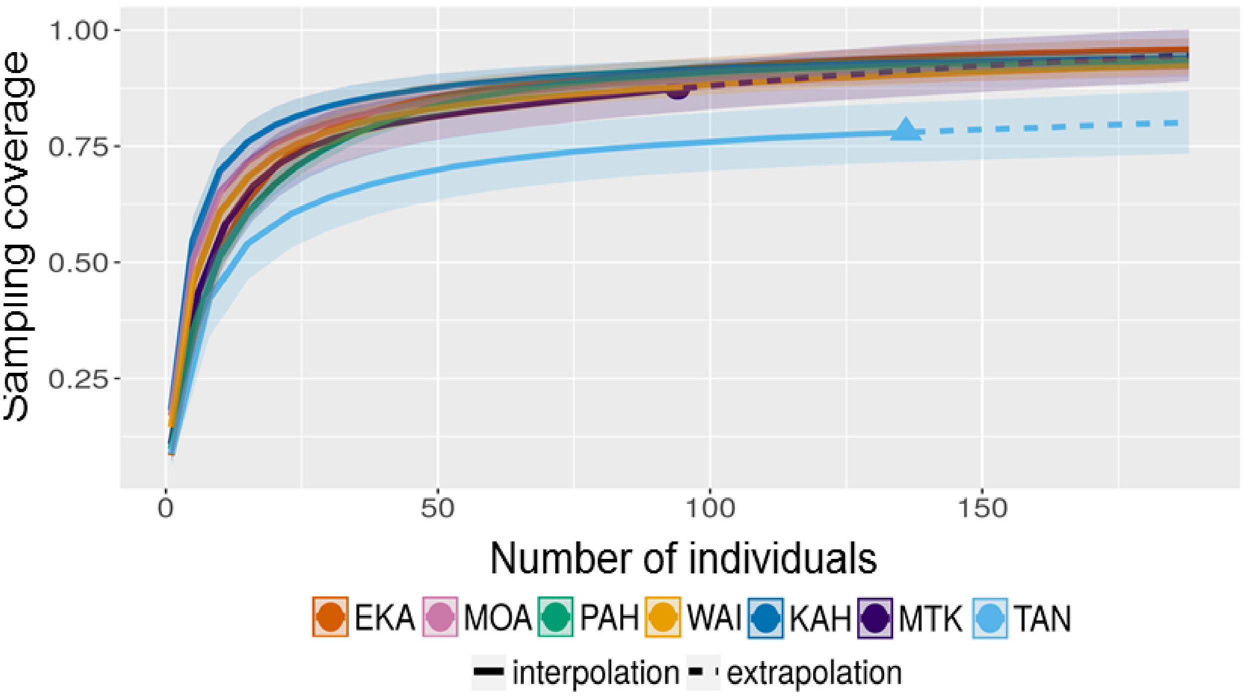

Fig. S5. Estimation of sampling coverage using interpolation/extrapolation method. Note that all sites had sampling coverage presenting an asymptotic tendency which indicates that the sampling was sufficient to detect at least 75% of the links in each site; 95% CI are built based on 1000 bootstrap iterations. *Methodological details:* In order to evaluate sampling completeness across sites, we estimated sampling coverage using individual-based extrapolation/interpolation methods proposed by (*56*). We replaced 'abundance' by the number of endozoochorous dispersal events recorded for each link (pairwise species). Curves of accumulation of detected links and confidence intervals (95%) were built based on 1000 iterations (bootstraps) of the original data for equally-large samples (interpolation-extrapolation method). The lowest number of foraging events was a benchmark to compare interpolation curves and the highest number, for extrapolation. We performed this analysis using the software iNEXT (57). We detected minimal differences among sites in the proportion of detected links and sampling was sufficient to detect >75% of links in each site. This indicates that sampling had a negligible influence on network metrics and sampling was similar or greater than in other studies (see Table S1 for site acronyms; *42*).

Table S1. **Details on sampling sites on Oahu.** Coordinates, elevation and mean annual rainfall (1978-2007) for each sampling site. Source: Rainfall Atlas of Hawaiʻi, http://rainfall.geography.hawaii.edu/

Site	Acronym	Latitude	Longitude	Elevation (m a.s.l.)	Rainfall (mm)
Ēkahanui	EKA	21°26'35.90"N	158°5'4.27"W	467	1107.8
Kahanahāiki	KAH	21°32'12.55"N	158°11'35.40"W	667	1345.8
Moanalua	MOA	21°22'33.75"N	157°52'24.09"W	108	1884.4
Mount Kaʻala	MTK	21°30'24.58"N	158° 8'41.17"W	1206	1953.7
Pahole	PAH	21°32'11.30"N	158°10'47.64"W	594	1533.5
Tantalus	TAN	21°20'18.19"N	157°48'39.29"W	549	3386.1
Waimea Valley	WAI	21°37'55.62"N	158° 2'26.69"W	190	1732.9

Table S2. **Birds sampled on Oahu.** Number of fecal samples sorted per bird species per site.

Species	Common name	Acronym	EKA	KAH	MOA	MTK	PAH	TAN	WAI	Total
Native birds										
Himatione sanguinea	‘Apapane	APAP	-	3	-	74	3*	-	-	80
Chlorodrepanis flava	Oahu ‘amakihi	OAAM	10	-	-	2*	-	2	-	14
Introduced birds										
†*Lonchura atricapilla*	Chestnut munia	CHMU	2		2	11	1		8	24
Estrilda astrild	Common waxbill	COMW	16	19	17	24	19	1	20	116
Haemorhous mexicanus	House finch	HOFI	106	6	9	3	5	-	17	146
Garrulax canorus	Hwamei	HWAM	4	1*	-	-	-	-	1	6
Horornis diphone	Japanese bush-warbler	JABW	12	7	1	20	5	-	9	54
†*Lonchura oryzivora*	Java sparrow	JASP	-	-	2	-	-	-	-	2
Zosterops japonicus	Japanese white-eye	JAWE	126	148	79	110	114	75	153	805
Cardinalis cardinalis	Northern cardinal	NOCA	24	11	8	-	8	4	9	64
Leiothrix lutea	Red-billed leiothrix	RBLE	192	201	290	29	161	123	152	1148
Paroaria coronata	Red-crested cardinal	RCCA	3	1	4	1	3	-	16	28
†*Amandava amandava*	Red avadavat	REAV	-	-	-	-	-	-	1	1
Pycnonotus cafer	Red-vented bulbul	RVBU	2	3*	18	2	6	4	9	44
Pycnonotus jocosus	Red-whiskered bulbul	RWBU	25	29	86	1*	41	14	75	271
†*Lonchura punctulata*	Scaly-breasted munia	SBMU	45	1	16	5	-	-	6	73
Spilopelia chinensis	Spotted dove	SPDO	9	-	5	-	-	1*	8	23
Kittacincla malabarica	White-rumped shama	WRSH	66	31	87	2	33	32	46	297
†*Crithagra mozambica*	Yellow-fronted canary	YFCA	-	2	10	-	-	-	-	12
†*Tiaris olivaceus*	Yellow-faced grassquit	YFGR	-	-	-	-	2	-	-	2
Geopelia striata	Zebra dove	ZEDO	5	-	56	-	-	-	7	68
		Total	647	463	690	284	401	256	537	3278

*Cases when the frequency of interaction at the site was estimated based on all samples collected for the species due to low sample size at the local scale. †Species for which no viable seeds were found in fecal samples.

Table S3. Plants found in bird feces in each site on Oahu. Number of fecal samples in which each native or introduced plant was found per site. Taxonomic classification and authors names follow www.tropicos.org.

Family	Species	Acronym	EKA	KAH	MOA	MTK	PAH	TAN	WAI	Sum
Native Plants										
Ericaceae	**Leptecophylla tameiameiae* (Cham. & Schltdl.) C.M.Weiller	LEPTAM	-	5	-	-	-	-	-	5
Araliaceae	*Cheirodendron platyphyllum* (Hook. & Arn.) Seem.	CHEPLA	-	-	-	2	-	-	-	2
Araliaceae	*Cheirodendron trigynum* (Gaudich.) A. Heller	CHETRI	-	-	-	-	-	1	-	1
Campanulaceae	*Clermontia kakeana* Meyen	CLEKAK	-	-	-	-	-	2	-	2
Campanulaceae	*Cyanea angustifolia* (Cham.) Hillebr.	CYAANG	-	-	-	-	-	1	-	1
Asphodelaceae	*Dianella sandwicensis* Hook. & Arn.	DIASAN	-	-	-	2	-	-	-	2
Pandanaceae	*Freycinetia arborea* Gaudich.	FREARB	-	-	-	-	-	1	-	1
Aquifoliaceae	*Ilex anomala* Hook. & Arn.	ILEANO	-	-	-	2	-	2	-	4
Rutaceae	*Melicope* sp.	MELICO	-	-	-	1	-	-	-	1
Primulaceae	*Myrsine lessertiana* A. DC.	MYRLES	-	1	-	-	-	-	-	1
Dipentodontaceae	*Perrottetia sandwicensis* A. Gray	PERSAN	-	-	-	1	-	-	-	1
Urticaceae	*Pipturus albidus* (Hook. & Arn.) A.Gray ex H.Mann	PIPALB	-	2	-	11	49	21	1	84
Rubiaceae	*Psydrax odorata* (G. Forst.) A.C. Sm. & S.P. Darwin	PSYODO	-	4	-	-	1	-	7	12
Urticaceae	*Touchardia latifolia* Gaudich.	TOULAT	-	-	-	-	-	2	-	2
Ericaceae	*Vaccinium calycinum* Sm.	VACCAL	-	-	-	1	-	-	-	1
Introduced Plants										
Primulaceae	*Ardisia elliptica* Thunb.	ARDELL	-	-	1	-	-	-	2	3
Arecaceae	Arecaceae sp.	ARECAC	-	-	1	-	-	-	-	1

Phyllanthaceae	*Bischofia javanica* Blume	BISJAV	-	-	-	-	-	-	1	1
Boraginaceae	*Carmona retusa* (Vahl) Masam.	CARRET	-	-	3	-	-	1	-	4
Urticaceae	*Cecropia obtusifolia* Bertol.	CECOBT	-	-	-	-	-	1	2	3
Solanaceae	*Cestrum nocturnum* L.	CESNOC	-	-	-	-	-	2	-	2
Lauraceae	*Cinnamomum burmannii* (Nees & T. Nees) Blume	CINBUR	-	-	-	-	-	11	-	11
Verbenaceae	*Citharexylum caudatum* L.	CITCAU	-	-	-	-	-	2	-	2
Melastomataceae	*Clidemia hirta* (L.) D. Don	CLIHIR	26	167	90	21	128	34	186	652
Moraceae	*Ficus* spp.	FICUS	-	-	1	-	-	1	1	3
Zingiberaceae	*Hedychium gardnerianum* Sheppard ex Ker Gawl.	HEDGAR	-	1	-	-	1	4	-	6
Verbenaceae	*Lantana camara* L.	LANCAM	6	1	3	-	1	-	1	12
Euphorbiaceae	*Macaranga mappa* (L.) Müll. Arg.	MACMAP	-	-	1	-	-	-	17	18
Euphorbiaceae	*Macaranga tanarius* (L.) Müll. Arg.	MACTAN	-	-	-	-	-	-	1	1
Cucurbitaceae	*Momordica charantia* L.	MOMCHA	-	-	2	-	-	-	-	2
Rubiaceae	*Paederia foetida* L.	PAEFOE	-	-	3	-	-	-	-	3
Passifloraceae	*Passiflora edulis* Sims	PASEDU	2	-	-	-	-	-	-	2
Passifloraceae	*Passiflora suberosa* L.	PASSUB	35	-	2	-	-	-	6	43
Myrtaceae	*Psidium cattleyanum* Sabine	PSICAT	22	27	14	2	11	2	3	81
Myrtaceae	*Psidium guajava* L.	PSIGUA	20	4	6	-	8	1	-	39
Petiveriaceae	*Rivina humilis* L.	RIVHUM	22	3	3	2	-	1	-	31
Rosaceae	*Rubus argutus* Link	RUBARG	-	-	-	37	-	-	-	37
Rosaceae	*Rubus rosifolius* Sm.	RUBROS	6	126	3	9	95	30	6	275
Araliaceae	*Schefflera actinophylla* (Endl.) Harms	SCHACT	-	-	5	-	-	-	-	5
Anacardiaceae	*Schinus terebinthifolia* Raddi	SCHTER	64	12	23	1	26	1	10	137
Myrtaceae	*Syzygium cumini* (L.) Skeels	SYZCUM	-	-	1	-	-	-	-	1
Cannabaceae	*Trema orientalis* (L.) Blume	TREORI	2	3	199	2	2	12	72	292
-	-	Unk_101	-	-	1	-	-	-	-	1
-	-	Unk_74	-	-	-	-	-	3	1	4

Sum	205	356	362	94	322	136	317	1792

[*] Synonym of *Styphelia tameiameiae* F. Muell.

Table S4. Structure of seed dispersal networks in Oahu. Regional and local structure of seed dispersal networks and the proportion of invasive birds and plants in each network. Bold indicates a structure that deviates from the null expectation. Parentheses include 95% confidence intervals of the null expectation.

Descriptor	Regional	Local (sites)						
	Island	EKA	KAH	MOA	MTK	PAH	TAN	WAI
N birds	15	6	8	6	5	7	6	10
N plants	44	10	13	19	14	10	22	16
N links	112	29	32	41	24	32	44	39
N interactions	1793	205	356	362	94	322	136	317
Connectance	0.17	0.48	0.31	0.36	0.34	0.45	0.33	0.24
Specialization (H2')	**0.20** **(0.06-0.09)**	**0.23** **(0.05-0.17)**	**0.23** **(0.05-0.12)**	**0.29** **(0.07-0.17)**	0.20 (0.07-0.22)	**0.19** **(0.02-0.07)**	**0.44** **(0.13-0.28)**	**0.35** **(0.10-0.23)**
Nestedness (wNODF)	**48.67** **(34.24-44.66)**	36.48 (47.41-77.10)	52.13 (42.52-65.03)	33.16 (39.18-56.15)	36.74 (39.65-62.01)	65.78 (55.62-78.54)	32.51 (37.16-53.99)	43.59 (32.33-51.79)
Modularity (Q)	**0.24** **(0.07-0.09)**	**0.16** **(0.05-0.14)**	**0.24** **(0.04-0.08)**	**0.21** **(0.05-0.11)**	0.15 (0.05-0.16)	**0.22** **(0.03-0.07)**	**0.43** **(0.10-0.20)**	**0.30** **(0.06-0.13)**
N modules	3	3	4	4	-	3	4	3
N invasive birds (%)	13 (86.7)	6 (100.0)	8 (100.0)	6 (100.0)	3 (60.0)	6 (85.7)	6 (100.0)	10 (100.0)
N invasive plants (%)*	29 (65.9)	10 (100.0)	9 (69.2)	19 (100.0)	7 (50.0)	8 (80.0)	15 (68.2)	14 (83.3)
% samples with seeds**	59.0	43.5	68.2	61.5	52.1	65.8	42.6	66.8

N= number. *Calculated assuming that morphotypes are invasive species; †Calculated considering the four most common frugivorous birds (Red-billed leiothrix, RBLE; Japanese white-eye, JAWE; Red-whiskered bulbul, RWBU; and Red-vented bulbul, RVBU).

Table S5. Interaction dissimilarity (B_{WN}) between each pair of sites in Oahu. The total dissimilarity occurs due to species turnover (β_{ST}) or linkage turnover among shared species (β_{OS}). Δ indicates the difference in Elevation/Invasion/Rainfall between two sites.

Pairs of sites	β_{WN}	β_{OS}	β_{ST}	Distance (km)	ΔElevation (m)	ΔInvasion	ΔRainfall (mm/yr)
EKA-KAH	0.44	0.20	0.23	15.29	200.00	30.80	237.96
EKA-MOA	0.44	0.22	0.22	23.13	359.00	0.00	776.56
EKA-MTK	0.62	0.20	0.42	9.40	739.00	46.20	845.89
EKA-PAH	0.37	0.07	0.30	14.28	127.00	20.00	425.66
EKA-TAN	0.64	0.25	0.38	30.66	82.00	35.00	2278.35
EKA-WAI	0.583	0.30	0.28	21.40	277.00	16.70	625.10
KAH-MOA	0.58	0.34	0.23	37.61	559.00	30.80	538.60
KAH-MTK	0.60	0.24	0.36	6.01	539.00	15.40	607.93
KAH-PAH	0.28	0.20	0.07	1.37	73.00	10.80	187.70
KAH-TAN	0.55	0.26	0.29	45.30	118.00	4.20	2040.39
KAH-WAI	0.57	0.33	0.24	18.99	477.00	14.10	387.14
MOA-MTK	0.75	0.33	0.41	31.65	1098.00	46.20	69.33
MOA-PAH	0.55	0.27	0.28	36.40	486.00	20.00	350.90
MOA-TAN	0.66	0.33	0.33	7.75	441.00	35.00	1501.79
MOA-WAI	0.62	0.34	0.27	33.26	82.00	16.70	151.46
MTK-PAH	0.57	0.20	0.37	4.95	612.00	26.20	420.23
MTK-TAN	0.64	0.25	0.39	39.29	657.00	11.20	1432.46
MTK-WAI	0.74	0.33	0.41	17.57	1016.00	29.50	220.79
PAH-TAN	0.52	0.25	0.27	44.09	45.00	15.00	1852.69
PAH-WAI	0.54	0.31	0.23	17.89	404.00	3.30	199.44
TAN-WAI	0.68	0.35	0.33	40.31	359.00	18.30	1653.25

Table S6. Top models of the test on the influence of abiotic and biotic factors on interaction dissimilarity. Top models (encompassing 95% of model weight) examining how differences between sites (Δ) in elevation, rainfall and proportion of invasive plants influence interaction dissimilarity in seed dispersal networks in Oahu.

Model	**d.f.**	**logLik**	**AIC_c**	**ΔAIC_c**	**weight**
ΔElevation+ΔRainfall	4	23.61	-36.73	0.00	0.59
ΔElevation+ΔRainfall+ΔInvasion	5	24.48	-34.95	1.78	0.24
ΔElevation	3	20.40	-33.39	3.33	0.11
ΔElevation+ΔInvasion	4	21.15	-31.80	4.93	0.05

Table S7. Influence of abiotic and biotic factors on interaction dissimilarity. Model averaged results for the variables that influence interaction dissimilarity in seed dispersal networks in Oahu. Bold indicates variables whose confidence intervals (95% CI) did not cross zero.

Predictors	β	Adjusted S.E.	Lower 95% CI	Upper 95% CI
ΔElevation	0.28	0.09	**0.11**	**0.51**
ΔRainfall	0.21	0.08	**0.05**	**0.38**
ΔInvasion	0.12	0.09	-0.07	0.31

Table S8. Top models of the test on the influence of abiotic and biotic factors on interaction dissimilarity due to species turnover. Top models (encompassing 95% of model weight) examining how differences between sites (Δ) in elevation, rainfall and proportion of invasive plants influence the proportion of interaction dissimilarity due to species turnover (B_{ST}) in seed dispersal networks in Oahu.

Model	d.f.	logLik	AIC_c	ΔAIC_c	weight
ΔElevation+ΔRainfall+ΔInvasion	5	30.08	-46.16	0.00	0.47
ΔElevation+ΔInvasion	4	27.79	-45.08	1.08	0.27
ΔRainfall+ΔInvasion	4	27.41	-44.33	1.83	0.19
ΔRainfall	3	24.96	-42.52	3.65	0.08

Table S9. Influence of abiotic and biotic factors on interaction dissimilarity due to species turnover. Model averaged results for the variables that influence the proportion of interaction dissimilarity due to species turnover (B_{ST}) in seed dispersal networks in Oahu. Bold indicates variables whose confidence intervals did not cross zero.

Predictors	β	Adjusted S.E.	Lower 95% CI	Upper 95% CI
ΔElevation	0.20	0.08	**0.04**	**0.43**
ΔRainfall	0.23	0.07	**0.02**	**0.39**
ΔInvasion	0.17	0.08	**0.06**	**0.37**

Table S10. Top models of the test on the influence of abiotic and biotic factors on interaction dissimilarity due to rewiring. Top models (encompassing 95% of model weight) examining how differences between sites (Δ) in elevation, rainfall and proportion of invasive plants influence the proportion of interaction dissimilarity due to rewiring (B_{OS}) in seed dispersal networks in Oahu.

Model	**d.f.**	**logLik**	**AIC_c**	**ΔAIC_c**	**weight**
Null (intercept)	2	24.60	-44.53	0.00	0.40
ΔElevation	3	25.70	-43.98	0.54	0.30
ΔInvasion	3	24.63	-41.85	2.68	0.10
ΔRainfall	4	24.60	-41.80	2.73	0.10
ΔElevation+ΔInvasion	4	26.08	-41.67	2.86	0.10

Table S11. Influence of abiotic and biotic factors on interaction dissimilarity due to rewiring. Model averaged results for the variables that influence the proportion of interaction dissimilarity due to rewiring (B_{OS}) in seed dispersal networks in Oahu. Bold indicates variables whose confidence intervals did not cross zero.

Predictors	**β**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**
ΔElevation	0.19	0.10	-0.05	0.32
ΔRainfall	0.08	0.09	-0.16	0.20
ΔInvasion	-0.09	0.10	-0.25	0.18

Table S12 (below). Seed dispersal networks included in the global dataset. Acronym, sources and details on locations of the avian seed dispersal network in the global dataset.

Code	Data	I/C	Zone	LOCATION	SOURCE	REFERENCE
AZOR	Binary	Island	Non-tropical	São Miguel, Azores	Web of life	Heleno et al. (2013) Integration of exotic seeds into an Azorean seed dispersal network. Biol. Inv., 15, 1143-1154
BAIR	Weighted	Continent	Non-tropical	New Jersey, USA	Rezende et al. 2007	Baird (1980) The selection and use of fruit by birds in an eastern forest. Wilson Bull., 92: 63-73
BAND	Weighted	Island	Non-tropical	Bandama, Canary Islands	literature	Gonzalez-Castro et al. (2012) Seed dispersal interactions in the Mediterranean Region: contrasting patterns between islands and mainland. J. Biogeog. 39, 1938-1947
BARB	Binary	Continent	Non-tropical	Santa Bárbara, Sierra de Baza	Fricke et al 2017	Data unpublished, however see Jordano 1993
BEEH	Weighted	Island	Tropical	Morobe Province, New Guinea	Rezende et al. 2007	Beehler (1983) Frugivory and polygamy in birds of paradise. Auk, 100, 1-12.
CACG	Weighted	Island	Tropical	Caguana, Puerto Rico	Rezende et al. 2007	Carlo et al. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. Oecol., 134, 119-131
CACI	Weighted	Island	Tropical	Cialitos, Puerto Rico	Rezende et al. 2007	Carlo et al. (2003)
CACO	Weighted	Island	Tropical	Cordillera, Puerto Rico	Rezende et al. 2007	Carlo et al. (2003)
CAFR	Weighted	Island	Tropical	Fronton, Puerto Rico	Rezende et al. 2007	Carlo et al. (2003)
ELPAL	Weighted	Island	Non-tropical	El Palomar, Canary Islands	literature	Gonzalez-Castro et al. (2012)
FADI04	Weighted	Continent	Tropical	Tropical Forest,Minas Gerais, Brazil	literature	Fadini & De Marco Jr (2004) Interação entre aves e plantas em um fragmento de mata atlântica de Minas Gerais. Rev. Bras. Ornitol., 12, 97–103.
FAUS06	Weighted	Continent	Tropical	Rocky outcrops, Brazil	literature	Faustino & Machado (2006) Frugivoria por aves em uma área de campo rupestre na Chapada Diamantina, BA. Rev. Bras. Ornitol., 14, 137–143.

FROS	Weighted	Continent	Non-tropical	Mtunzini, South Africa	Rezende et al. 2007	Frost (1980) Fruit-frugivore interactions in a South African coastal dune forest. Pages 1179-1184 in: R. Noring (ed.). Acta XVII Congresus Internationalis Ornithologici, Deutsches Ornithologische Gessenshaft, Berlin.
GEN1	Weighted	Continent	Tropical	Santa Genebra Reserve T1. SE Brazil	Rezende et al. 2007	Galetti & Pizo (1996) Fruit eating birds in a forest fragment in southeastern Brazil. Rev. Bras. Ornitol., 4: 71-79.
GEN2	Weighted	Continent	Tropical	Santa Genebra Reserve T2. SE Brazil	Rezende et al. 2007	Galetti & Pizo (1996)
GUIT	Binary	Continent	Non-tropical	Temperate forest.,Spain	Fricke et al 2017	Guitián (1983) Relaciones entre los frutos y los passeriformes en un bosque montano de la cordillera cantábrica occidental. PhD Thesis. Univ. Santiago. Spain
HAMM	Binary	Island	Tropical	North Negros Forest Reserve, Philippine Islands	Rezende et al. 2007	Hammann & Curio (1999) Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. Conserv. Biol. 13, 693-950
HRAT	Weighted	Continent	Non-tropical	Hato Ratón, Sevilla, Spain	Rezende et al. 2007	Jordano (1985) El ciclo anual de los paseriformes frugívoros en el matorral mediterráneo del sur de España: importancia de su invernada y variaciones interanuales. Ardeola, 32, 69-94.
KANT	Binary	Continent	Tropical	Campeche state, Mexico	Rezende et al. 2007	Kantak (1979) Observations on some fruit-eating birds in Mexico. Auk, 96: 183-186.
LAMB	Binary	Continent	Tropical	Kuala Lompat, Krau Game Reserve, Malaysia	Rezende et al. 2007	Lambert (1989) Fig-eating by birds in a Malaysian lowland rain forest. J. Trop. Ecol., 5, 401-412.
MACK	Binary	Island	Tropical	Crater Mountain Biol. Res. Station, Chimbu Province, Papua New Guinea	Rezende et al. 2007	Mack & Wright (1996) Notes on occurrence and feeding of birds at Crater Mountain Biological Research Station, Papua New Guinea. Emu 96: 89-101.
MARQ	Binary	Continent	Non-tropical	Sabinar del Marqués, Reserva de la Estación Biológica de Doñana, Spain	Fricke et al 2017	Data unpublished, however see Jordano 1993

MINV1	Weighted	Island	Tropical	Makawao Forest Reserve and Waikamoi Preserve, Mesic wet forest, Hawai‘i (Plot1)	unpublished	Data unpublished, however see Foster & Robinson (2007)
MINV2	Weighted	Island	Tropical	Makawao Forest Reserve and Waikamoi Preserve, Mesic wet forest, Hawai‘i (Plot4)	unpublished	Data unpublished, however see Foster & Robinson (2007)
MNAT	Weighted	Island	Tropical	Makawao Forest Reserve and Waikamoi Preserve, Mesic wet forest, Hawai‘i (plots 3+5+Hanawi)	unpublished	Data unpublished, however see Foster & Robinson (2007)
MONT	Binary	Continent	Tropical	Monteverde, Costa Rica	Rezende et al. 2007	Wheelwright et al. (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica, 16, 173-192.
NCOR	Weighted	Continent	Non-tropical	Nava Correhuelas. S. Cazorla, SE Spain.	Rezende et al. 2007	P. Jordano, unpublished
NNOG	Binary	Continent	Non-tropical	Nava Noguera, Sierra de Cazorla, SE Spain	Rezende et al. 2007	P. Jordano, unpublished
OTER	Binary	Continent	Non-tropical	Campos de Otero, Sierra Nevada, Spain	Fricke et al 2017	Data unpublished, however see Jordano 1993
POUL99	Weighted	Continent	Tropical	Semideciduous tropical forest, Panama	IWDB	Poulin et al. (1999) Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. J. Trop. Ecol, 15, 213–227.
SAAV14	Weighted	Continent	Tropical	Montane forest, Bolivia	literature	Saavedra et al. (2014) Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. Oecol. 176, 837–848.
SABI	Binary	Continent	Non-tropical	Cañada de las Sabinas, Nava e	Fricke et al 2017	Data unpublished, however see Jordano 1993

				Correhuelas, Sierra de Cazorla		
SAPF	Weighted	Island	Non-tropical	Yakushima Island, Japan	Rezende et al. 2007	Noma (1997) Annual fluctuations of sapfruits production and synchronization within and inter species in a warm temperate forest on Yakushima Island, Japan. Tropics, 6: 441-449.
SCHL	Weighted	Continent	Tropical	Kakamega Forest, Kenya	Web of life	Schleuning et al. (2011) Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. Ecology, 92, 26-36.
SILV14	Weighted	Continent	Tropical	Cerrado- Neotropical Savanna, Brazil	literature	Silva & Pedroni (2014) Frugivoria por aves em área de cerrado no município de Uberlândia, Minas Gerais. Rev Árvore, 38, 433–442.
SNOW	Weighted	Island	Tropical	Tropical rainforest, Trinidad	Rezende et al. 2007	Snow & Snow (1971) The feeding ecology of tanagers and honeycreepers in Trinidad. Auk, 88, 291-322.
SNOW88	Binary	Continent	Non-tropical	UK	IWDB	Snow & Snow (1988) Birds and berries, Calton, England.
SORE81	Weighted	Continent	Non-tropical	Temperate woodland, UK	IWDB	Sorensen (1981) Interactions between birds and fruit in a temperate woodland. Oecol. 50, 242–249.
SREA	Binary	Island	Non-tropical	Son Real, Balearic islands	literature	Gonzalez-Castro et al. (2012)
STRI	Binary	Island	Non-tropical	Son Trias, Balearic islands	literature	Gonzalez-Castro et al. (2012)
TRAV	Binary	Continent	Non-tropical	Cañada Travina, Sierra de Cazorla, Spain	Fricke et al 2017	Data unpublished, however see Jordano 1993
WES	Binary	Continent	Tropical	Intervales and Saibadela, São Paulo, Brazil	Rezende et al. 2007	Silva et al. (2002) Patterns of fruit-frugivores interactions in two Atlantic Forest bird communities of South-eastern Brazil: implications for conservation. Pp. 423-435. In: Levey, Silva & Galetti (eds.) Seed dispersal and frugivory: ecology, evolution and conservation. Wallinford: CAB International.
*EKA	Weighted	Island	Tropical	‘Ēkahanui, Oahu Island, Hawai‘i, USA	unpublished	this study

*KAH	Weighted	Island	Tropical	Kahanahāiki, Oahu Island, Hawai‘i, USA	unpublished	this study
*MOA	Weighted	Island	Tropical	Moanalua, Oahu Island, Hawai‘i, USA	unpublished	this study
*MTK	Weighted	Island	Tropical	Mount Ka'ala, Oahu Island, Hawai‘i, USA	unpublished	this study
*PAH	Weighted	Island	Tropical	Pahole, Oahu Island, Hawai‘i, USA	unpublished	this study
*TAN	Weighted	Island	Tropical	Tantalus, Oahu Island, Hawai‘i, USA	unpublished	this study
*WAI	Weighted	Island	Tropical	Waimea Valley, Oahu Island, Hawai‘i, USA	unpublished	this study

Zone/Location	Weighted				Binary						
	N nets	H_2’	wNODF	Qw	N nets	NODF	Qb	ranP	degP	ranA	degA
All (Isls+Conts.)	26	−0.11-0.39	−33.27-13.28	−0.03-0.31	42	−16.16-36.78	−0.03-0.13	−0.18-0.22	−0.25-0.11	−0.18-0.04	−0.32-0.22
Islands only	12	−0.19-0.27	−16.04-19.82	−0.03-0.29	17	−12.49-30.02	−0.12-0.12	−0.28-0.02	−0.25-0.08	−0.28-0.04	−0.35-0.16
Continents only	14	0.05-0.41	−37.73-1.59	0.04-0.29	25	−18.74-40.75	−0.03-0.06	−0.05-0.28	−0.21-0.16	−0.08-0.03	−0.14-0.16
Tropical Islands	3	−0.02-0.08	−15.34-20.49	−0.03-0.30	6	−9.76-3.09	−0.14-0.12	−0.15-0.02	−0.20-0.08	−0.15-0.03	−0.34-0.18
Non-tropical Islands	9	−0.21-0.27	−15.47-5.82	−0.02-0.09	11	−13.00-30.25	−0.01-0.12	−0.31-0.02	−0.27-0.04	−0.31-0.03	−0.30-0.08
Tropical Continents	8	0.03-0.20	−14.83-1.55	0.03-0.23	12	−14.55-0.77	−0.03-0.08	−0.06-0.17	−0.14-0.08	−0.09-0.01	−0.16-0.10
Non-tropical Cont.	6	**0.14-0.43**	−40.70-16.65	**0.11-0.30**	13	−18.96-43.69	−0.02-0.02	−0.03-0.33	−0.23-0.19	−0.03-0.04	−0.11-0.20
Oahu(7 networks)	7	−0.01-0.09	−14.99-−1.65	−0.02-0.07	7	−6.65-11.99	−0.04-−0.01	−0.03-0.02	−0.09-0.07	−0.03-0.03	−0.05-0.13

Only 26 out of 42 networks had weighted data, which were converted to binary data to also calculate binary metrics. Bold indicates a significant difference between Oahu *vs.* non-Oahu networks. H_2’= complementary specialization; wNODF and NODF= nestedness; Qw and Qb=modularity; ranP, ranA, degP and degA= network robustness to the sequential extinction of animals (A) and plants (P) by random (ran) or from the most generalist to the most specialist (deg). The latter is calculated only for binary data. Δ-correction (i.e. the subtraction of an observed value of a metric and the mean value of a metric obtained from null matrices) was applied on all metrics to account for variation in sampling intensity and network dimensions across studies (see methods).

Table S13. Calculated structure and robustness of global and Oahu networks. A comparison of the structure and stability of 42 seed dispersal networks from islands and continents in tropical and non-tropical communities around the world in comparison to novel networks on Oahu.

Table S14. Data on vegetation surveys per site. Number and proportion of introduced and native (indigenous and endemic) plant species along transects in each site. *Methodological details:* Plants were documented using the point-intercept method, at 1-m intervals along transects. Plant cover for each species was recorded in three strata: 0-2 m, >2-4 m, and > 4 m.

Sites	**Transect (m)**	**N species**	**N introduced (%)**	**N native (%)**
MTK	600	22	2 (09.1)	20 (90.9)
PAH	1271	46	14 (30.4)	32 (69.6)
KAH	824	33	14 (42.4)	19 (57.6)
TAN	594	35	23 (65.7)	12 (34.3)
MOA	703	25	23 (92.0)	2 (08.0)
EKA	913	28	26 (92.9)	2 (07.1)
WAI	678	21	17 (81.0)	4 (19.0)