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Trophic interactions and feedbacks maintain intact and degraded states of Hawaiian tropical forests

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Abstract. Feedbacks within ecosystems can lead to internal reinforcement of the current state providing ecosystem resilience. Often, multiple biotic interactions across trophic levels play a role in such feedbacks, yet these are generally studied independently, obscuring the relative importance of interactions among different factors. We look at various potential feedbacks in intact and degraded mesic forests on Hawai'i Island where managers have planted native *Acacia koa* (koa) trees in an attempt to jumpstart succession in former cattle pastures. These restoration forests, however, have not undergone secondary succession, instead maintaining a koa overstory with an exotic pasture grass understory. We contrasted different trophic level processes that influence the capacity for natural understory regeneration: feedbacks between bird-mediated seed rain and fruiting understory ("top-down"), as well as links between understory composition and microhabitats for native seed germination ("bottom-up"). We quantified bird-mediated seed rain under canopy trees along transects spanning intact, fragmented, and restoration forests. Along these transects, we established plots around focal overstory trees to measure abundance of fruiting understory species, ground cover (e.g., exotic grass, bryophyte), and obtained estimates of bird density to evaluate the contribution of each of these factors to seedling abundance. We also used a factorial seed addition/grass removal experiment to directly compare the influence of seed rain and germination substrate. We found evidence of both top-down and bottom-up feedbacks that reinforced the current state of each forest type. In the intact and fragmented forests, the combination of comparatively high seed rain and ample germination substrate is likely critical for maintaining a diverse forest system. In contrast, exotic grasses exhibit priority effects in restoration forests, inhibiting seed germination and effectively negating any benefits that could be derived from bird-mediated seed rain. Such internal reinforcement suggests that active, rather than passive, restoration would be beneficial to increase forest diversity in restoration areas.

Key words: *Acacia koa;* bird-mediated seed rain; ecosystem resilience; feedbacks; forest restoration; Hawai'i; *Metrosideros polymorpha;* secondary succession; seedling recruitment; tropical forest.

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Introduction

Positive feedbacks within ecosystems can lead to internal reinforcement of the current state and thus ecosystem resilience (Suding et al. 2004). For example, an exotic plant species may cultivate a soil microbial community that has a more positive effect on its own growth than other species' growth, thereby reinforcing its own abundance (Levine et al. 2006, Kulmatiski et al. 2008). Such

positive feedbacks can lead to alternative stable states wherein different plant communities (e.g., exotic vs. native-dominated) can become dominant in the same location depending on starting conditions (Beisner et al. 2003). The seeming resilience of exotic-dominated states has led to great interest in studies of ecosystem feedbacks, including plant–soil feedbacks, which have been the subject of many experiments, reviews, and meta-analyses (e.g., Kulmatiski et al. 2008, Van der Putten et al. 2013, Crawford et al. 2019). While there are likely multiple feedback mechanisms functioning simultaneously to hold a degraded system in place, rarely is more than one feedback considered in a single study (Van der Putten et al. 2013). In this manuscript, we explore feedbacks across different trophic levels in a subtropical forest that was converted to exotic pasture for cattle.

In the tropics and sub-tropics worldwide, forests are often cleared for agricultural purposes, such as cattle pasture; however, subsequent restoration of pasture to forest often proves difficult (Austin et al. 2017). Exotic pasture grasses often persist after grazers are removed, inhibiting native woody species regeneration, suggesting priority effects and internal reinforcement of the degraded state (Holl 1999, Fukami and Nakajima 2011, Kéfi et al. 2016). The early stages of secondary succession in disturbed tropical forests are influenced by factors that drive plant colonization, notably seed arrival rates and suitable germination sites (Inman-Narahari et al. 2013), and a lack of either of these two variables can act to constrain natural regeneration (Guariguata and Ostertag 2001). Importantly, background rates of seed arrival and the availability of suitable germination sites are rarely studied in conjunction, making it difficult to determine their relative importance in stalling succession and thus difficult to identify the best, first steps toward restoration.

Both seed arrival and subsequent recruitment in suitable germination sites can be affected by ecosystem feedbacks. Seed dispersal in many tropical forests is facilitated by animal frugivores, which are critical for tree and understory plant recruitment, particularly in degraded areas (Holl 1999, Jordano 2000). Tropical plant seed banks are generally short-lived, and seeds often fail to survive periods of long-term grazing (Vázquez-Yanes and Orozco-Segovia 1993). Furthermore, degraded areas often lack mature plants that could provide local, passively dispersed seeds (Holl 1999). While birds can be important drivers of secondary forest succession, a lack of food (i.e., fruit), and suitable habitat (i.e., structure), often discourages avian seed dispersers from visiting degraded sites, leading to internal reinforcement of a degraded state (Holl 1998, Zahawi and Augspurger 2006, Wandrag et al. 2017). Conversely, in intact forests, abundant food and habitat resources maintain bird populations, which in turn disperse seeds, leading to reinforcement of a native-dominated state. For brevity, we refer to avian-mediated seed dispersal processes as "top-down" processes (Fig. 1).

Another potential constraint to natural regeneration is a lack of suitable germination sites. In degraded tropical forests, suitable germination sites are often limited by the presence of highly competitive exotic pasture grasses (Denslow et al. 2006). Within intact tropical forests, trees and understory can limit the spread of exotic grass species by preempting resources such as light and nutrients. In addition, native woody species deposit leaf litter and woody debris that can lower grass biomass directly by physically covering it, or indirectly by immobilizing nitrogen (Rhoades et al. 1998, Yelenik 2017). Leaf litter and woody debris can also ameliorate extreme temperature fluctuations, thereby promoting germination and survival of native seeds (Gomez-Aparicio et al. 2004, Batllori et al. 2009, Rehm and Feeley 2013). Thus, the presence of native woody plants facilitates germination and survival of native species to the detriment of exotic grasses, reinforcing the native-dominated state. Once these internally reinforcing mechanisms are missing however, grasses often exhibit priority effects that stall community succession and natural forest regeneration, even when seed dispersal to these pasture sites occurs (Young et al. 2005, Fukami and Nakajima 2011). For brevity, we refer to this myriad of microsite-based constraints to seedling establishment as "bottom-up" processes.

In our study, we explored how top-down and bottom-up feedbacks work to stall succession of restoration forests in Hawai'i. In Hawai'i, intact mid-elevation mesic native forests are dominated

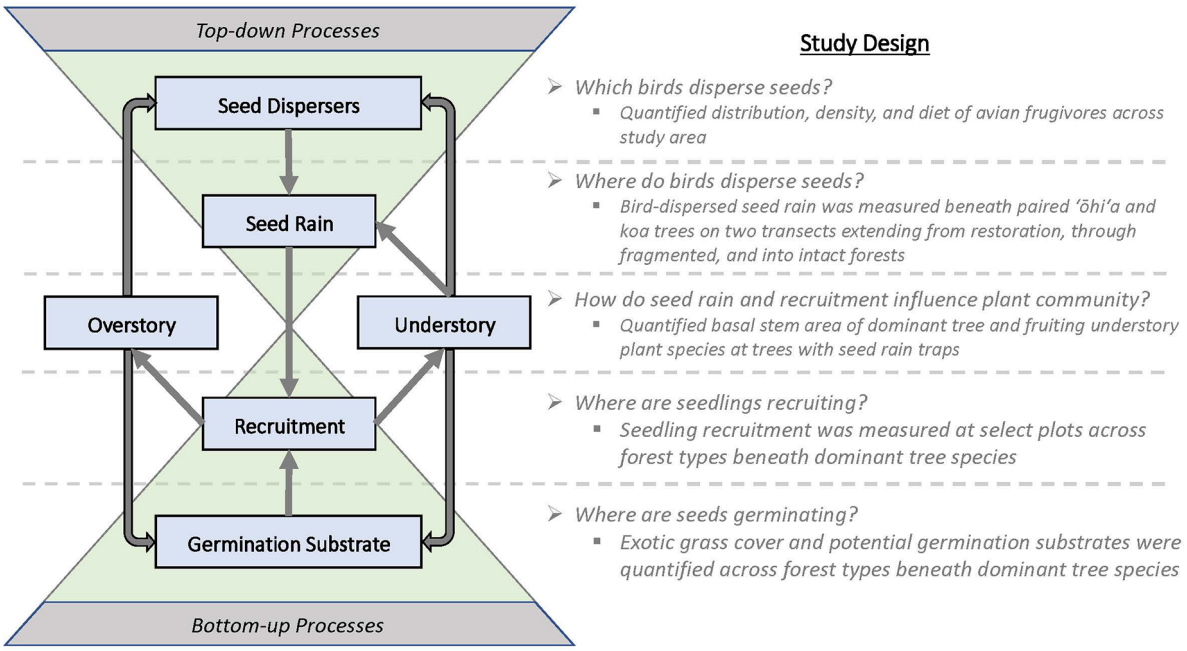


Fig. 1. Conceptual diagram of study design to understand how different factors affect top-down and bottom-up processes influencing intact forest stability and degraded forest recovery. Elements of our study included quantifying the diet and density of avian seed dispersers, measuring seed rain across the study area, evaluating the contributing effects of overstory and understory plants, and evaluating how germination substrate and environment contribute to seedling recruitment across three different forest types.

by two canopy trees, *Acacia koa* (koa) a nitrogen (N) fixing Leguminosae and *Metrosideros polymorpha* (ʻōhiʻa) a non-fixer in the Myrtaceae family. Intact forests have a dense understory of subcanopy trees and shrubs (Mueller-Dombois et al. 2013), many of which produce fruit that is dispersed by frugivorous birds (Drake 1998). In contrast, koa and ʻōhiʻa do not produce fleshy fruit, although they may offer other food resources (nectar, insects) to other bird species (Banko et al. 2015*a*). Like subtropical forests worldwide (Guariguata and Ostertag 2001, Corbin and Holl 2012), many of the mesic forests in Hawaiʻi were cleared of understory and planted with exotic pasture grasses for livestock grazing (Ripperton and Hosaka 1942, McDaniel and Ostertag 2010). Even after cattle have been excluded, exotic grasses continue to dominate much of what used to be mesic forest, even where remnant scattered canopy trees remain, and there is little evidence of natural forest regeneration (McDaniel and Ostertag 2010, McDaniel et al. 2011). In some of these areas, notably Hakalau Forest National Wildlife Refuge (Hakalau), exotic pasture grasses remain persistent in the understory some 30 yr after cattle removal (Yelenik 2017).

Within Hakalau, managers planted koa extensively across the degraded pasture areas in the late 1980s in an attempt to jumpstart succession. Mass planting of koa was chosen as a method because, relative to ʻōhiʻa, it is fast growing, easy to propagate, and has high survivorship (Scowcroft et al. 2004, Scowcroft and Yeh 2013). Restoration goals at Hakalau include creating shade and deep litter layers to reduce exotic grass growth, which would theoretically facilitate regeneration of native understory species while creating habitat for endangered forest birds (McDaniel and Ostertag 2010). While koa has grown successfully and created greater overstory cover in former pasture lands (Scowcroft and Yeh 2013), surveys indicate that native understory is not regenerating under koa trees, and exotic grasses such as kikuyu grass, *Cenchrus clandestinus*, remain dominant (Yelenik 2017). As

a result, managers have begun outplanting native woody understory species into koa restoration sites to accelerate restoration. However, scattered remnant ʻōhiʻa trees in the former pasture lands often have native woody species recruiting in their understory, many of which are fruit bearing (Yelenik 2017) suggesting that natural regeneration can occur in the degraded systems given the right conditions. The remanent ʻōhiʻa trees may differ from the koa trees by providing microhabitat differences in light, soil properties, or germination substrate, and a preferred roosting tree for birds which then deposit seeds.

Thus, Hakalau provides a unique opportunity to explore the roles of top-down and bottom-up processes and show how feedbacks change across different forest states (Appendix S1: Table S1): "intact" forest (native woody understory and abundant ʻōhiʻa and koa canopy trees), "fragmented" forest (scattered remnant canopy trees with exotic grass understory), and "restoration" forest (scattered remnant ʻōhiʻa trees, planted koa, and exotic grass understory). Forests at Hakalau are representative of the species richness and range of conditions that can exist in upland, mesic Hawaiian forests (Scowcroft et al. 2004, Mueller-Dombois et al. 2013) and offer a relatively simple ecosystem that enables asking complex ecological questions (Denslow 2003). To address the influence of top-down feedbacks on forest regeneration (Fig. 1), we measured bird-mediated seed rain and quantified factors that could influence the number of seeds entering an area. These variables included frugivorous bird density, diet composition, and density of local fruiting tree/shrub species and overstory tree species. We hypothesized that rates of bird-mediated seed rain would be greater in areas with more fruiting trees and shrubs that might attract birds to the local area, which would reinforce the intact forest state. We also hypothesized that seed rain would be higher under ʻōhiʻa than under koa, reinforcing the koa-grass state that lacked succession with native woody understory.

To address bottom-up feedbacks, we evaluated the extent to which different interacting variables influenced seedling abundance. We asked if the amount of available germination substrate (e.g., bare soil, woody litter, moss), the amount of grass biomass, and the density of local fruiting trees and shrubs influenced seedling recruitment (Fig. 1). We hypothesized that native seedling density would be positively related to local fruiting tree/shrub density, which could provide suitable microhabitats and seeds, and lead to a positive reinforcement of intact forest states. Similarly, we hypothesized that native seedling density would be negatively related to grass cover, with grass cover greater in koa restoration forests, leading to a lack of succession and reinforcement of the koa-grass state.

Finally, we used two lines of evidence to evaluate the relative importance of bottom-up and top-down factors for making intact forest and restoration forest resilient to change. First, we evaluated statistical relationships between seedling abundance measured at out study lots and the associated bird density, bird-mediated seed rain, and understory abundance. Second, we experimentally tested for interactions between seed arrival and germination substrate in native plant regeneration by altering seed inputs and grass biomass in replicated plots across degraded and intact forests. This multi-trophic approach to understanding feedbacks and forest recovery can provide important insights into the stability of altered systems, and help to prioritize strategies for forest restoration. In other words, if degraded forests are shown to have feedbacks and be resilient, then planting or other expensive management may be needed; but if forests are not resilient, this suggests that less expensive passive restoration will be successful (Suding et al. 2004).

Materials and Methods

Site description

Our study was conducted within Hakalau National Wildlife Refuge on Hawaiʻi Island, which was established in 1985 to protect endangered Hawaiian forest birds and their habitat (U.S. Fish and Wildlife Service 2010). Hakalau ranges from 610 to 1900 m elevation, receives an annual rainfall of 2700 mm, and has a mean annual temperature of 12°C (Giambelluca et. al. 2013).

Upper elevations at Hakalau were cleared of trees and understory plants in the late 1900s for livestock grazing, while the lower elevations were protected to retain watershed function and remain dominated by mesic forest. Beginning in 1987, over 390,000 koa trees were planted in corridors running from intact forest upslope into

former pastures to create new forest habitat (Jeffrey and Horiuchi 2003). Due to this land-use history, the upper portion of the refuge is dominated by koa restoration corridors with some scattered remnant ʻōhiʻa and an exotic pasture grass understory; we refer to this habitat type as "restoration" hereafter. Moving down in elevation below koa restoration corridors, there are scattered remnant koa and ʻōhiʻa surrounded largely by pasture grass, which we refer to as the "fragmented" habitat type. Finally, just below these habitats is mature, intact closed-canopy forest, which we refer to as "intact" habitat (Fig. 2). Intact forest canopy is dominated by koa and ʻōhiʻa, with subcanopy trees including *Cheirodendron trigynum* (ʻōlapa), *Myrsine lessertiana* (kōlea), and *Coprosma rhynchocarpa* (pilo). Common understory shrubs include *Leptecophylla tameiameiae* (pukiawe), *Rubus hawaiensis* (ʻākala), the invasive *Rubus argutus* (blackberry), and two

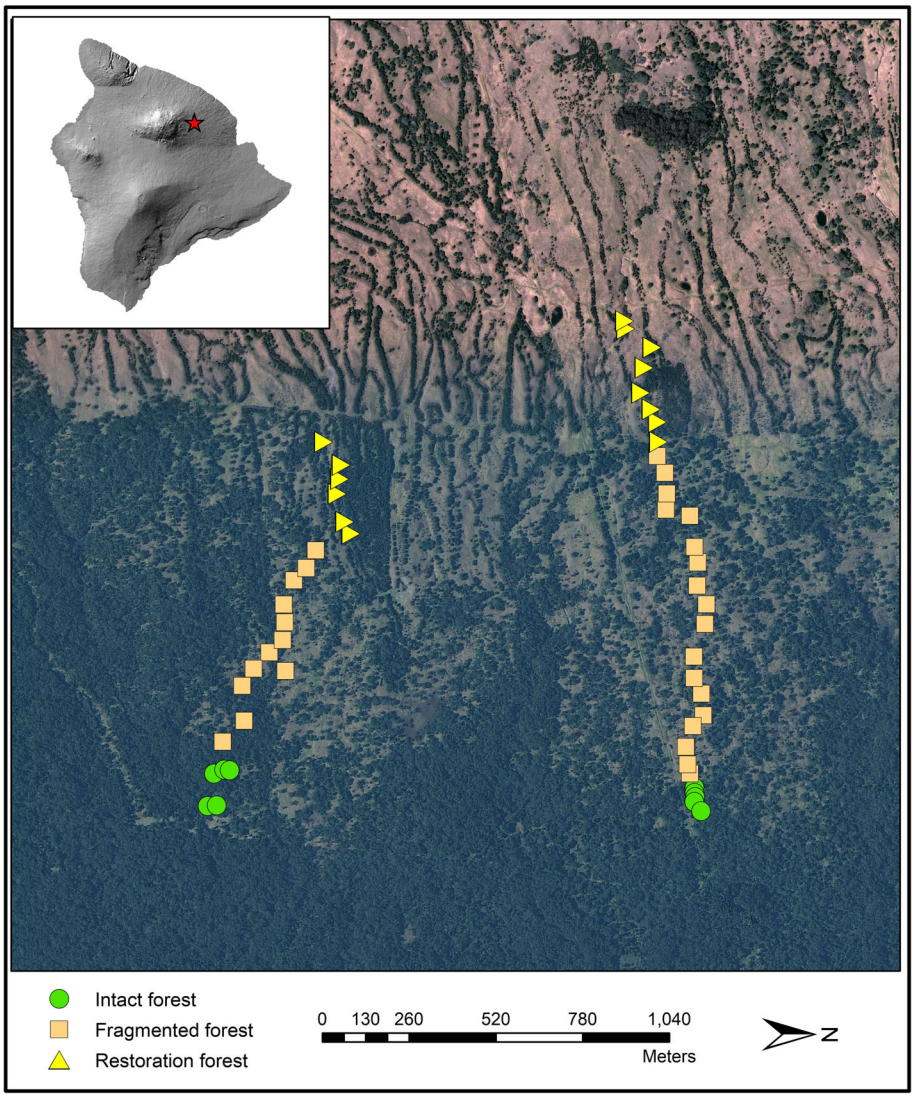


Fig. 2. Two seed rain transects provide an illustration of the type and distribution of habitats sampled to quantify trophic interactions within Hakalau Forest National Wildlife Refuge, Hawaiʻi. Seed rain transects started within restoration forest to the west and descended in elevation through fragmented remnants of historical intact forest and into existing intact forest to the east. Base map is from 2006 Quickbird satellite imagery.

species of *Vaccinium* (ʻōhelo), *V. reticulatum*, and *V. calycinum*. All of these common subcanopy trees and understory shrubs produce fleshy fruit eaten by forest birds. Native ferns were also present and abundant, particularly in intact forest areas. Exotic pasture grasses such as kikuyu grass, *Holcus lanatus* (velvet grass), *Anthoxanthum odoratum* (sweet vernal grass), and *Ehrharta stipoides* (weeping rice grass) occur throughout the refuge with the highest percent cover in fragmented and restoration areas, and very little in intact forest.

Bird distribution and diet

Bird communities within Hakalau are surveyed annually across the refuge using an 8-minute point-count survey methodology (Camp et al. 2016). We used detection-corrected estimates of bird density at each survey station (Camp et al. 2016) for the 3 yr of data leading up to and including our seed rain study (2010, 2011, 2012) to calculate average density of frugivorous bird species in each of the three habitat types.

We quantified diet of potentially frugivorous forest birds by opportunistically collecting fecal samples from birds captured in a banding study (2012–2016) at three locations within Hakalau. Capture periods occurred throughout the year, with the highest frequency during peak breeding season, February through July. Once collected, fecal samples were placed in plastic vials with a 90% ethanol solution until they were processed using a dissecting microscope to search for and identify seeds within each sample. We examined a total of 949 fecal samples from five bird species believed to be potential seed dispersers (based on literature searches). We used chi-square tests to determine whether the proportion of fecal samples containing each seed species differed across bird species to evaluate differential fruit diets among frugivorous species.

Bird-mediated seed rain

In order to quantify the number of bird-dispersed seeds available for germination, we measured seed rain using hoop style traps (Rose et al. 2017) from May 2015 to August 2016, spanning the peak of two fruiting seasons. We established 108 (0.38 m^2 area) seed rain traps along transects in two different forest tracts, in paired koa and ʻōhiʻa trees (which were approximately 30 m apart), approximately every 50 m (Fig. 2). Both seed rain transects started in intact forest and extended upslope through fragmented and into restoration forest. Traps were hung above existing understory plants to avoid capturing seeds that were not bird-dispersed. We collected seed rain from traps twice monthly, sorting and identifying seeds with dissecting scopes (Rose et al. 2017 for detailed methods). All seeds without a pericarp were considered bird-dispersed.

We quantified fruit phenology to assess the degree of linkage with observed patterns of seed rain. During each seed rain collection visit, observers recorded whether they encountered any of five focal plant species (blackberry, ʻākala, ʻōhelo, ʻōlapa, pukiawe) and which species were fruiting in the vicinity of each trap. The proportion of plants fruiting was then calculated for each visit as the number of traps where the species was seen fruiting, divided by the number of traps where the species was present. We visually compared patterns in seed rain and fruit phenology using the daily seed rain for each month averaged across all traps.

We used daily seed rain averaged over the entire sample period for a given trap ("average seed rain") as a response variable to evaluate different variables affecting bird-dispersed seed rain. First, we developed a linear mixed model for each species to determine whether habitat type influenced the average seed rain. To control for possible effects of tree type, these models incorporated tree species as a random effect. Second, we used a similar approach to develop linear mixed models to determine if canopy tree species influenced the average seed rain. To control for possible effects of habitat, these models incorporated habitat type as a random effect. Finally, we used linear mixed models and an AIC (Akaike information criterion) model selection approach (Burnham and Anderson 2002) to evaluate the relative effects of an index of local seed availability (plant basal area, see "*Understory surveys*" for methods) and a measure of expected seed contributions that incorporated bird density and diet (adjusted bird density), on bird-mediated seed rain. We developed linear mixed models for each covariate, in addition to an additive model incorporating adjusted bird density and plant basal area, as well as a null model. Each model incorporated nested random effects

of tree species and habitat type to control for any variation associated with those variables. To meet the assumption of normality, we cube-root-transformed average seed rain prior to analyses. We used the AICmodavg package in R version 4.0.0, and an AIC-weighted model averaging approach (Buckland et al. 1997) to calculate a natural average for each parameter of interest (Burnham and Anderson 2002). This weighted model averaging approach incorporates AIC model weights into model-averaged parameter estimates.

Adjusted bird density was used to explore the effects of frugivorous bird density on bird-mediated seed dispersal for each fruiting plant species and to account for the different proportion of fruit that was found in each bird's diet. Adjusted bird density was calculated as the sum of frugivorous bird contributions for a given fruiting species. Each birds' contribution was calculated as its density from the closest point-count station multiplied by the proportion of its diet comprised of the target fruit as follows, where fruiting plant species is denoted as $f1 \ldots fn$, and each bird species is denoted as $b1 \ldots bn$:

$$\begin{aligned}\text{AdjDen}_{f1} = {} & (\text{Density}_{b1} \times \text{Fecal Proportion}_{b1,f1}) \\ & + \ldots + (\text{Density}_{bn} \\ & \times \text{Fecal Proportion}_{bn,f1})\end{aligned}$$

By controlling for possible effects of habitat type and tree species, we could use plant basal area (a proxy for local seed source) and adjusted bird density (an expected rate of avian dispersed seed for a given plant) to ask whether the abundance of fruit in an area facilitated frugivore dispersal of seed.

Understory surveys

We characterized fruiting plant communities by measuring plant basal area of the five focal plant species in a 20 m radius circle around seed rain trap trees. These species were chosen due to their prevalence in bird diet as measured by bird fecal data (97% of seed species in diet) and bird-mediated seed rain (99% of seed rain). We surveyed plots under two, nine, and seven koa and ʻōhiʻa trees from the two seed rain transects in intact, fragmented, and restoration forests, respectively. We stratified the plots to account for the high degree of understory patchiness in fragmented and restoration forests, and consistently high basal area in intact forests. We counted the number of stems of each focal species in four basal diameter classes: 0–2, 2–5, 5–10, >10 cm. We estimated basal area per plot by assuming that the midpoint of each size class represented the average diameter for all stems in that class and used 10cm as the diameter for the largest category. While this may have underestimated basal area per plot, we note that less than 0.8% of all stems (n = 59,804 stems) were in the >10 cm basal diameter size class.

To ask whether basal area of different understory species differed between habitat type and overstory tree species, we developed four zero-inflated mixture models (i.e., null, tree species, habitat type, tree species + habitat type) for each fruiting understory plant species and evaluated model performance using AIC. Zero-inflated mixture models incorporated a binomial component with a logit link function to account for the point mass at zero, and a negative binomial component with a log link to account for non-zero basal stem area. Although non-zero basal stem area was initially continuous, values were rounded to the nearest integer and treated as counts for the analysis. Because we were most interested in incremental changes in basal area, we used an inflated parameterization to assign a single probability of belonging to the zero component for each model. For this analysis, we again used an information theoretic approach and calculated a weighted model-averaged estimates for the parameters of interest.

Understory plant recruitment

To better understand relationships between understory, germination substrate, and native seedling recruitment, we quantified the type and number of native seedlings, the substrate each seedling was found growing in, and the availability of different germination substrates. This was done at a subset of seed rain trap trees: three koa and three ʻōhiʻa from the two seed rain transects, in intact, fragmented, and restoration forests, for a total of 36 trees, from July to October 2015. At each tree, we sampled 20 consecutive 0.5 × 0.5 m quadrats placed along a 10-m north–south transect centered at the base of the tree. We visually estimated percent cover of substrates

(grass, woody species' litter, grass litter, soil, moss, rock, nurse log, buttressed root) and counted all woody seedlings in the quadrat, identifying them to species when possible. However, a number of seedlings could not be identified, including native *V. calycinum*, *V. ovatum*, and ʻōhiʻa because they all have small (<1 mm wide) cotyledons and first leaves that look similar. Thus, we included unknown seedlings in the native seedling category. Preliminary analyses showed that >95% of seedlings were found on moss, woody litter, and soil; thus, we summed these substrate types to estimate potentially available "germination substrate" at each tree. Data were averaged across the 20 quadrats per individual tree prior to analysis.

We included both "top-down" and "bottom-up" factors potentially affecting seedling recruitment using linear models and an AIC information theoretic approach. We developed eight linear mixed-effects models, incorporating all possible additive combinations of the effects of bird-mediated seed rain, fruiting plant density, and germination substrate availability on seedling recruitment for each overstory tree species. All models incorporated a random effect of habitat to control for variation across habitat types. Seedling recruitment was cube-root-transformed prior to modeling to improve residual distribution.

Grass competition and seed limitation

We implemented a fully factorial seed addition, grass removal experiment beneath the different canopy dominant trees to compare the degree to which seed limitation and grass competition limit native understory recruitment. We established four 0.5 × 0.5 m plots under ʻōhiʻa and koa trees and randomly assigned them to the following treatments: (1) control (grass intact, no seed added); (2) grass removed, no seed added; (3) grass intact, seed added; or 4. grass removed, seed added. To capture the full range of growing conditions beneath each tree type, we established three replicate sites of this design under each canopy species in intact, fragmented, and restoration forests for a total of nine ʻōhiʻa and nine koa trees.

All grass found within grass removal plots was removed by hand. Grass was clipped to soil level leaving the soil undisturbed. Grass vegetative matter was collected from each of the 36 selected plots and placed into a labeled paper bag for transport and drying. Grass samples were oven dried at 70° for 1 week and weighed to provide estimates of dry grass biomass.

Seed augmentation was done in July 2015 using 0.15 g each of ʻākala and ʻōhelo seeds, which we estimated to be approximately 50 ʻākala and 3000 ʻōhelo seeds based on weight (Rose et al. 2017). Seeds were collected as ripe fruit on site, and fruit of both species were processed to remove fruit pulp according to the recommendations of Lilleeng-Rosenberger (2005). All native woody seedlings present at that time were recorded. Plots were visited monthly to monitor native woody seedling emergence and trim grass for 14 months. Seedlings were marked with numbered cocktail swords to keep individuals separate, and here, we only report total native woody seedling emergence over 14 months.

To ask how experimental seed additions and grass removal affected native woody seedling recruitment, we used separate logistic mixed-effects models for each canopy tree species (koa and ʻōhiʻa). Each model included a random effect for habitat type to account for sampling structure and used a logistic response, as well as a logit link, to accommodate the large number of zeros in the data set. These models retained the experimental blocking structure through a fixed effect for treatment (i.e., grass/no seed, grass/seed added, grass removed/no seed, grass removed/seed added). We also used a linear model with a normal distribution to ask how overstory canopy tree, habitat type, and the tree × habitat interaction affected pre-treatment grass biomass in the grass removal plots. We used a chi-squared effects test with $P \leq 0.05$ to determine which parameters were significant in each of these models.

In addition, to better understand microhabitat differences under koa and ʻōhiʻa, we quantified light transmittance levels in experimental plots using a light meter (Apogee MQ-301 PAR Meter, Logan, Utah) during cloudless, midday conditions. Four readings were taken directly over experimental plots and paired with four open sky readings (outside of any tree canopy) to quantify percent transmittance using the ratio of the average treatment plot to average open sky readings.

Results

Frugivorous bird diet and distribution

Three of the five bird species regularly contained seeds within fecal samples: ʻōmaʻo (*Myadestes obscurus*), warbling white-eye (*Zosterops japonicus*), and red-billed leiothrix (*Leiothrix lutea*) (Table 1). Although the literature suggests Hawaiʻi ʻamakihi (*Chlorodrepanis virens*) will occasionally eat fruit, examination of 146 fecal samples found no seeds. Another potential seed disperser, northern cardinals (*Cardinalis cardinalis*), had seeds in 29% of fecal samples collected, but many were damaged suggesting that cardinals are largely seed predators. Therefore, we focused our analyses on the ʻōmaʻo, white-eye, and leiothrix.

The proportion of different plant species in samples varied among these three bird species, indicating differences in the degree of frugivory and dietary preferences (Fig. 3). ʻŌmaʻo had the highest level of frugivory, with 81% of samples containing seeds, while warbling white-eye had the lowest level of frugivory, with seeds in only 38% of fecal samples. Red-billed leiothrix had a moderate level of frugivory with 59% of fecal samples containing seeds. Similarly, ʻōmaʻo had the highest number of seeds within each sample, warbling white-eye had the lowest, and red-billed leiothrix was in between (Table 1). We found significant differences in seed composition across bird species (Appendix S1: Fig. S1) for blackberry ($\chi^2 = 15.32$, df = 2, $P < 0.01$), ʻōlapa ($\chi^2 = 173.94$, df = 2, $P < 0.01$), pukiawe ($\chi^2 = 68.80$, df = 2, $P < 0.01$), and ʻōhelo ($\chi^2 = 15.32$, df = 2, $P < 0.01$); however, we did not see this pattern for ʻākala ($\chi^2 = 2.74$, df = 2, $P = 0.25$). Warbling white eyes consumed more of the exotic blackberry than the other bird species, while ʻōmaʻo consumed more native ʻōhelo and ʻōlapa fruit than the warbling white eyes,

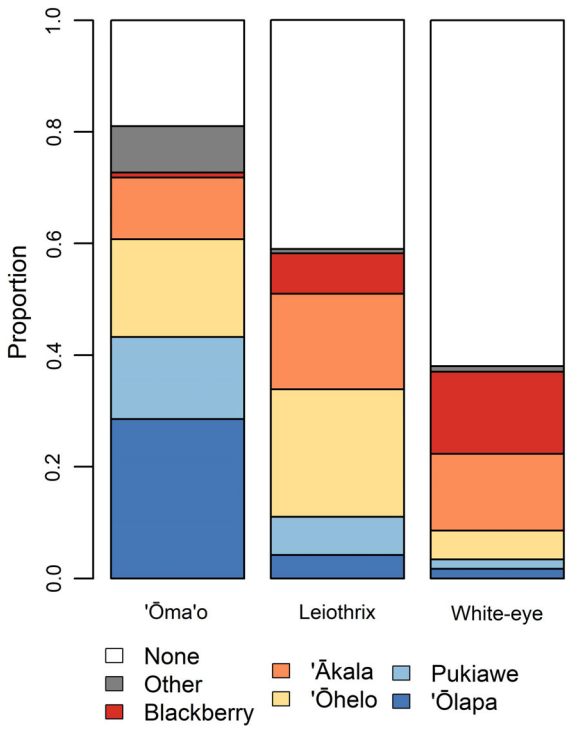


Fig. 3. Seed composition of fecal samples for three avian frugivores, ʻōmaʻo, red-billed leiothrix, and warbling white-eye, at Hakalau Forest National Wildlife Refuge, Hawaiʻi. Seed composition per bird species was calculated in two steps, first overall proportion of fecal samples with one or more seeds was calculated; then, the relative proportion of each plant species detected in those fecal samples with seeds is shown.

Table 1. The total number of fecal samples (Total samples) collected for each bird species, along with the number of samples that contained seeds (Samples with seeds), the total number of seeds found across samples (Total seeds), and the average ± SE (standard error) of seeds found across samples (Seeds per sample) during 2012 through 2016 mist netting efforts within Hakalau Forest National Wildlife Refuge.

Species	Total samples	No. of samples with seeds (%)	Total seeds	No. of seeds/sample (mean ± SE)
Hawaiʻi ʻamakihi	147	0	0	0
ʻŌmaʻo	73	59 (81%)	569	7.8 ± 1.7
Warbling white-eye	456	171 (38%)	670	1.5 ± 0.1
Red-billed leiothrix	259	154 (59%)	1455	5.6 ± 0.7
Northern cardinal	17	5 (29%)	29	1.7 ± 1.3

Note: Although some Vaccinium seeds can make it through intact, most seeds are destroyed by the Northern Cardinal during ingestion/digestion and are no longer viable.

and more native pukiawe than both exotic bird species (Appendix S1: Fig. S1).

The distribution and density of frugivorous birds varied across the study site with the two birds eating the greatest proportion of fruit, ʻōmaʻo and red-billed leiothrix, being more abundant in intact forest than restoration forest (Fig. 4). For ʻōmaʻo, there was a significant difference in density among habitats (df = 2,63, $F = 80.82$, $P < 0.01$), with density in intact forest being 24 times that of the restoration forest, but densities were similar within intact and fragmented forests. Red-billed leiothrix density also differed among habitats (df = 2,63, $F = 33.6$, $P < 0.01$), with density being five times higher in intact forest compared with restoration forests, and three times higher in fragmented compared to restoration. A markedly different pattern was observed with the warbling white-eye, which ate the least fruit, where bird densities were nearly double in the restoration forest compared to intact, and 50% higher in the restoration forest compared to fragmented (df = 2,63, $F = 14.03$, $P < 0.01$).

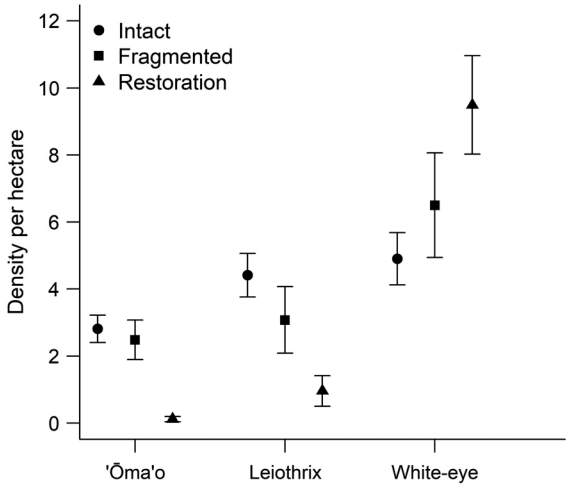


Fig. 4. Average density of three frugivorous birds by habitat type at Hakalau Forest National Wildlife Refuge, Hawaiʻi. Average detection-corrected densities (2010–2012) were based on line-transect surveys conducted across the refuge (Camp et al. 2016). Survey points were grouped by habitat type (intact, fragmented, restoration) prior to calculating the average number of birds per hectare. Error bars represent ± SE.

Bird-mediated seed rain

We monitored bird-mediated seed rain from 108 traps operated over 461 d and intercepted 8298 seeds representing 11 plant species (Fig. 5). The average bird-mediated seed rain was 0.47 ± 0.07 seeds·m^{-2}·d^{-1}. After controlling for potential variance associated with forest type, seed rain rates were not significantly different beneath the two canopy trees (blackberry: $F = 2.27$, $P = 0.13$, ʻākala: $F = 2.13$, $P = 0.15$, ʻōlapa: $F = 0.45$, $P = 0.51$, pukiawe: $F = 2.96$, $P = 0.09$, ʻōhelo: $F = 0.00$, $P = 0.97$).

Similarly, after controlling for potential variance associated with tree species, overall seed rain rates did not differ significantly across habitat types (df = 108, $F = 0.53$, $P < 0.58$), although they were lowest in restoration forest traps (0.35 ± 0.13 seeds·m^{-2}·d^{-1}), higher in intact forest traps (0.49 ± 0.16 seeds·m^{-2}·d^{-1}), and highest in fragmented forest traps (0.51 ± 0.09

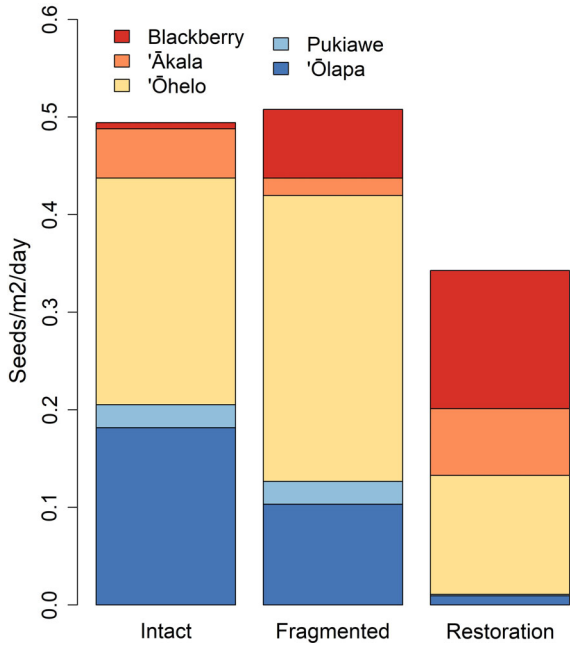


Fig. 5. Average seed rain (seeds·d^{-1}·m^{-2}) across three habitat types within Hakalau Forest National Wildlife Refuge, Hawaiʻi, from June 2015 to August 2016. Seed rain was measured using 108 hoop traps deployed across the three habitat types. While more species were found, they were in low enough numbers to not include in this figure, which we limited to our five focal fruiting species.

seeds·m^{-2}·d^{-1}). While overall seed rain rates were not significantly different, seed rain rates differed across habitat types for blackberry (F = 3.95, P = 0.02, intact = 0.00 ± 0.03 seeds·m^{-2}·d^{-1}, fragmented =0.07 ± 0.02 seeds·m^{-2}·d^{-1}, restoration = 0.14 ±0.03 seeds·m^{-2}·d^{-1}), ʻākala (F = 11.65, P < 0.01, intact = 0.05 ± 0.01, fragmented = 0.02 ± 0.01seeds·m^{-2}·d^{-1}, restoration = 0.07 ± 0.01 seeds·m^{-2}·d^{-1}), and ʻōlapa (F = 5.86, P < 0.01, intact = 0.18 ± 0.04 seeds·m^{-2}·d^{-1}, fragmented = 0.10 ± 0.02 seeds·m^{-2}·d^{-1}, restoration = 0.01 ± 0.03 seeds·m^{-2}·d^{-1}). Seed rain of the exotic blackberry and native ʻākala was greater in the upper elevation restoration habitat as compared to fragmented or intact forests, and this pattern was the most dramatic for the exotic blackberry (Fig. 5). In contrast, seed rain of ʻōlapa and ʻōhelo was greatest in the intact forest and decreased moving across habitats into fragmented and then restoration areas.

Seed rain rates generally reflected species-specific patterns of fruit phenology within the study area (Appendix S1: Fig. S2), with blackberry, ʻākala, and ʻōhelo showing distinct seasonal variation in rates of seed rain throughout the year. Notably, exotic blackberry fruiting and abundance in seed rain peaked in late summer, which was at a different time than the native ʻākala and ʻōhelo, which both peaked in late spring. In contrast, natives ʻōlapa and pukiawe showed little seasonal variation in fruiting phenology or abundance in seed rain traps. Seed of all five understory species were found in seed rain traps that did not have an adult of that species within a 20-m radius of the seed rain trap tree, indicating dispersal greater than 20-m distances. We note, however, that understory was only surveyed at a subset of seed rain trap trees and that 20 m may not be a good indicator of long-distance dispersal.

While model selection indicated that the variables most strongly associated with bird-mediated seed rain differed somewhat across plant species (Table 2), total plant basal area of the dominant understory fruiting species (ʻākala, blackberry, ʻōlapa, ʻōhelo, and pukiawe), and adjusted bird density were consistently in top models, with the exception of ʻōhelo and to a

Table 2. Model selection and AIC-weighted model-averaged parameter estimates for the effects of fruiting plant basal area, adjusted bird density, and their additive effects on daily seed rain (seeds·m^{-2}·d^{-1}).

Species	Model	K	AICc	Δ	Wt	LL	Model-averaged estimates (lower, upper)
ʻŌlapa	Plant basal area	5	−51.73	0.00	0.65	31.16	**Plant basal area: 0.19 (0.10, 0.28)**
	Bird density + plant basal area	6	−50.47	1.12	0.35	31.65	Bird density: −0.17 (−0.46, 0.12)
	Null	4	−38.95	12.78	0.00	23.67	
	Bird density	5	−36.77	14.96	0.00	23.68	
Pukiawe	Bird density + plant basal area	6	−125.71	0.00	0.81	69.27	**Plant basal area: 0.05 (0.02, 0.08)**
	Plant basal area	5	−122.59	3.12	0.17	66.59	**Bird density: 0.31 (0.07, 0.56)**
	Bird density	5	−117.60	8.11	0.01	64.10	
	Null	4	−104.15	21.56	0.00	56.27	
Blackberry	Bird density + plant basal area	6	−55.90	0.00	0.70	34.36	**Plant basal area: 0.19 (0.02, 0.37)**
	Bird density	5	−53.77	2.12	0.24	32.18	**Bird density: 0.66 (0.24, 1.09)**
	Plant basal area	5	−50.85	5.04	0.06	30.72	
	Null	4	−45.94	9.95	0.00	27.17	
ʻĀkala	Bird density + plant basal area	5	−113.31	0.00	0.81	63.07	**Plant basal area: 0.20 (0.09, 0.23)**
	Plant basal area	6	−110.40	2.91	0.19	60.49	**Bird density: −0.40 (−0.74, −0.06)**
	Null	4	−102.52	10.78	0.00	55.46	
	Bird density	5	−101.99	11.32	0.00	56.29	
ʻŌhelo	Bird density	5	40.55	0.00	0.39	−14.98	Plant basal area: 0.02 (−0.06, 0.10)
	Null	4	40.75	0.20	0.35	−16.18	Bird density: 0.29 (−0.01, 0.59)
	Plant basal area	5	42.68	2.13	0.13	−16.05	
	Bird density + plant basal area	6	42.74	2.19	0.13	−14.96	

Notes: Model average estimates are weighted based on the relative importance (AIC weight) of each model. Model-averaged parameter estimates with 95% confidence intervals that do not overlap zero are bold. Parameter estimates indicate the effect on the cube square root of seed rain (seeds·m^{-2}·d^{-1}), as the response variable was transformed prior to analysis. Abbreviations: K, number of parameters; AICc, Akaike information criterion; Δ, the change in AICc from the top model; Wt, model weight; LL, log likelihood for each model.

lesser extent ʻōlapa. Basal area of fruiting understory was positively related to bird-mediated seed rain in all cases. The relationship between seed rain and adjusted bird density was positive for pukiawe, blackberry, and ʻōhelo, but negative for ʻōlapa and ʻākala, although the relationship with ʻōlapa was not significant. The significant negative relationship with ʻākala may reflect a combination of ʻākala having higher basal area in the restoration forest vs. the fragmented forest, and the propensity of white eyes to consume ʻākala, and the highest density of white eyes in the restoration area (thus providing high seed rain rates) but the overall lower bird densities in the restoration forest.

Understory plant communities

Basal areas for four of the five fruiting species —native ʻōlapa, ʻōhelo, ʻākala, and pukiawe— measured within 20 m of seed rain trap trees were greatest in the intact forest and decreased markedly in fragmented and restoration areas (Table 3). For example, ʻōlapa averaged 0.98 ± 0.20 cm^2/m^2 in the intact forest, decreased nearly fivefold in the fragmented forest (0.21 ± 0.03 cm^2/m^2), and was largely absent (0.003 ± 0.01 cm^2/m^2) in the restoration forest. The two *Rubus* species, however, showed contrasting patterns. The native ʻākala had the most basal area in intact forest (0.49 ± 0.11 cm^2/m^2), little in fragmented areas (0.08 ± 0.04 cm^2/m^2), and unlike the other native fruiting species, basal area was higher in restoration (0.14 ± 0.05 cm^2/m^2) than in fragmented forests. Conversely, exotic blackberry basal area was greatest in fragmented areas (0.26 ± 0.02 cm^2/m^2), with no difference between intact (0.13 ± 0.05 cm^2/m^2) and restoration forests (0.16 ± 0.04 cm^2/m^2). Generally, the two *Rubus* species were the only understory plants with appreciable basal area in the restoration habitat. Although we initially hypothesized that basal area of understory plants within a 20 m radius of focal canopy trees would be greater under ʻōhiʻa vs. koa, this was only the case for ʻōhelo, but not for any other fruiting understory plant species, nor for total basal area of fruiting

Table 3. AIC model results and weighted model-averaged estimates for the effects of habitat type and tree species on fruiting plant basal area (cm^2/m^2) at Hakalau Forest NWR.

Species	Model	*K*	AICc	Δ	Wt	LL	Model-averaged estimates (lower, upper)
ʻŌlapa	Habitat type + tree species	6	1204.48	0	0.79	−595.82	**Tree species: −0.72 (−1.38, −0.07)**
	Habitat type	5	1207.11	2.63	0.21	−598.26	**Fragmented: −1.61 (−2.33, −0.89)**
	Null	3	1252.07	47.59	0	−622.92	**Restoration: −5.87 (−7.05, −4.69)**
	Tree species	4	1253.09	48.61	0	−622.35	
Pukiawe	Habitat type	5	1378.01	0	0.6	−683.71	Tree Species: 0.41 (−0.28, 1.10)
	Habitat type + tree species	6	1378.83	0.81	0.4	−683	**Fragmented: −1.28 (−2.01, −0.54)**
	Null	3	1400.38	22.36	0	−697.07	**Restoration: −3.66 (−4.99, −2.34)**
	Tree species	4	1402.26	24.25	0	−696.93	
ʻŌhelo	Habitat type + tree species	6	1523.17	0	0.91	−755.17	**Tree species: 0.56 (0.14, 0.99)**
	Habitat type	5	1527.78	4.62	0.09	−758.6	**Fragmented: −1.03 (−1.53, −0.52)**
	Null	3	1589.84	66.68	0	−791.8	**Restoration: −3.76 (−4.44, −3.08)**
	Tree species	4	1591.05	67.89	0	−791.33	
ʻĀkala	Habitat type	5	1156.15	0	0.74	−572.78	Tree species: −0.12 (−0.82, 0.59)
	Habitat type + tree species	6	1158.3	2.14	0.25	−572.73	**Fragmented: −1.56 (−2.42, −0.69)**
	Null	3	1166.26	10.1	0	−580.01	**Restoration: −1.06 (−2.06, −0.07)**
	Tree species	4	1166.7	10.54	0	−579.16	
Blackberry	Habitat type + tree species	6	1412.36	0	0.55	−699.77	Tree species: −0.36 (−0.75, 0.02)
	Habitat type	5	1413.57	1.2	0.3	−701.49	**Fragmented: 0.72 (0.20, 1.24)**
	Tree species	4	1416.09	3.72	0.09	−703.85	Restoration: 0.33 (−0.29, 0.94)
	Null	3	1416.54	4.17	0.07	−705.15	

Note: Model-averaged parameter estimates with 95% confidence intervals that do not overlap zero are bold. Model-averaged parameter estimates incorporate weighted estimates from all models and indicate the effect on plant basal area per plot (cm^2/1256 m^2). A positive estimate for tree species indicates a corresponding increase in basal stem area beneath *Metrosideros polymorpha* (ʻōhiʻa) trees relative to *Acacia koa* (koa) trees. Similarly, a positive estimate for habitat type indicates a corresponding increase in basal stem area relative to intact forest. Abbreviations: *K*, number of parameters; AICc, Akaike information criterion; **Δ,** the change in AICc from the top model; Wt, model weight; LL, log likelihood for each model.

understory (koa = 2.07 ± 2.11 cm^2/m^2, ʻōhiʻa = 2.34 ± 2.41 cm^2/m^2).

Understory plant recruitment

Understory seedling recruitment varied across tree species and habitat type (Fig. 6). In the restoration and fragmented areas, there were 8.5 and 4.5 times as many seedlings under ʻōhiʻa than koa, respectively. However, intact forest sites, which had the most seedlings overall, had similar numbers under koa (37.3 ± 15.2 seedlings/m^2) and ʻōhiʻa (36.6 ± 10.7 seedlings/m^2). The only seedling species that substantially differed from this pattern was exotic blackberry, which had more seedlings under koa than ʻōhiʻa on average, and more in the fragmented and restoration forests than the other habitats. Indeed, blackberry accounted for about 96%, 21%, and 0.1% of all seedlings found under koa in restoration, fragmented, and intact forest habitats, respectively. In contrast, blackberry only accounted for 2%, 3%, and zero in those same habitats under ʻōhiʻa. Richness of seedlings was generally greater in the intact forest than other habitat types (species richness of seedlings under ʻōhiʻa—intact: 4.5 ± 0.6, fragmented: 4.2 ± 1.1, and restoration: 2.2 ± 0.7; under koa—intact: 4.3 ± 0.4, fragmented: 2.7 ± 0.7, and restoration: 0.8 ± 0.3; linear models with normal distribution: habitat effect, $\chi^2 = 16.9$, $P < 0.01$; tree species effect $\chi^2 = 3.51$, $P = 0.06$).

After controlling for variation associated with habitat type, modeling efforts identified plant basal area as the strongest predictor of seedling recruitment beneath both ʻōhiʻa and koa. The amount of germination substrate (the sum of moss, woody litter, and soil substrates) available to seedlings, the basal area of fruiting understory species, and bird-mediated seed rain were all positively related to seedling recruitment under ʻōhiʻa; however, germination substrate played a larger role under ʻōhiʻa than under koa (Table 4). As seen in Figure 6, exotic grass cover was greater under koa than ʻōhiʻa and increased in cover moving upward in elevation from intact to restoration forests. Cover of suitable native seedling germination substrate (the sum of moss, woody litter, and soil substrates) showed the opposite pattern, which was not surprising given the negative relationship between grass cover and germination substrate ($r^2 = 0.95$, $P < 0.01$).

Overall, the majority of seedlings (89%) were found growing on mossy substrates, even though moss only constituted about 10% cover in sampling plots. Of the 2520 seedlings found on mossy substrates, about 50% were in moss found on a nurse log, 30% were in moss on the soil surface, and 14% were found in moss on the focal tree itself. In contrast, substrate with grass cover contained the fewest seedlings (2%), even though grass constituted 46% cover of the plots, on average (Table 5). Exceptions to this pattern were exotic blackberry, most of which occurred in exotic grasses, and koa stems, which occurred relatively evenly across moss, woody litter, and grass litter. Both species can send up suckering shoots from larger nearby individuals.

Grass competition and seed addition

Seedling recruitment within experimental plots varied across tree species and habitat type (Fig. 7). Experimental grass removal, with and without seed addition, significantly increased seedling recruitment under koa trees (grass/seed added = 3.07 ± 1.71, $z = 1.80$, $P = 0.07$; grass removed/no seed = 5.32 ± 2.07, $z = 2.57$, P =0.01; grass removed/seed added = 4.37 ± 1,90, $z = 2.31$, $P = 0.02$), but not under ʻōhiʻa trees (grass/seed added = 0.49 ± 0.99, $z = 0.49$, $P = 0.62$; grass removed/no seed = 1.44 ± 1.02, $z = 1.40$, $P = 0.16$; grass removed/seed added = 2.02 ± 1.01, z = 1,83, $P = 0.07$). While seed addition, combined with grass removal beneath ʻōhiʻa canopy, did increase seedling recruitment compared to the other three treatments, this pattern was not significant. Grass biomass, which was collected when plots were established (Appendix S1: Fig. S3), was greatest in restored forest under koa, but under ʻōhiʻa, grass was greatest in the fragmented forest, leading to significant habitat by tree species effect in the statistical model for grass biomass (habitat effect, $\chi^2 = 9.28$, $P = 0.01$; tree species effect, $\chi^2 = 0.11$, $P = 0.75$; habitat by tree species effect, $\chi^2 = 7.12$, $P = 0.03$). Light levels tended to be greater under koa than ʻōhiʻa, particularly in the restoration sites, where koa had light levels three times greater than ʻōhiʻa (habitat effect, $\chi^2 = 24.77$, $P < 0.01$; tree species effect, $\chi^2 = 24.77$, $P < 0.01$; habitat by tree species effect, $\chi^2 = 18.50$, $P < 0.01$) (Appendix S1: Fig. S3). On average across habitat types and canopy tree species,

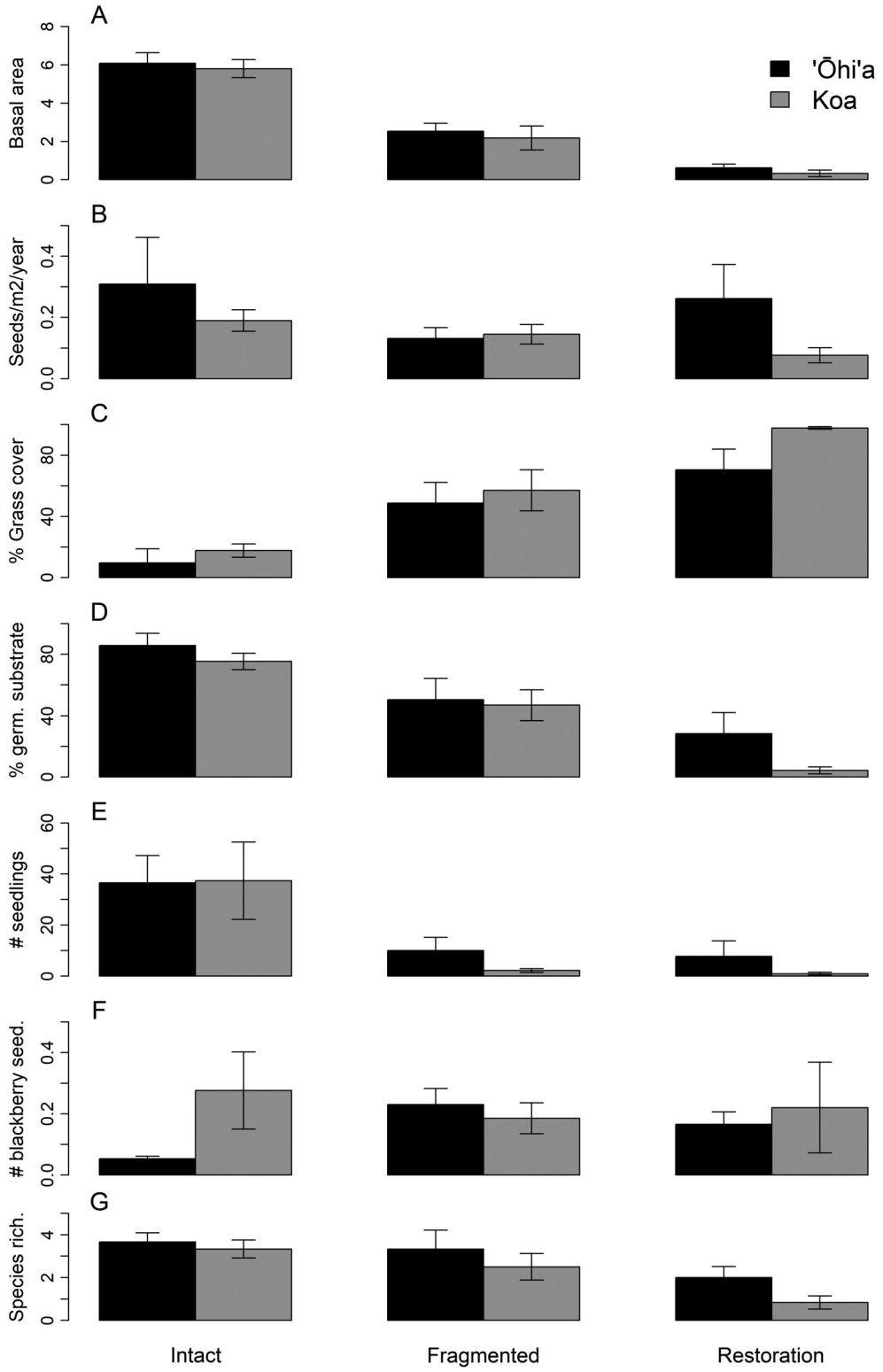


Fig. 6. Multiple ecological attributes vary by overstory tree species and the habitat type at Hakalau Forest

(Fig. 6. *Continued*)

National Wildlife Refuge, Hawai'i. Basal area (A) of understory plants within 20 m radius of overstory trees varies by habitat type but not tree species. Seed rain (B) (seeds·d^{-1}·m^{-2}) indicates variation by habitat type and overstory tree species. Percent grass cover (C) over a 10-m transect center on the focal tree showed large differences by habitat and higher percentages under koa trees. Percent germination substrate (D), a combination of bare soil, moss, and nurse log, is largely the inverse of percent grass cover and indicates substrates that promote germination. Number of native seedlings (E) under overstory trees in the different habitats indicates significantly higher seedling recruitment in intact forests. The number of non-native blackberry seedlings (F) was similar across habitats under koa, but much lower under 'ōhi'a in intact forests. Species richness of understory plants (G) was highest in the intact forest, and lowest in the restoration forest. Error bars represent mean ± SE.

Table 4. AIC model results and weighted model-averaged parameter estimates for the effects of fruiting understory basal area, germination substrate cover, and bird-mediated seed rain on seedling recruitment under *Acacia koa* (koa) and *Metrosideros polymorpha* ('ōhi'a) trees.

Canopy species	Model	df	AICc	Δ	Wt	Model-averaged estimates (lower, upper)
'Ōhi'a	Basal area + substrate	5	47.64	0	0.45	**Basal area: 0.17 (0.04, 0.30)**
	Substrate	4	48.22	0.58	0.34	Seed rain: 0.35 (−0.22, 0.93)
	Basal area + seed rain + substrate	6	50.53	2.89	0.11	**Substrate: 0.05 (0.03, 0.08)**
	Seed rain + substrate	5	51.03	3.4	0.08	
	Basal area + seed rain	5	54.87	7.24	0.01	
	Basal area	4	58.44	10.8	0	
	Seed rain	4	59.12	11.48	0	
	Null	3	61.88	14.24	0	
Koa	Basal area	4	48.35	0	0.5	**Basal area: 0.39 (0.18, 0.60)**
	Basal area + substrate	5	49.68	1.33	0.26	Seed rain: −0.42 (−1.85, 1.01)
	Basal area + seed rain	5	51.22	2.87	0.12	Substrate: 0.05 (−0.01, 0.12)
	Substrate	4	51.97	3.62	0.08	
	Basal area + seed rain + substrate	6	54.17	5.82	0.03	
	Seed rain + substrate	5	54.92	6.57	0.02	
	Null	3	58.91	10.56	0	
	Seed rain	4	62.27	13.92	0	

Notes: Model-averaged parameter estimates incorporate weighted estimates from all models, and indicate effects on the cube square root of seedling recruitment. Model-averaged parameter estimates with 95% confidence intervals that do not overlap zero are bold. Abbreviations: df, degrees of freedom; AICc, Akaike information criterion; Δ, the change in AICc from the top model; Wt, model weight.

Table 5. Seedling occurrence in the different substrate types as a percentage of total seedlings across all plots.

Seedling species	Moss	Nurse log	Live tree	Woody litter	Bare soil	Grass litter
Koa	30.77	0.00	0.00	38.46	0.00	30.77
'Ōlapa	46.51	0.00	6.98	39.53	0.00	6.98
Pukiawe	58.95	0.00	0.00	38.95	1.05	1.05
'Ōhi'a	69.14	7.41	0.00	19.75	3.70	0.00
Kōlea	16.67	0.00	0.00	83.33	0.00	0.00
Blackberry	1.64	0.00	0.00	21.31	0.00	77.05
'Ākala	25.00	0.00	0.00	62.50	0.00	12.50
'Ōhelo	95.35	1.26	1.09	1.89	0.00	0.25
Unidentified	72.22	0.69	0.00	25.00	0.00	1.39
Total	88.76	1.30	1.06	6.31	0.14	2.25
Cover of substrate (%)	10.29	1.74	3.53	37.09	1.10	46.21

Note: The average percent cover of each substrate type is shown in the bottom row for comparison.

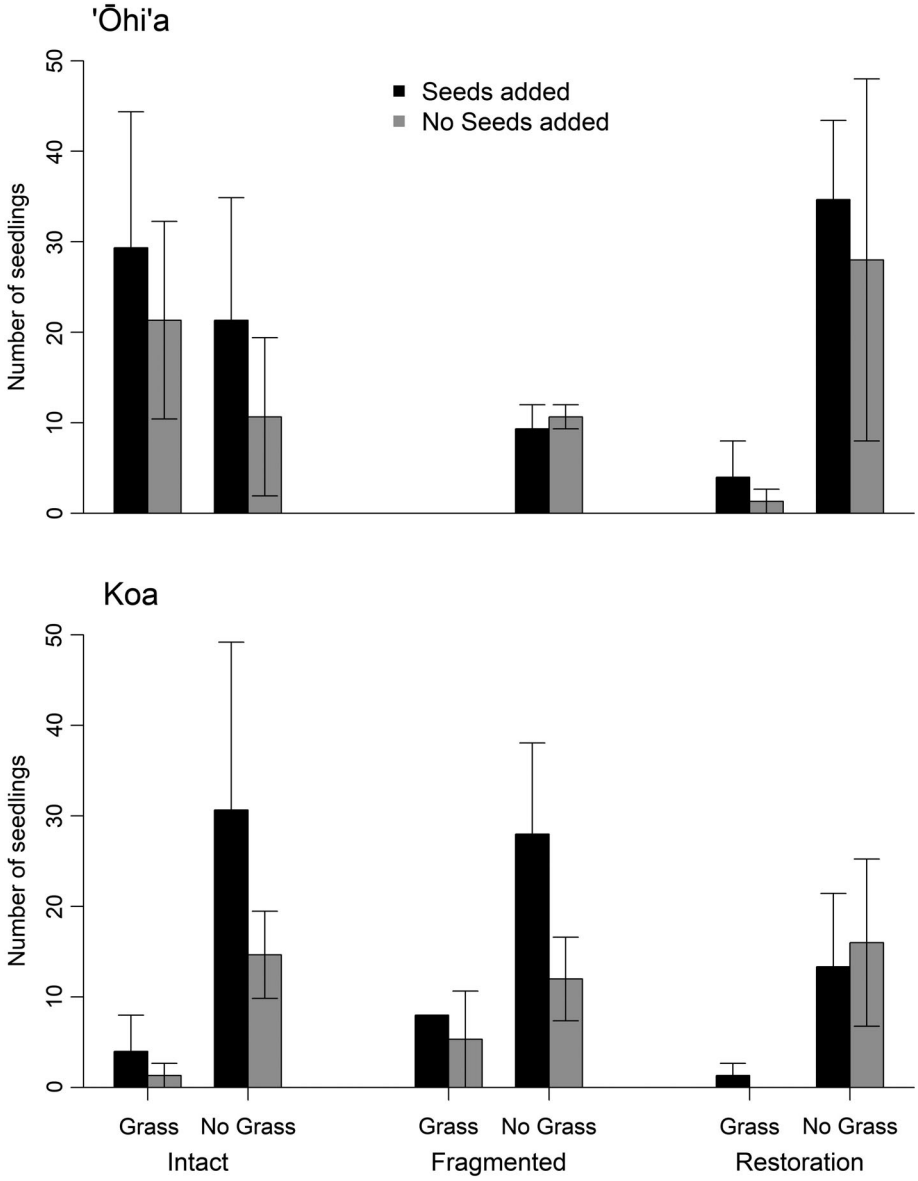


Fig. 7. Removal of grass and the addition of seed influenced the number of seedlings recruited in plots under ʻōhiʻa and koa trees at Hakalau Forest National Wildlife Refuge, Hawaiʻi. Nine ʻōhiʻa and nine koa were selected to establish experimental plots for a full factorial study of seed addition and grass removal. Four plots (0.5 × 0.5 m) were established beneath each tree, and each was randomly assigned one of the following treatments: grass/seeds added, grass/no seeds added, no grass/seeds added, no grass/no seeds added. Error bars represent ± SE.

removing grass led to 4.3 times the number of seedlings, adding seed led to 1.7 times the number of seedlings, and removing grass and adding seeds simultaneously led to 4.6 times the number of seedlings as compared to controls (no grass removal, no seed addition).

Discussion

We found evidence of both top-down and bottom-up internal reinforcement within intact and restoration forest areas (Fig. 8). These processes reinforced the current state of each forest

type, showing the importance of multiple processes, across trophic levels, influencing natural regeneration within Hawaiian mesic pasture/forest sites. Intact forests have several processes that provide positive feedbacks likely critical for maintaining a diverse forest system: comparatively high seed rain and native seedling recruitment, leading to high native woody understory basal area and ample germination substrate. Once those positive feedbacks are lost due to forest clearing, reforestation with koa may inhibit recovery due to new positive feedbacks between koa and exotic grass. Pasture grasses exhibit priority effects where they are already established, inhibiting seed germination and effectively negating any benefits that could be derived from bird-mediated seed rain. This was observed in the seed addition, grass removal experiment, where removing grass had a greater effect on seedling recruitment than seed additions. While this study demonstrates how multiple feedback loops can contribute to alternative states, this experiment provided evidence that bottom-up feedback processes may be the strongest driver in this system. The amount of seeds in the seed addition study were far greater than measured at Hakalau, even in intact forest areas where there is strong reinforcement of bird/native woody understory feedbacks, reinforcing the difficulty of overcoming the grass priority effect.

Top-down reinforcement of ecosystem state

Our results illustrate how internal top-down processes can reinforce intact forest ecosystems, and how the absence of these processes in former pastures inhibits forest regeneration. Intact forests had the highest density of frugivorous birds, the largest basal area of fruiting understory, and the highest rates of seed rain. This provides evidence for a positive feedback loop where abundant fruiting plants encourage bird visitation that increases bird-mediated seed rain and results in high seedling numbers in intact forest areas. Such internal reinforcement can lead to dominance stabilization of native woody understory communities (Suding et al. 2004, Pejchar 2015). Recently, the term "seed rain-successional

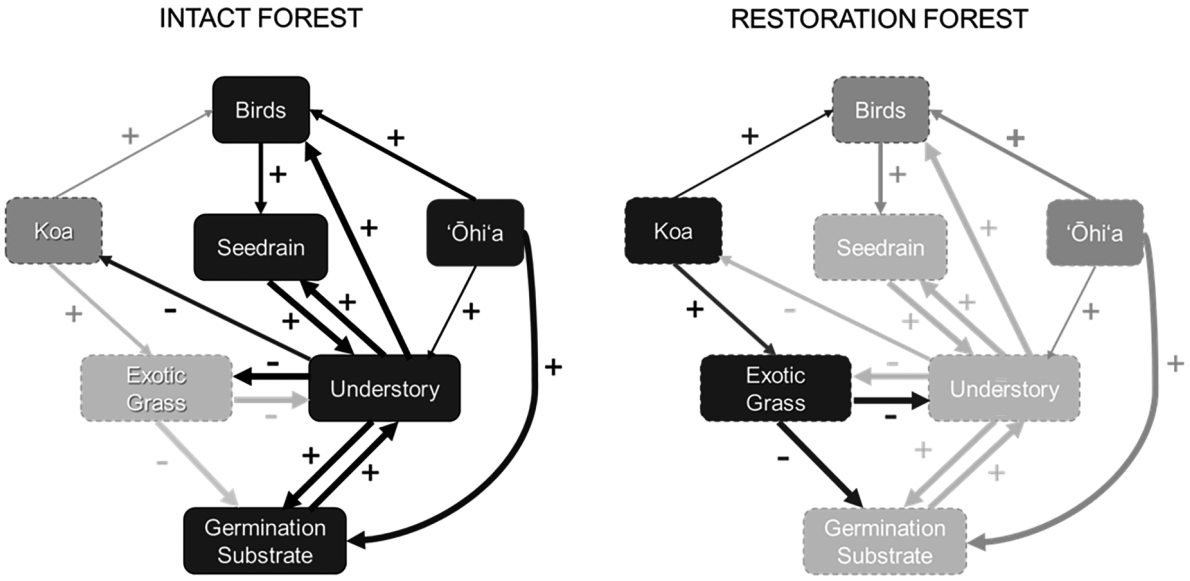


Fig. 8. Trophic interactions and feedbacks within intact and restoration forests of Hakalau Forest National Wildlife Refuge, Hawai'i. The direction (arrow), nature (positive or negative), and intensity (line thickness) of trophic relationships documented during this study are shown. Grayscale of boxes indicates the prevalence and importance of that factor in an ecosystem. For example, 'ōhi'a are abundant in intact forest (dark gray), where they are positively correlated with greater understory cover and germination substrate, but these are all uncommon in the restoration forest (light gray).

feedbacks" was used by Huanca Nuñez et al. (2021) to describe a similar phenomenon in Costa Rica.

The ʻōmaʻo, the only native frugivorous bird, illustrates the positive relationships between birds and intact forest. The largest frugivore (2.3–4.4 times larger than red-billed leiothrix and warbling white-eye, respectively), ʻōmaʻo, had the highest diversity of seed and the highest percentage of seeds in fecal samples (81% compared to 59% for red-billed leiothrix and 38% in warbling white-eye; Fig. 3). However, ʻōmaʻo were largely restricted to the intact and fragmented forests, with low densities in the restoration forest (Fig. 4), which was likely an important contributor to the higher seed rain in intact and fragmented forests. A similar pattern was found with a study that measured seed rain across sites with and without ʻōmaʻo on Hawaiʻi Island, where sites with ʻōmaʻo showed a greater proportion of native species and a more diverse assemblage in seed rain than sites with only warbling white-eye and red-billed leiothrix (Pejchar 2015). Red-billed leiothrix were the second most important seed dispersers, in terms of percent seeds in diet and species diversity, and they also had the highest densities in intact forest and lowest in the restoration forest.

In the restoration forest, a lack of fruiting understory shrubs likely contributed to the lower density of frugivorous birds. Both the ʻōmaʻo and the leiothrix have been slow colonizers of the restoration forest and are mostly restricted to areas closest to intact forest (Paxton et al. 2018). Given the prevalence of seed in their fecal samples, fruiting plants are presumably a key component of habitat selection for these two birds. Further, an important plant in the diet of ʻōmaʻo, the year-round fruiting ʻōlapa (Fig. 3, Appendix S1: Fig. S2), is largely absent from the restoration site, and the lack of this and other plant species may lead to ʻōmaʻo avoiding restoration forests during foraging bouts. Similar to the idea that top-down processes are reinforcing species composition in intact forest areas, our data suggest that the lack of a native woody understory in restoration areas is being reinforced via a lack of bird-mediated seed rain. Thus, while birds may be providing the important function of dispersing seeds and maintaining forests where understory diversity and abundance is high, areas with low abundance appear less likely to attract frugivorous birds, limiting seed dispersal and slowing recovery.

The omnivorous warbling white-eye occurs in a wide variety of habitats across Hawaiʻi and was an early colonizer of the restoration forest when it was remnant pasture grasses and small planted koa (Paxton et al. 2016). The warbling white-eye remains the most common species in the restoration forest (Fig. 4) and is likely the main contributor to seed rain there, particularly non-native blackberry and ʻākala given the prevalence of these species in their fecal samples (Fig. 3) and the seed rain (Fig. 5). This may set up a self-reinforcing cycle in restoration forests where the bulk of the understory basal area is made up of blackberry and ʻākala. Multiple studies have found that warbling white-eye diets were primarily composed of smaller seeded *Rubus* and ʻōhelo, or invasive *Lantana camara* and *Bocconia frutescens* in dry forest areas (Foster and Robinson 2007, Chimera and Drake 2010, Wu et al. 2014, Pejchar 2015, Kaushik et al. 2018), and many of the Hakalau understory species that are abundant in intact forest (e.g., ʻōlapa, pukiawe) have larger seeds than the warbling white-eye prefers.

Together, our data suggest internal reinforcement of restoration vs. intact forest states, mirroring global patterns of bird-mediated seed rain in degraded vs. intact ecosystems. There is a pattern of bird-mediated seed rain being greater in late succession than early succession and/or restoration forest (Castillo and Ríos 2008, McConkey et al. 2012) and in forest fragments rather than remnant pasture (Holl 1999, Zahawi and Augspurger 2006, Herrera and Garcia 2010), suggesting that mutualisms between birds and fruiting species lead to stabilization of plant communities in many ecosystems.

However, birds can break down this barrier through seed dispersal across habitats, and our data also show some evidence for bird-mediated seed dispersal away from zones of high fruit production. Seed of all five fruiting species studied were found in seed rain traps that were not within a 20 m radius of an adult plant of that species, suggesting that there may be some long-distance dispersal. Many studies from tropical systems have shown that birds disperse seeds away from parent plants into secondary forest or restoration areas (Holl 1998, Zahawi and Augspurger 2006, Parejo et al. 2014). For example,

Holl (1998) found that adding bird perching structures to tropical pastures in Costa Rica increased seed rain. At Hakalau, many remnant ʻōhiʻa in fragmented areas today are surrounded by "halos" of native woody understory even though those forests did not have these woody understory communities in 1985 when the refuge was established (L. Pratt, U.S. Geological Survey, *oral communication*, 2013). These "halos" are similar to "fruit orchards" in Sweden (Arnell et al. 2021) and "fruit islands" in Guam (Kastner et al. 2021), wherein avian dispersers create aggregated patches of fruiting plants. Halos around ʻōhiʻa suggest that birds moved seeds from intact forest areas into the grazed zones, starting new foci of native woody understory. It may also be the case that smaller birds take seeds shorter distances (Jordano et al. 2007, Sperry et al. 2021), which would suggest that ʻōmaʻo could be dispersing seeds farther than warbling white eyes. Thus, while we call the koa-exotic grass state "stable", it may be more akin to a transient state that moves to a more diverse, forested condition extremely slowly (Holling 1973, Fukami and Nakajima 2011). Studies of long-distance dispersal, avian behavior, and movement patterns would help inform how far patches can be from intact forest for bird-mediated seed rain to reach those areas, and expected time scales for this (Corlett 2009, Pegman et al. 2017, Rehm et al. 2019*a*).

Bottom-up reinforcement of ecosystem state

In addition to top-down reinforcement, we also documented bottom-up internal reinforcement of the intact forest and koa-exotic grass states stemming in part from positive associations between understory and suitable germination substrate. Intact forest areas had high basal area of native woody understory species, which likely led to low exotic grass cover (Fig. 6), a trend seen in previous work (Yelenik 2017). Dense, diverse patches of native understory preempt resources such as light, nutrients, or water (Tilman 1982), reducing grass growth and creating priority effects that lead to a resilient native state (Fukami and Nakajima 2011, Young et al. 2015). In particular, light has been found to limit exotic grasses in Hawaiian mesic forests (Funk and McDaniel 2010, McDaniel and Ostertag 2010) and tends to be lower in intact forest areas (Appendix S1: Fig. S3).

Intact forest sites also had greater prevalence of mosses, bare soil, and woody litter than fragmented and restoration sites, and these substrates were positively correlated with native woody seedling abundance (Fig. 6). Associations between native woody seedlings and mossy substrates were also found in more extensive surveys of Hakalau and other Hawaiian mesic forests (Santiago 2000, Inman-Narahari et al. 2013, Tweiten et al. 2014, Rehm et al. 2019*b*) and have been found to be important in forest regeneration and restoration more generally (Mallik and Kayes 2018, Blankenship et al. 2019). In Hawaiʻi, it has been proposed that mosses accumulate on decaying logs, which raise the seedlings above grass competition or disturbance from feral pigs (Santiago 2000, Inman-Narahari et al. 2013). However, about 30% of the seedlings found in bryophytes in this study were in moss that was growing on the soil surface, suggesting that other potential benefits such as mycorrhizae, microtopography to catch seeds, and favorable moisture microclimates may also help seedlings germinate and grow (Hörnberg et al. 1997, Kowal et al. 2016). The relatively undisturbed native woody understory of intact forests likely facilitates such mossy substrates by having low-light, high-humidity conditions as compared to areas with lower canopy cover, such as the koa restoration forests (Dovčiak et al. 2006, Caners et al. 2010, Rehm et al. 2019*b*). In addition, ʻōhiʻa may facilitate native woody understory regeneration by having horizontal woody structure and buttressed roots that, similar to nurse logs, form surfaces above exotic grasses that become mossy and tend to have epiphytic recruitment (Rehm et al. 2021*b*). Put together, the low light, high bryophyte abundance, and higher seed rain in intact forests facilitate native woody seedlings, which in turn facilitate bryophytes, creating positive feedbacks (Fig. 8).

Restoration sites, relative to intact forest sites, have higher grass biomass, lower native fruiting understory basal area (Figs. 6 and 8), lower seed rain, and less mossy substrate, all of which likely contributed to a lack of native woody recruitment (Table 4). We know from previous work in Hawaiʻi across many ecosystem types and sites that exotic grass is detrimental to native woody seedling emergence and survival (e.g., Cabin et al. 2002, Denslow et al. 2006, Yelenik and

D'Antonio 2013). Exotic grasses in our sites were pasture relicts likely facilitated by koa's effects on soil nitrogen (Yelenik 2017) and the higher light levels under koa than ʻōhiʻa (Appendix S1: Fig. S3). Grass-free seedling recruitment microsites could be created via tree mortality and subsequent availability of nurse logs (Santiago 2000). However, the majority of canopy trees in the restoration forest are widely spaced young koa, with a low probability of mortality (Lugo and Scatena 1996) making nurse logs unlikely. In addition, our seed addition, grass removal experiment showed that native woody seedlings rarely recruited under koa when grasses were left intact, even when seeds were added (Fig. 7), demonstrating exotic grasses' priority effects.

The only fruiting species regularly found growing in the thick grass in fragmented sites, and restoration koa corridors was non-native blackberry and to a lesser extent ʻākala and koa itself (Table 5). These three species have relatively high foliar nitrogen content as compared to the other fruiting understory (Banko et al. 2015*a*,*b*), suggesting high growth rates (Lambers and Poorter 1992, Wright et al. 2004) especially in the high soil nitrogen conditions found under koa (Scowcroft et al. 2004, Yelenik 2017), and being more competitive with species such as kikuyu grass, the dominant exotic grass under koa (Funk et al. 2008, Drenovsky et al. 2012). In addition, these three species can regenerate via suckers (Scowcroft and Yeh 2013) and more easily break exotic grass priority effects by bypassing recruiting from seed (Young et al. 2015). In contrast, other native woody species are most commonly associated with bryophyte mats not found under koa, potentially due to the higher light and high grass environment not being suitable for bryophytes (Rehm et al. 2019*b*). Koa's effects on soil and microclimate thus act similar to warbling white eyes in reinforcing the prevalence of blackberry in koa restoration forests.

These results, in combination with past work (Yelenik 2017, Paxton et al. 2018, Rehm et al. 2019*b*), suggest that koa facilitates exotic grass to the detriment of most native woody species except koa itself and *Rubus* species. In turn, we suggest that grasses facilitate koa due to a lack of dense, diverse, woody species that compete for resources. Thus, our results provide additional support for the idea that koa-exotic grass states, similar to the intact forest sites, are reinforced internally leading to resilience of the degraded state (Suding et al. 2004, Fukami and Nakajima 2011, Yelenik and D'Antonio 2013).

Comparing top-down and bottom-up effects

Our experiments indicated that grass removal was necessary to increase native woody seedling recruitment, particularly under koa, which is the current dominant tree in restoration areas. These findings reinforce that grasses incur strong priority effects and are the main constraint to passive regeneration, although seed additions also contributed to overall seedling recruitment. Indeed, we found that on average grass removal increased seedling abundance at least twice as much as seed addition did, despite the fact that we added an estimated 3.7 times and 34.6 times the annual bird-dispersed seed rain of ʻākala and ʻōhelo, respectively. It is possible that gut passage via birds may increase germination rates of seeds (Culliney et al. 2012), making a direct comparison of seed addition (where pulp was simply removed, but did not pass through the gut of a bird) and grass removal difficult. However, recent studies from the Micronesian island of Saipan showed that pulp removal in and of itself accounts for a large proportion of "gut passage" benefits normally attributed to birds (Fricke et al. 2019), evidence that a direct comparison is possible. Similar to our experiment, Holl (1998) found that while bird-mediated seed rain increased in abandoned pasture areas where bird perching structures were added in Costa Rica, there was a lack of seedling recruitment, which she attributed to highly competitive exotic pasture grasses. Also in Costa Rica, recent work by Huanca Nuñez et al. (2021) suggests that tight linkages between existing plant communities and seed rain help to shape successional trajectories in forest remnants.

More generally, our work adds an important case study to the broader work on alternative stable states, which is more often talked about theoretically than quantitatively (Holling 1973, Beisner et al. 2003, Anderson et al. 2009). Didham et al. (2005) suggest that species depauperate systems with strong abiotic gradients and disturbance regimes are more prone to exhibiting stable states. While most tropical forests have diverse flora and weak abiotic gradients and do not fit this model, Hawaiʻi differs in certain

ways. Hawai‘i has strong abiotic gradients that limit forest expansion via freezing and drought tolerance (Fortini and Jacobi 2018, Rehm et al. 2021*a*), and unlike other tropical forests, Hawai‘i is species depauperate due to its distance from continental seed sources (Ostertag et al. 2014). We also note, however, that it is possible that rather than being in alternative stable states, koa-grass sites are in "alternative transient states", as defined by Fukami and Nakajima (2011). It has only been ~35 yr since koa corridors were planted, and with more time, the forest may naturally transition to a more diverse assemblage as koa fall and create moss covered nurse logs above the grass layer (Santiago 2000, Rehm et al. 2021*a*). In addition, we often see native woody species in the crotches of koa which may be the start of new "halos" (S. Yelenik, E. Paxton, and E. Rose, *personal observation*). However, from a management perspective, this is still too slow to effectively create habitat for birds that need climate and disease refugia (Paxton et al. 2016), making these koa-grass systems alternative stable states within the time period of conservation planning (Suding et al. 2004).

Management implications and lessons learned

If restoration of a diverse forest assemblage is the management goal, would promoting bottom-up or top-down processes be beneficial for managers? In koa restoration forests that are dominated by exotic pasture grasses in the understory, native woody understory planting would be needed to break internal reinforcement of the koa—exotic grass state. We predict that passive seed rain and effects on exotic grasses (i.e., lower grass biomass) from these native woody understory plants will lead to native understory regeneration before bird densities and bird-mediated seed rain reaches a level high enough to lead to passive regeneration. Therefore, in areas where native understory exists or is planted, bottom-up processes would lead to regeneration of those species that were already planted prior to seeing any impacts of bird-mediated seed rain. Indeed, Reid et al. (2015) found that even in secondary tropical forests undergoing succession, it was the large seeded, animal dispersed plant species that were not recruiting into sites, even after a decade. Similarly, they suggested enrichment planting of these species.

A strategic landscape-level plan for increasing diversity in the restoration forest may facilitate more rapid recovery over the entire refuge. Given the large areas requiring restoration with limited resources, it may be advantageous to experiment with different strategies to maximize restoration benefits, such as varying planting densities, patch sizes, and species mixtures. For example, a forest node approach to restoration might be a cost-effective strategy (Corbin and Holl 2012), but this has yet to be tested in Hawai‘i. A node strategy may work well because the small patches can be densely packed with plants and take less time to lower light availability and take up excess soil nitrogen, potentially leading to lower grass biomass and secondary succession more quickly than sparse plantings. Spatially explicit models that take into account bird movement, seed rain, probability of germination and survival in different substrates, and the availability of these substrates across the landscape may help to inform planting strategies in terms of size and distance from intact forest (Xi et al. 2008, Wandrag et al. 2017).

Another strategy would be to restore natural top-down processes. One approach would be to augment native woody understory adjacent to intact, species-rich forests that could be visited by neighboring bird species carrying seeds from the diverse forest. This rolling front approach might take longer than other approaches such as the node strategy but could prove more manageable as work and costs are spread across years. Another approach would be to translocate bird species to areas of restoration, especially where bird species have been extirpated. There are plans to translocate the ‘ōma‘o to the western side of Hawai‘i Island where the bird once occurred but was extirpated over 100 yr ago. The reintroduction of ‘ōma‘o into these forests would increase seed dispersal of larger seeded species than the warbling white-eye can disperse. In sites where this is a consideration, we note that ‘ōlapa and pukiawe offer year-round food resources, as opposed to the *Rubus* and *Vaccinium* spp., and may be important to have on site prior to any translocations. Fortunately, ‘ōlapa is fairly easy to germinate and grows relatively quickly and had high survivorship in mesic forest sites as compared to some other native understory species (Yelenik et al. 2021).

As land managers attempt to restore increasingly more degraded lands across tropical systems, they are finding that some systems resist recovery, presenting an ecological puzzle with expensive consequences. Our study can help managers understand how different feedbacks lead to slow recovery of degraded ecosystems, knowledge which can help to prioritize management actions. Because feedbacks and constraints often exist across multiple trophic levels (Holl 1999, Zahawi and Augspurger 2006), the multitrophic approach of this study provides insights into forest ecosystem functions and guidance for land managers.

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Data Availability

Data for this publication are available from the U.S. Geological Survey (Yelenik et al. 2020): https://doi.org/10.5066/P9BKTXB3.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2./full