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Crossing the threshold: Invasive grasses inhibit forest restoration on Hawaiian islands

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Abstract

Forest removal for livestock grazing is a striking example of human-caused state change leading to a stable, undesirable invasive grass system that is resistant to restoration efforts. Understanding which factors lead to resilience to the alternative grass state can greatly benefit managers when planning forest restoration. We address how thresholds of grass cover and seed rain might influence forest recovery in a restoration project on Hawai'i Island, USA. Since the 1980s, over 400,000 *Acacia koa* (koa) trees have been planted across degraded pasture, and invasive grasses still dominate the understory with no native woody-plant recruitment. Between this koa/grass matrix are remnant native *Metrosideros polymorpha* ('ōhi'a) trees beneath which native woody plants naturally recruit. We tested whether there were threshold levels of native woody understory that accelerate recruitment under both tree species by monitoring seed rain at 40 trees (20 koa and 'ōhi'a) with a range of native woody understory basal area (BA). We found a positive relationship between total seed rain (but not bird-dispersed seed rain) and native woody BA and a negative relationship between native woody BA and grass cover, with no indication of threshold dynamics. We also experimentally combined grass removal levels with seed rain density (six levels) of two common understory species in plots under koa ($n = 9$) and remnant 'ōhi'a ($n = 9$). Few seedlings emerged when no grass was removed despite adding seeds at densities two to 75 times higher than naturally occurring. However, seedling recruitment increased two to three times once at least 50% of grass was removed. Existing survey data of naturally occurring seedlings also supported a threshold of grass cover below which seedlings were able to establish. Thus, removal of all grasses is not necessary to achieve system responses: Even moderate reductions (~50%) can increase rates of native woody recruitment. The nonlinear thresholds found here highlight how incremental changes to an inhibitory factor lead to limited restoration success until a threshold is crossed. The resources needed to fully eradicate an invasive species may be unwarranted for state change, making understanding where thresholds lie of the utmost importance to prioritize resources.

KEYWORDS
alternative stable state, ecological thresholds, establishment inhibition, nonnative grasses, priority effects, seed limitation, seed rain, tropical forest restoration

INTRODUCTION

Alternative stable equilibrium (ASE) theory hypothesizes that a system can exist as one of multiple stable states under the same general environmental conditions (Beisner et al., 2003; Holling, 1973; Scheffer et al., 2001). The current state is determined by starting conditions (i.e., priority effects) and is nontransitory or weakly transitory due to positive feedback between species and environmental factors (Fukami & Nakajima, 2011). Only when certain thresholds are reached do systems experience phase shifts from one stable state to an alternative state (Suding & Hobbs, 2009). Such shifts can occur when nonlinear ecosystem dynamics are present. Nonlinear dynamics are characterized by threshold responses whereby a small increment in a causative variable leads to a sudden state shift (Andersen et al., 2009). In contrast, systems that undergo linear change typically change slowly and unidirectionally through time, exhibiting classic successional dynamics (Andersen et al., 2009; Suding & Hobbs, 2009). One way to ask whether thresholds exist is to manipulate controlling factors to test for sudden changes in system responses. For example, multiple experiments using rainfall exclusion shelters show that tropical rainforest trees are resistant to soil moisture deficits up to 50% after which mortality rates dramatically increase (Meir et al., 2015).

The large commitment of time and resources needed to study thresholds in systems dominated by long-lived organisms means that few examples of threshold dynamics are available in forested systems, particularly during restoration (Andersen et al., 2009; Germino et al., 2018; Young et al., 2005, but see Meir et al., 2015). Yet, ASE theory and threshold dynamics are important to consider during ecological restoration because they can direct practitioners to evaluate the vulnerability of a system to sudden change with either positive or negative outcomes for the restoration goal (Bestelmeyer, 2006). An ASE/threshold approach can also help identify the causes of resilience of an undesirable state and how to achieve success in reversing degradative processes or altering compositional states (Suding et al., 2004; Suding & Hobbs, 2009). For example, ASE theory can guide management by determining how much of an exotic species would need to be reduced to allow native recovery. As such, ASE theory can also help determine the potential cost and time commitment involved in active restoration (Rohr et al., 2018; Suding & Hobbs, 2009).

The clearing of forest to create pastures for livestock grazing is a striking and common example of human-caused state change that may lead to ASE (Austin et al., 2017). During the transition of forests to pasturelands, an almost complete loss of woody plants occurs (Guariguata & Ostertag, 2001). Often, this process includes the introduction of grazing tolerant grasses (D'Antonio & Vitousek, 1992), and, depending on the size of the converted area, a large decline in seed rain of forest species may occur (Holl, 1999). Together these factors can create priority effects that inhibit succession back to forest once livestock grazing has ceased (Holl, 1999; Yelenik, Rose, & Paxton, 2022).

The level to which native species seed rain would need to increase or dominant exotic grasses (exerting priority effects) would need to decrease before natural native forest regeneration takes place is critical for setting management goals, such as intensity of tree planting or invasive grass control. Whether these relationships are linear or follow threshold dynamics is currently unknown.

We address the importance of seed rain and invasive grass cover to recovery processes in midelevation invasive grass-dominated pastures on Hawai'i Island, where active reforestation has been taking place for 35+ years with the goal of converting pasturelands to diverse, native forest (Scowcroft, 2013). Despite planted native *Acacia koa* (henceforth koa) trees being 35+ years old, little to no native plant recruitment has occurred in the understory of restoration areas, which instead continue to be 100% dominated by invasive pasture grasses (McDaniel & Ostertag, 2010; Yelenik, 2017). Because of this, managers have been planting understory woody species under the planted koa monocultures. Whether planting would need to reach a critical level whereby grasses would be suppressed, leading to higher native seed germination and establishment, is unknown. Similarly, a threshold of understory native density may need to be reached to attract seed-dispersing birds, which could greatly increase woody plant recruitment and understory development.

Past work suggested that multiple feedbacks worked to promote two alternative states: resilient intact forest or a persistent, restoration-koa/grass state (Yelenik, Rehm, D'Antonio, & Caldwell, 2021; Yelenik, Rose, & Paxton, 2022). The majority of woody understory species are bird-dispersed (although koa is not), so there is potentially a positive feedback between fruiting understory and bird density: Birds benefit from fruiting resources, and understory development benefits from bird-mediated seed dispersal. While this feedback appears to have been broken by forest clearing (Chimera & Drake, 2010; Pejchar, 2015), seed dispersal has begun to recover as birds use the koa restoration areas (Paxton et al., 2018; Rose et al., 2017; Yelenik, Rose, & Paxton, 2022). Yet initial work comparing bird density and seed rain between koa restoration sites lacking understory and intact forest provides evidence that seed rain is substantially lower in koa restoration areas (Yelenik, Rose, & Paxton, 2022).

Past work also suggested that feedback exists between native understory cover and suitable germination habitat (Rehm et al., 2019; Yelenik, Rose, & Paxton, 2022).

In intact forest, dense understory was positively related to the prevalence of bryophytes and lack of grass, both of which have been found to facilitate native plant recruitment and greater understory seedling and sapling abundance (Rehm et al., 2019). In contrast to native forest, restoration koa areas have high grass cover and almost no bryophytes (Rehm et al., 2019).

Together, prior observations and experiments led to the following questions: (1) How much woody understory is needed to encourage greater bird-mediated seed dispersal? From the perspective of thresholds, we are asking whether there is a point at which a small increase in shrub cover results in large increase in bird-mediated seed rain. (2) What is the relationship between native woody-species seed rain and seedling establishment, and does this relationship indicate a threshold of seed rain that would be needed to promote native woody recruitment? This latter question is intertwined with a final question: (3) Is there a relationship between grass cover and native woody recruitment? This last question can directly inform grass control efforts.

To address Questions 1 and 2, we evaluated the relationship between understory density/basal area and bird-mediated seed rain. We made use of existing variation in the planting density of outplanted fruit-bearing woody understory to see whether a threshold of understory woody plants would be needed to attract birds and, thus, initiate a large increase in native seed rain. If these processes exhibited threshold dynamics, then we would expect to see a threshold level of understory density/basal area associated with a sharp rise in seed rain. To address Questions 2 and 3, we conducted a seed addition experiment that varied seeding density and crossed this experimental variation with grass removal. In this way, we evaluated whether a threshold level of seed addition and/or grass removal would be needed to observe seedling establishment (over the 2-year study period). Because grass cover is difficult to manipulate in a continuous way, we conducted a grass reduction treatment in combination with the seed addition treatments and identified a likely range of grass reduction that would be needed to initiate woody plant establishment. Finally, to further clarify the relationship between grass cover and native seedling recruitment, we reanalyzed grass cover and seedling survey data from Yelenik, Rose, and Paxton (2022) to specifically look for threshold effects in seedling establishment across a gradient of grass cover.

METHODS

Study area

The study took place at Hakalau Forest National Wildlife Refuge (Hakalau NWR) on Hawai‘i Island, Hawai‘i USA. Hakalau NWR extends from high-quality low- to midelevation forests (<1000 m above sea level [asl]) to high-elevation (~1600–2000 m asl) invasive grass-dominated pasturelands that were once covered in native forest. Forests were cleared during the 19th century, planted with introduced pasture grasses, and actively grazed until the 1980s. Since the late 1980s, active restoration has consisted in planting over 400,000 individuals of a native tree, koa, in corridors that extend from the invasive grass-native forest boundary at ~1600 m asl upslope through the invasive grasslands to the upper boundary of the refuge (~2000 m asl). Koa were originally used for restoration since they are relatively easy to propagate and grow quickly (Scowcroft et al., 2004). Kikuyu (*Cenchrus clandestinus*) is one of the most dominant invasive grasses at the site, grows well in the light and nutrient conditions found under koa (McDaniel & Ostertag, 2010; Yelenik, 2017), and often compose >90% of grass biomass within our plots.

To increase native plant recruitment within koa corridors, managers have been manually outplanting native understory species and individuals of the other canopy-forming tree species, *Metrosideros polymorpha* (henceforth ‘ōhi‘a), since the late 1990s. Planting composition includes a variety of understory plants not listed here, but the most common species planted include the following: *Coprosma rhynchocarpa* (pilo), *Cheirodendron trigynum* (‘ōlapa), *Ilex anomala* (kāwa‘u), and *Myrsine lessertiana* (kōlea). This has resulted in some corridors having a sparse but diverse understory, although these areas are very limited in spatial extent. In addition, invasive grasses persist even in areas that have relatively dense understory outplanting. The majority of old pasture area planted with koa (~1400 ha) has not received supplemental understory outplanting and is solely grass dominated.

In addition to restoration corridors, remnant ‘ōhi‘a are present within the grassland matrix. These are trees that were not removed during the initial forest conversion to grassland. Unlike under the planted koa, native plant recruitment has occurred at the base of some remnant ‘ōhi‘a since the exclusion of livestock, which results in “halos” of native vegetation of various sizes that extend from the tree base out to the edge of the tree canopy (Rehm et al., 2020). Under other remnant ‘ōhi‘a, the understory remains dominated by invasive grasses. The reasons for understory recruitment under some and not other remnant ‘ōhi‘a is unclear, but it may be related to soil conditions, distance to intact forest, seed rain by frugivores, tree architecture, the presence of bryophytes, or additional factors not yet studied (Rehm et al., 2019, 2020; Yelenik, Rehm, & D’Antonio, 2022). We compare thresholds of understory cover to seed rain under these trees as well as

under koa because these trees may play an important role in initiating forest succession.

Understory basal area

From August to October 2017, we measured the basal area of all fruit-producing native and one nonnative species (*Rubus argutus*) at 20 koa within restoration corridors and 20 remnant ʻōhiʻa near these corridors. At each focal tree, we established a 5-m-radius plot with the base of the tree as the plot center. A 5-m-radius plot was chosen to capture most or all of the area under the canopy of the focal tree (Yelenik, 2017). Every understory woody stem was identified, and the basal diameter was measured to the nearest 0.1 mm. Trees were distributed across three transects that extended from the intact forest boundary upslope into the open grassland and transects were ~1.5 km away from other transects. By distributing trees along the transect moving away from the intact forest boundary, we limited the influence that proximity to intact forest may have in attracting frugivores for the bulk of our study trees.

Seed rain

To estimate seed rain, we deployed 0.5-m-radius (~0.8 m^2) circular hoop-style seed traps lined with a 0.13-mm silkscreen (Rose et al., 2017) to catch all vertebrate-dispersed seeds at each of the 40 trees where we measured the understory basal area. At each tree, one trap was placed 1 m off the ground, and a second was suspended in the tree canopy just above any understory fruiting plants (height depended on understory canopy height). Canopy traps were anchored to the ground with a rope to minimize trap movement, and a weight was placed in all traps so seeds would pool in the middle to minimize seed loss due to wind. The canopy traps represented seeds dispersed by vertebrates, and our assumption was that any seeds found in these traps would be dispersed by one of three birds: the native frugivore, *Myadestes obscurus* (hereafter ʻŌmaʻo), or the nonnative omnivores, *Zosterops japonicus* (Warbling white-eye) or *Leiothrix lutea* (Red-billed Leiothrix). Seed traps placed 1 m above the ground within the understory would capture both bird-dispersed and passive seed rain of the understory itself.

Although rodents can occur in the forest within the refuge, we assumed rodents were at low densities within our sites, and therefore seed removal by rodents was relatively low for the following reasons: We saw no evidence of rodents at the site over the 2 years of the study (no visual sightings, no droppings in traps, no partially chewed seeds or fruit), a lower amount of food sources outside of the forest would not support high densities of rodents, and traps were elevated to reduce access by mammals. However, we do acknowledge that without directly measuring seed predation by rodents, we cannot determine how much seed was potentially lost. This is likely more important in our seed traps near to the ground rather than those above the canopy.

Traps were deployed from October 2017 to October 2018 and were collected every 2 weeks. Seeds were mostly identified to species except for seeds of the genera *Vaccinium* and *Rubus*, which were grouped by genus.

Relationship between grass cover and grass biomass

To evaluate the relationship of understory basal area, grass presence, and seed rain, we measured both grass cover and biomass. In our study system, a small change in the amount of grass biomass may result in a large change in the percentage cover of grass in a plot due to the structure of the grass species present. Furthermore, understanding how much grass biomass would need to be removed before influencing seedling establishment (see following discussion) has important management implications. Here we evaluated the relationship of cover to biomass at the same 40 trees where we measured understory basal area and seed rain. In June and July 2017, we established 0.5-m^2 (1.0×0.5-m) plots at 2.5 m from the base of each tree in each cardinal direction ($n = 4$ plots per tree). At each plot we estimated the percentage grass cover inside quadrats using a 10×10-cm grid and point-intercept method, then clipped, dried, and weighed the grass to obtain total aboveground grass biomass.

Seed addition and grass removal

One of our goals was to determine how seed rain and grass cover interacted to influence native seedling recruitment under remnant ʻōhiʻa and restoration koa and if these exhibited threshold-type effects. Therefore, we conducted a full-factorial random-block design experiment that contained three fixed factors: overstory tree (restoration koa or ʻōhiʻa), grass removal (none, medium, high removal), and seed density (0, 10, 20, 50, 100, 200/400 seeds added per 0.25 m^2). Because most of the restoration area of the refuge consists of trees (koa in corridors or remnant ʻōhiʻa) with an understory dominated by invasive grasses, we focused this experiment on trees

with little to no native plant understory development. We chose nine koa and ʻōhiʻa that were a subset of the 40 trees from the understory basal area and seed rain component. At least two individuals of each tree species were chosen on each of the three study transects. Trees were selected that had relatively low understory basal area of native species, had no understory plants of the species used for seed addition (see following discussion), and contained at least 80% grass coverage of the soil surface.

At each tree, we established three 1 × 1.5-m rectangular plots 1 m from the base of the tree in three randomly chosen cardinal directions. Plots were oriented with the long edge facing the tree and were completely under the focal tree's canopy, and each plot was randomly chosen for a grass removal treatment consisting of none, medium, or high grass removal, corresponding to 100%, 50%, and 0% grass coverage, respectively. True grass cover values, which were measured at each time point with a plot frame, were often close to target values (Appendix S1: Table S1), with the medium (50%) grass removal treatment deviating from the desired value by the largest margin (mean grass removal was between 39% and 35% instead of 50%). We originally clipped grass to desired removal values, then estimated grass cover at each survey and grass regrowth was clipped every 2 to 4 weeks for the duration of the study, depending on the rate of regrowth. All grass clippings were removed from the plot. Each grass treatment plot was divided into six 0.25-m^2 subplots (0.5 m × 0.5 m), where we manipulated the seed density of two common understory species, *C. rhynchocarpa* (hereafter pilo) and *C. trigynum* (hereafter ʻōlapa). For each species, we randomly assigned to each subplot the addition of 0, 10, 20, 50, 100, and 200 (pilo) or 400 (ʻōlapa) seeds. During August and September 2017, seeds were collected from at least six individuals of each species within the refuge, manually separated from the pulp, and mixed.

Initial plot clearing took place in August and September 2017, and seeds were added to plots in late September and early October 2017. Every subplot was surveyed for seedling germination and establishment for roughly every 2 weeks from October 2017 to January 2018 and then monthly from January 2018 to April 2019. At each survey, subplots were thoroughly searched, and we marked every individual germinating seed and seedling with a unique identifier. During subsequent surveys, each marked individual was revisited and tracked until death or until the end of the experiment. Seed addition treatments possibly created seedling competition as high seed density plots were receiving up to 600 seeds from the two species (200 pilo and 400 ʻōlapa). However, low to modest germination rates were found across all seed addition plots, indicating a small but consistent proportion of seeds germinated. Seeds were also evenly distributed throughout the 0.25 m^2, and rarely did we find seeds germinating and growing near enough to other individuals to inhibit initial growth through competition. In the time course of the study, seedlings did not reach sizes large enough to affect growth of other individuals within their vicinity by shading and given ample moisture and soil nutrients, we feel competition between seedling individuals played a minimal role in our experimental results.

Grass cover versus seedling abundance

To further explore how grass cover influences seedling establishment, and to see whether thresholds existed in previous work, we reanalyzed data from another study located nearby (Yelenik, Rose, & Paxton, 2022). The previous analyses of these data focused on how multiple factors (germination substrate, bird-mediated seed rain, fruiting plant density) affected seedling recruitment. Germination substrate was defined as moss, litter, or bare soil (favorable microsites for native seedling recruitment) and did not include grass cover. Thus, the relationship between grass cover and seedling recruitment from these data had gone unexplored until now.

In this previous study, we established 20 consecutive 0.25-m^2 plots placed along a 10-m north–south transect centered at the base of each of 36 trees (18 koa and 18 ʻōhiʻa) throughout the refuge. In each 0.25-m^2 plot, we counted and identified all seedlings and estimated the percentage grass cover (for a full description, see Yelenik, Rose, & Paxton, 2022). For the previous publication, plot data were averaged per tree prior to analysis, whereas in this reanalysis, we retained plot-level variation. The 36 trees in the previous study were distinct from the 40 trees used in the current study.

Data analysis

All analyses were conducted in R version 4.2.1 (R Core Team, 2022). We were interested in determining whether the understory basal area related to total and bird-dispersed seed rain. For bird-dispersed seed rain, we first summed the total number of seeds collected in canopy traps at each focal tree. We then modeled this total against the log of total understory basal area (adding 0.01 to remove zero values) at each focal tree and the interaction with overstory tree species (restoration koa or ʻōhiʻa) using a generalized linear model (GLM) with a negative binomial error distribution. We modeled total seed rain similarly, except that we summed the total number of

seeds collected in both the canopy and ground traps at each tree, as this represents both bird-dispersed and passive seed rain from the understory itself. We then performed model selection on total and bird-dispersed seed rain models using AIC following Burnham and Anderson (2002). A model was considered better if it had an AIC at least two units lower than competing models. When multiple models were within two AIC units of each other, the simpler model was selected.

In grass removal and seed addition plots, to determine the relationship between grass percentage cover and biomass, we modeled grass percentage cover against a fixed effect of dry weight grass biomass (g) at all subplots (four subplots per 40 trees, $n = 160$) using a beta regression and the package betareg (Cribari-Neto & Zeileis, 2010). We first converted percentage cover into proportion, then added or subtracted a small value (0.01) to remove zeros and ones.

In grass removal and seed addition plots, we determined whether seed germination and seedling establishment of pilo and ʻōlapa were dependent on the overstory species (restoration koa or ʻōhiʻa), grass removal, or seed density and whether these dynamics exhibited threshold effects. If threshold processes operated, we predicted we would observe seed germination and/or seedling establishment increase rapidly once a threshold of seed density or grass removal treatment was reached. We conducted a separate analysis for each seed addition species. In all exploratory analyses and initial statistical approaches, overstory species did not play a role in seedling germination or seedling survival. Therefore, to simplify the modeling and aid in model convergence, overstory species was excluded from final analyses.

For seed germination, we first summed the total number of seeds that germinated for each subplot for each species during the entire study. We then modeled this total against grass removal, seed density, and a quadratic effect of seed density to allow for nonlinear, threshold-like responses with a random effect of focal tree ID using a generalized linear mixed model with a negative binomial distribution in the glmmTMB package (Brooks et al., 2017). We did not include a quadratic term for grass removal because we only had three removal levels, but we addressed possible grass cover thresholds in the reanalysis of the Yelenik, Rose, and Paxton (2022) data. In addition, we included the interaction of grass removal and seed density because large changes in seed germination may occur as thresholds of grass removal and seed density are crossed simultaneously. We compared four competing models testing the effects of linear and nonlinear seed density and grass removal using the AIC selection criterion. When grass removal was found to be significant ($p < 0.05$), we looked for differences between treatments using the emmeans package.

We modeled the number of seedlings per subplot using a similar approach to seed germination but counted only those seedlings surviving until the end of the study. We used the same model formulas and model selection process as outlined for seed germination.

For our reanalysis of data from Yelenik, Rose, and Paxton (2022), we modeled seedling abundance using a mixed-effects hurdle model due to the large number of plots where no seedlings occurred (623 of 720). We used fixed effects of percentage grass cover and overstory species (restoration koa or ʻōhiʻa) for both the zero-count and positive-count processes, with a random effect of individual trees using the GLMMadaptive package (Rizopoulos, 2022). When fixed effects were not significant in either the zero- or positive-count models, we simplified models using an AIC approach until the simplest and best explanatory model was found. In this analysis, we limited seedlings to those that produce fleshy fruit nad were identified to at least the genus level and excluded species of *Rubus* because it is difficult to determine the native (*Rubus hawaiensis*) from the invasive (*R. argutus*) seedlings.

RESULTS

Seed rain versus understory density

Seed rain was highly variable across the study area, with the number of seeds falling into individual traps ranging from 1 to 6172 seeds, with every trap having at least one seed collected during the 12-month collection period (Appendix S1: Table S2). In total, we found seeds of eight understory fruiting plant species, and these eight represented the most common plants present in the understory of intact forest (Appendix S2: Figure S1). For the two species used in the seed addition and grass removal experiment, average total seed rain ranged from 0.13 to 2.06 seeds/0.25 m^2 (pilo) and 0.45 to 5.28 seeds/0.25 m^2 (ōlapa; Appendix S1: Table S3).

We selected sites to achieve a large range of understory basal area to explore for a possible threshold on seed rain and understory recruitment. Indeed, understory basal area was highly variable, ranging from 0 to 4407 cm^2 within each 5-m-radius plot (Appendix S1: Table S2), but on average, basal area was greater under ʻōhiʻa with a mean (SD) of 808.5 (1279.1) cm^2 compared to koa with 401.2 (465.3) cm^2. While the best-fit model for bird-mediated seed rain (e.g., seed rain above the understory canopy) contained understory basal area, model selection criteria favored the simpler model with

only overstory tree basal area (Figure 1A, Table 1, Appendix S1: Table S4). Bird-mediated seed rain was higher under ʻōhiʻa than the restoration koa with mean seed rain (SD) of 53.7 (68.2) cm^2 for ʻōhiʻa versus 24.7 (33.1) cm^2 for koa (Table 1, Appendix S1: Table S4).

In addition to seeds caught in aerial traps, we evaluated total seed rain (bird-mediated + passive). The best model to explain variation in total seed rain included both understory basal area and overstory species (Figure 1B, Table 1, Appendix S1: Table S4), with a positive effect of understory basal area on total seed rain. This, combined with the lack of an understory effect on bird-dispersed seed rain, indicates that seed rain increases as understory basal area increases, but this was largely due to passive seed fall rather than bird dispersal. As before, total seed rain was higher under ʻōhiʻa than the koa with mean seed rain (SD) under ʻōhiʻa of 746.15 (1500.1) cm^2 versus koa of 48.8 (75.2) cm^2. The relationship between total seed rain and understory basal area was linear, supporting the lack of a threshold response.

Relationship of grass cover and biomass

We found a strong asymptotic relationship between grass cover and biomass (pseudo-$R^2 = 0.8$, $p < 0.001$, Appendix S1: Table S5, Appendix S2: Figure S2). A small

TABLE 1 Model outputs from generalized linear models with negative binomial error structure with model structure, df (degrees of freedom), AIC (Akaike's information criterion), and ΔAIC (difference in AIC score relative to lowest AIC score).

Seed rain	Model structure	df	AIC	ΔAIC
Bird-dispersed seed rain	Log total basal area + Overstory species	4	375.1	0
	Overstory species	**3**	**375.2**	**0.10**
	Log total basal area × Overstory species	5	377.6	2.54
	Log total basal area	3	377.7	2.58
	Null	2	377.9	2.82
Total seed rain	**Log total basal area + Overstory species**	**4**	**508.9**	**0**
	Log total basal area × Overstory species	5	510.5	1.65
	Overstory species	3	521.3	12.41
	Log total basal area	3	532.4	23.59
	Null	2	543.9	35.09

Note: Response variable is bird-dispersed seed rain or total seed rain that includes passive and bird-dispersed seeds. Fixed effects include log-transformed total understory basal area, overstory species (restoration koa or ʻōhiʻa), and their interaction. Best model is indicated in bold and was chosen based on the simplest model that was within two AIC units of the lowest AIC score.

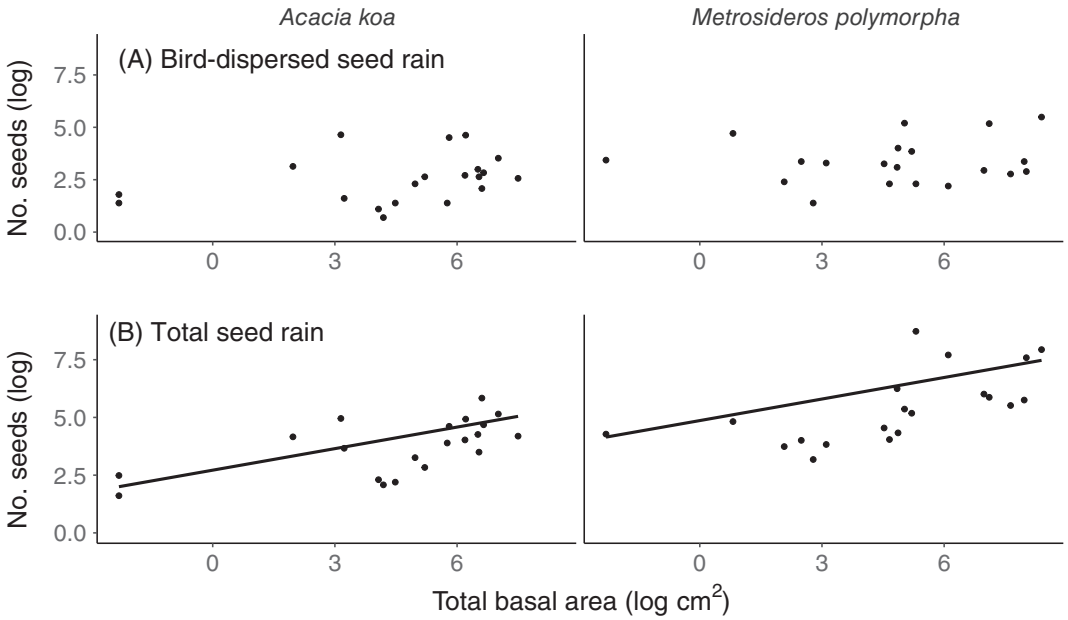

FIGURE 1 Total number of seeds per trap (~0.8 m^2) against log of total understory basal area at 40 trees, 20 *Acacia koa* (koa) within restoration corridors (left column) and 20 *Metrosideros polymorpha* (ʻōhiʻa; right column) as remnant trees within same corridor areas at Hakalau Forest National Wildlife Refuge. The top row (A) represents bird-dispersed seeds captured in traps suspended in tree canopy above any understory plants. The bottom row (B) represents total seed rain, which includes both the bird-dispersed seed rain (A) and that falling passively from the understory itself (data not shown). Solid line is the model-fitted relationship and is present only when model selection identified a statistically significant relationship between seed rain and total basal area ($p < 0.05$).

increase in grass biomass results in a large increase of grass cover at values below roughly 80% grass coverage. Thus, removing grass to 50% cover, which is what we aimed for in our medium grass treatment, would lead to more than 50% of grass biomass being removed. Above 80% cover, grass biomass continued to increase but with smaller changes to grass coverage up to 100%. Actual treatment levels in our medium grass removal treatments, as measured with a plot frame and averaged over time, were quantified as 40%–45% grass cover removal, which would equate to ~75 g dry grass biomass removed per plot.

Seed rain and grass removal versus recruitment

Focusing first on the effects of varied levels of seed addition in our seed addition and grass removal experiment, ignoring the subplots where no seeds were added (54 subplots), of the remaining 280 subplots, only 34 subplots (12.1%) had no pilo seeds germinate in them. For pilo, every subplot within the highest seed density treatment (200 seeds/0.25 m^2) had at least one seed germinate during the study. For ʻōlapa, overall seed germination was lower, with 145 of 280 subplots (51.7%) that received seed having no seeds germinate within them. Furthermore, despite adding 400 seeds in the highest seed density treatment subplots, 24 of 54 subplots had no ʻōlapa seeds germinate, with 15 of these 24 occurring in the subplots where no grass was removed.

The best model of the number of seeds germinated of both pilo and ʻōlapa included grass removal, seed density (with the quadratic term), and their interaction (Table 2, Appendix S1: Table S6, Figure 2). Seed germination increased with seed density, and seed germination was highest with medium grass removal, moderate in the high grass removal, and lowest when no grass was removed ($p < 0.032$ for all pairwise comparison across both species; Appendix S1: Table S7). The significant shifts in germination that occurred at medium grass removal relative to no grass removal coupled with no gains made with further grass removal indicate a threshold. Furthermore, a threshold of seed density may also be present as the number of seeds germinated increased faster after 20 or 50 seeds were added to plots but plateaued as seed densities approached the highest seed densities.

The best-fit model for seedling survival was similar to that of germination for both species but with no interaction between seed density and grass removal. The number of seedlings surviving at the end of the study of pilo and ʻōlapa increased with grass removal and seed density, with no difference between the medium or high grass removal treatments (Table 2, Appendix S1: Table S7, Figure 3). The inclusion of the quadratic term of seed density in the best-fitting model indicates a

TABLE 2 Models considered during model selection of seed germination totals and number of seedlings alive at end of experiment across grass removal and seed addition.

Dependent variable	Species	Model structure	df	AIC
Seed germination	Pilo	**Grass removal × (Seed density + Seed density^2)**	**11**	**6441.7**
		Grass removal + (Seed density + Seed density^2)	7	6487.6
		Grass removal × Seed density	8	6702.0
		Grass removal + Seed density	6	6720.0
	ʻŌlapa	**Grass removal × (Seed density + Seed density^2)**	**11**	**3339.8**
		Grass removal + (Seed density + Seed density^2)	**7**	3346.3
		Grass removal × Seed density	8	3428.2
		Grass removal + Seed density	6	3437.3
Seedlings alive at end of study	Pilo	Grass removal × (Seed density + Seed density^2)	11	1276.1
		Grass removal + (Seed density + Seed density^2)	**7**	**1275.5**
		Grass removal × Seed density	8	1295.2
		Grass removal + Seed density	6	1294.4
	ʻŌlapa	Grass removal × (Seed density + Seed density^2)	11	341.4
		Grass removal + (Seed density + Seed density^2)	**7**	**340.0**
		Grass removal × Seed density	8	342.7
		Grass removal + Seed density	6	343.3

Note: The best-chosen model is in bold.
Abbreviation: AIC, Akaike information criterion.

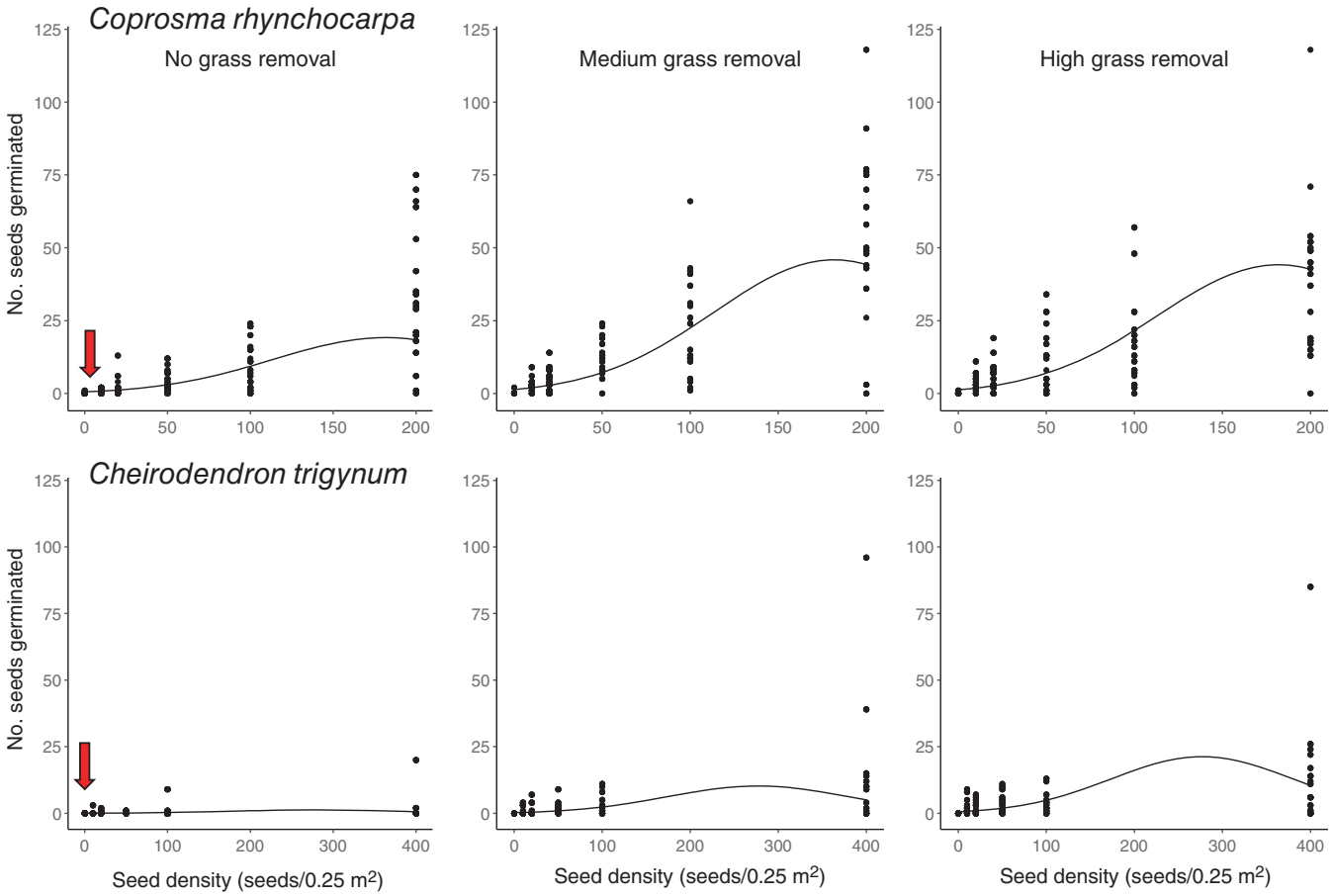

FIGURE 2 Seed germination within 0.25-m^2 subplots for each seed species (top: *Coprosma rhynchocarpa*, bottom: *Cheirodendron trigynum*) across grass removal treatments (columns within panels) and seed density (*x*-axis for each subpanel). Points represent plot values, and black line represents predicted relationship with shaded area the 95% CI from the mixed-effect modeling. Arrows in the first column show current average total seed rain rate for each species (see Appendix S1: Table S3 for more details).

threshold effect of seed density on seedling survival similar to seed germination: Seedling survival increases fastest after 50 seeds are added to the plot but levels off at high seed densities (Figure 3).

Grass cover versus seedling abundance

By reanalyzing data from Yelenik, Rose, and Paxton (2022) to look specifically at the effects of naturally occurring grass cover (not previously tested), we found support similar to our experimental findings that grass cover affects seedling establishment (Figure 4, Appendix S1: Table S8). The zero-count portion of the hurdle model showed that the probability of encountering no seedlings in a plot increased with grass cover and was higher under koa than ʻōhiʻa (Appendix S1: Table S8). Indeed, only 97 of the 720 plots had at least a single seedling, indicating substantial barriers to seedling establishment across the entire restoration area. Of these 97 plots with at least a single seedling, 92 had grass coverage of <50%. In the current portion of our study looking at seed rain and recruitment, over 83% (113 of 160 plots) of 0.5-m^2 plots under trees where seed rain and understory basal area were quantified had grass coverage values ≥50%. Therefore, most of the plots did not achieve this low threshold level of grass, potentially preventing us from detecting a threshold.

In contrast to our experimental findings, we did find support that seedling presence was influenced by overstory species, with seedling presence being higher under ʻōhiʻa than koa (69 of 97 plots that had at least a single seedling present were under ʻōhiʻa). The count-process part of the hurdle model showed that no fixed effects were better than a null model in explaining the quantity of seedlings that occurred (no competing model had ΔAIC <2 from the null model). This indicates a strong influence of grass cover and overstory species on the presence of seedlings, but not on how many seedlings established.

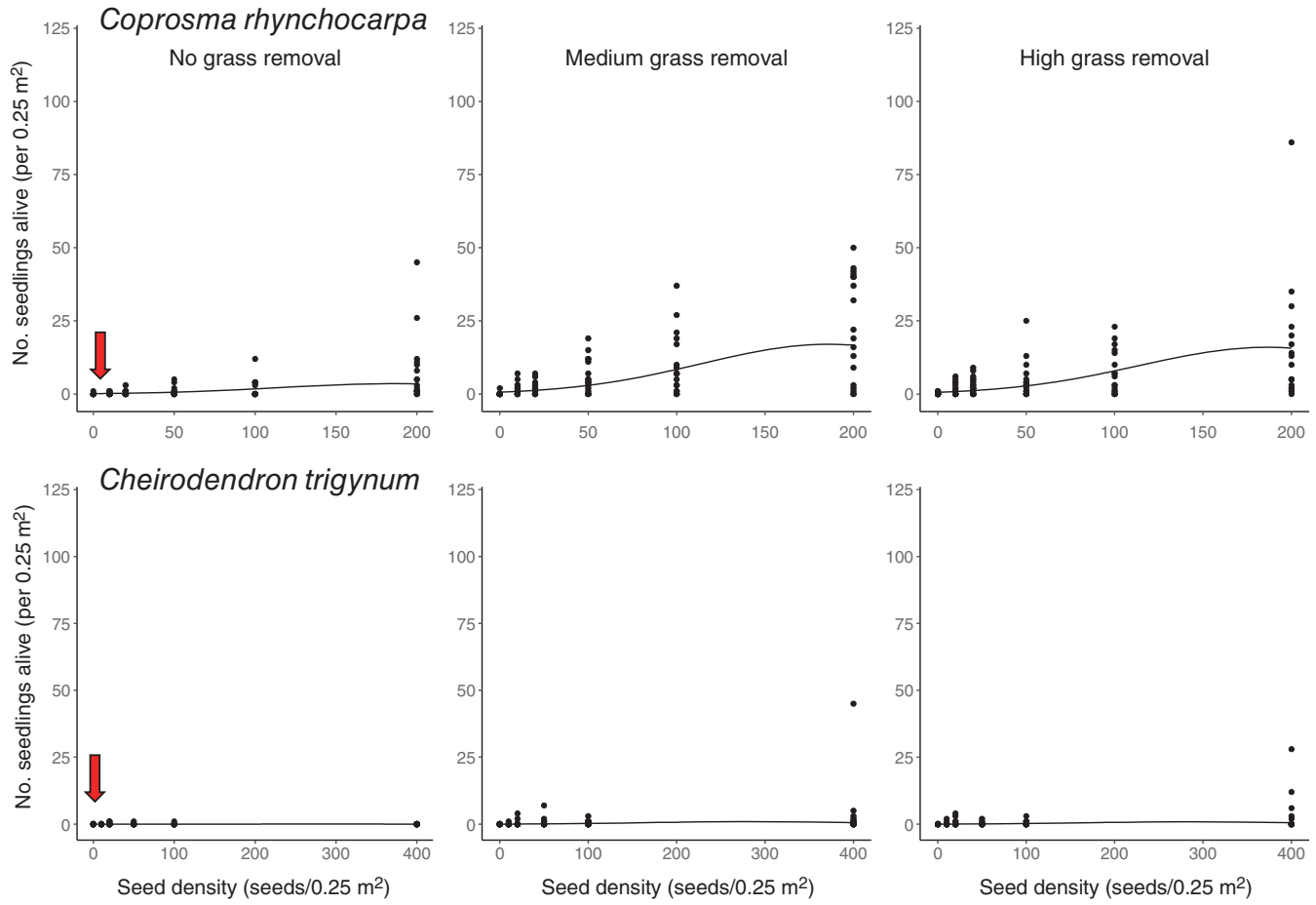

FIGURE 3 Number of seedlings alive at end of study within 0.25-m^2 subplots for each seed species (top: *Coprosma rhynchocarpa*, bottom: *Cheirodendron trigynum*) across grass removal treatments (columns within panels) and seed density (*x*-axis for each subpanel). Points represent plot values, and black line represents predicted relationship with shaded area the 95% CI from the mixed-effect modeling. Arrows in first column show current average total seed rain rate for each species (see Appendix S1: Table S3 for more details).

DISCUSSION

Our study provided evidence that thresholds to passive restoration/succession exist in this ecosystem, but they are not universal across species, cover conditions, or processes. For example, total seed rain (passive + bird-mediated) increased linearly with understory basal area. Hence, there did not appear to be a sudden influx of bird-mediated seed rain in plots with high understory basal area and fruit resources that would have been indicative of a threshold effect. Conversely, we found that seedling establishment exhibited a nonlinear relationship with grass cover, where moderate amounts of grass removal (~50%) resulted in large amounts of seed germination and seedling establishment. We also show that seed germination and seedling establishment exhibited nonlinear relationships with seed density. Still, the seed densities applied here that created a large increase in seed germination and seedling establishment (~50 seeds) were at least 18 times higher than average bird-mediated or total seed rain (passive + bird-mediated) in these restoration forests. As such, our results showed that neither passive nor bird-mediated seed rain was likely to lead to the natural recruitment of understory species unless grass cover is depressed to or below a threshold level. Indeed, reanalysis of survey data showed that grass cover thresholds would need to be below the 50% threshold before seedlings naturally establish.

Grass-mediated thresholds

As tropical forest is cleared and converted to grassland, sites may cross a threshold beyond which the probability of passive recovery is substantially reduced, resulting in persistent grassland domination (Lamb et al., 2005). We show that on the Hawaiian islands, clearing forests for grasslands operates in a similar manner and that recovery back to the natural forested state may only occur when a threshold of lower grass cover is reached. When no grass was removed, few seedlings emerged and/or survived until

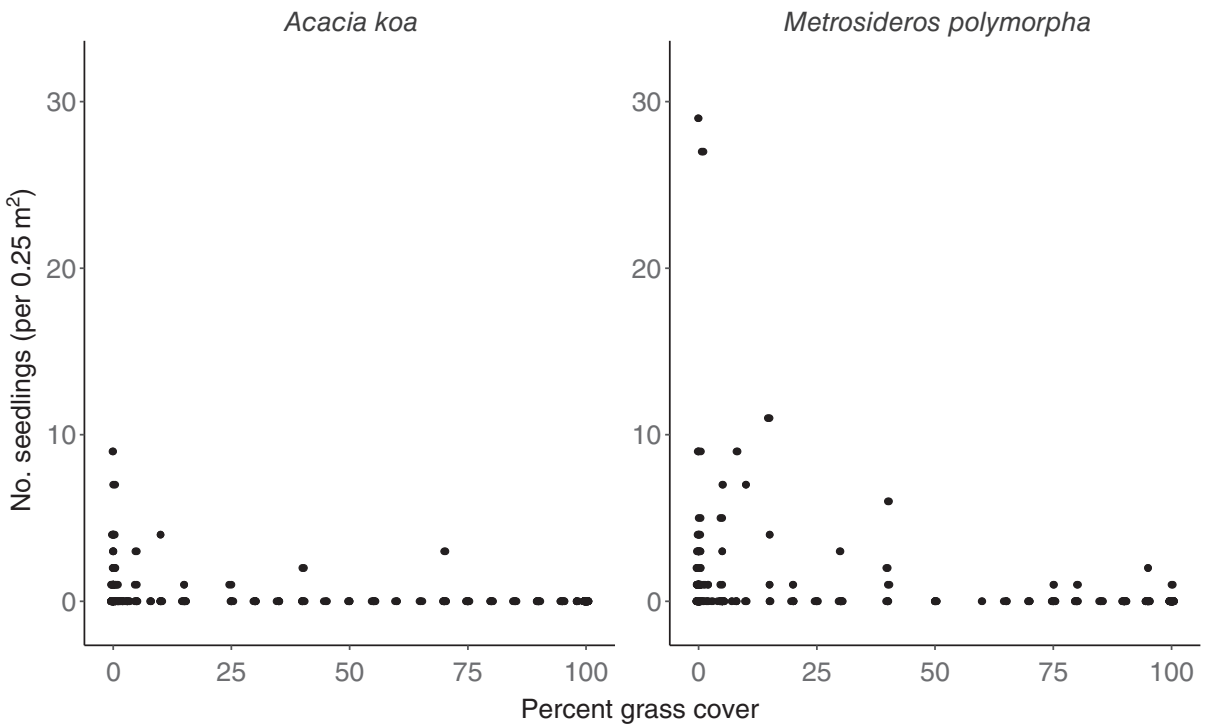

FIGURE 4 Data reanalyzed from Yelenik et al. (2023). The number of fruit-producing seedlings (excluding *Rubus* spp.) against percentage grass cover in ten 0.5-m^2 subplots each in the north and south direction from the base of the tree to 4.5 m from the tree ($n = 20$ subplots at each tree) at 36 trees, 18 *Acacia koa* (koa) and 18 *Metrosideros polymorpha* (ʻōhiʻa) ($n = 720$ plots total) in 2015. Points were jittered to show all points. Model summary can be found in Appendix S1: Table S7 but includes a significant effect of percentage grass cover and overstory species on seedling numbers. After grass percentage cover decreases below ~50%, the number of seedlings increases.

seed was added at levels that simply do not occur in natural or restoration settings. Seedling recruitment roughly doubled or tripled (depending on species) relative to controls once ~50% of grass was removed, yet there were no more gains made by removing all grass cover. Additionally, our analysis of plant survey data from Yelenik, Rose, and Paxton (2022) showed a similar pattern: Few seedlings occurred until grass cover was less than ~50%. Because these data included a continuous range of grass cover, they provided complementary evidence of a threshold effect when grass cover is reduced. While seed availability may limit seedling recruitment in native Hawaiian forest with little invasive grass cover (Inman-Narahari et al., 2013), in the restoration setting, grass cover is a stronger limiting factor than seed rain to native seedling recruitment.

Invasive grasses on the Hawaiian islands have long been shown to be detrimental to native forest regeneration and restoration, across various ecosystem types (Cabin et al., 2002; D'Antonio et al., 1998; Denslow et al., 2006). The main invasive grass in our study site is kikuyu (*C. clandestinus*), which produces very dense rhizome mats. We observed that seeds often germinated while suspended within the kikuyu rhizome mat but not in contact with the soil surface. These germinating seeds mostly did not transition into seedlings. Furthermore, seedling establishment is greatly restricted within the grass, as evidenced by the reanalysis of the data from Yelenik, Rose, and Paxton (2022) and previous work done at our site (Rehm et al., 2019, 2020; Yelenik, Rehm, D'Antonio, & Caldwell, 2021). Similar to seed germination, evidence of grass impacts on seedling survival and growth in tropical pastures is equivocal. Grass can have a negative (Elgar et al., 2014; García-Orth & Martínez-Ramos, 2011; Hooper et al., 2005; Zahawi et al., 2013), positive (Meli & Dirzo, 2013) or no impact (Meli & Dirzo, 2013) on seedling growth and survival. Zahawi et al. (2013) found that seedlings recruited best when woody canopy cover was present and grass cover was ≤25% in their Costa Rican restoration sites. These findings indicate a grass reduction threshold, below which seedling establishment and survival greatly increase. That grass cover reduction threshold may be as little as 50% (as evidenced by our experiment) or above 75% (as evidenced by previous work).

Feedbacks between seed rain, understory, and recruitment

We hypothesized that there would be a strong positive relationship between the basal area of fleshy-fruiting understory

and bird-mediated seed rain due to more birds visiting sites with greater fruit resources. This might lead to a threshold density of fruiting understory beyond which seed rain greatly increases due to attractiveness to birds. However, we did not see a significant relationship between bird-mediated seed rain and understory basal area. The lack of a relationship may be partly due to the fragmented nature of our sites. For example, birds may not move into forest fragments because fragments exist in a matrix of inhospitable open areas, exhibit large edge-to-interior ratios, and can be long distances from each other (Herrera & García, 2010; San-José et al., 2020). Instead, early successional forest fragments may show evidence of seed rain successional feedbacks (Huanca Nuñez et al., 2021), which reinforce local species distributions as seeds move (either passively or by birds) only within their own fragments. The fact that total seed rain (passive + bird-mediated) was positively related to basal area of understory hints at such relationships, and previous work showed that bird-mediated seed rain was correlated to the number and identity of fruiting shrubs within 20 m of seed rain traps (Yelenik, Rose, & Paxton, 2022).

Although experimentally increased seed rain did result in increased seed germination and establishment, it did so only when grass had been removed or at extremely high levels of seed rain not naturally found in this system. Our lowest experimental seed addition amount (10 seeds/0.25 m^2) was an order of magnitude higher than average bird-mediated seed rain for our two target species. This lowest addition seed treatment was also double the passive seed rain rate under trees with the largest amount of fruiting understory plants or over 100 times greater under trees with little to no understory plants. This indicates that neither bird movement into restoration corridors nor planting understory and waiting for passive seed rain is enough by itself to initiate passive restoration/natural regeneration. This finding further highlights the importance of grass-mediated thresholds and establishment limitation being greater than seed-dispersal limitation, unlike in some other mid- to high-elevation tropical systems (e.g., Cierjacks et al., 2007; Holl, 1999; Rehm & Feeley, 2013). Our results are somewhat consistent with findings by Clark et al. (2007), who conducted a meta-analysis of seed addition studies that demonstrated that, although most plant populations are seed limited to some degree, the effect sizes were small enough to suggest that establishment limitation (e.g., competition, herbivory) was often more important in driving recruitment dynamics.

Effects of canopy species

We found both bird-mediated and passively falling seed rain was higher under ʻōhiʻa than koa trees. ʻOmaʻo, the only native seed-dispersing bird in this region and a species that disperses native seeds (Culliney et al., 2012; Yelenik, Rose, & Paxton, 2022), often sing from high perches in remnant ʻōhiʻa as these are the tallest and most visible trees (E. M. Rehm and S. Yelenik, personal observation). Therefore, ʻomaʻo may disperse seeds under ʻōhiʻa even when fruiting understory is not present. How the other nonnative bird species that also disperse seeds (Warbling white-eye and Red-billed Leothrix) use koa and ʻōhiʻa is unclear, but ʻōhiʻa is a prominent nectar source and is associated with distinct yet important insect prey species that may attract these omnivorous birds (Banko et al., 2022). Both species are present in the koa restoration corridors and disperse understory plants that are present at our sites (Culliney et al., 2012; Vizentin-Bugoni et al., 2019; Yelenik, Rose, & Paxton, 2022), with warbling white-eyes having the greatest densities but dispersing few native species (Paxton et al., 2018). Therefore, these nonnative species may be using our study site to forage for insects or nectar or for perching, inadvertently dispersing seeds (native and nonnative) from the nearby forest.

Another possible reason that ʻōhiʻa had higher seed rain under the canopy than koa might be due to a greater prevalence of nearby understory, even if not directly under the canopy of sampled trees. Observationally, ʻōhiʻa tended to have other ʻōhiʻa nearby in the grass matrix, often with at least some understory. Thus, even when a sampled ʻōhiʻa did not have an understory, birds may have deposited seed in our traps while transiting between ʻōhiʻa with understory. In addition, although we attempted to find the highest understory basal area possible under koa, values were lower on average under koa than ʻōhiʻa (Appendix S1: Table S2), with a mean (SD) of 808.5 (1279.1) cm^2 for ʻōhiʻa and 401.2 (465.3) cm^2 for koa, likely equating to lower quantities of fruits and seeds available to disperse. A critical mass of understory basal area may be needed before birds start to frequent an area (Huanca Nuñez et al., 2021), and if so, our data indicate that koa restoration corridors did not get to that critical mass because the understory is still sparse despite outplanting efforts. Meanwhile, ʻōhiʻa trees do reach this critical mass, at least at lower elevations, where birds tend to be abundant (Paxton et al., 2018). Together, these factors may be helping to facilitate pockets of understory under ʻōhiʻa, similar to "fruit islands" in Guam (Kastner et al., 2021) and "fruit orchards" in Sweden (Arnell et al., 2021), in which frugivorous birds help create dense, aggregated patches of fruiting plants.

We found inconclusive impacts of overstory species on seed germination or seedling establishment between the seed addition/grass removal experiment and reanalysis of the Yelenik, Rose, and Paxton (2022) data. Microhabitat

characteristics, such as light, soil nutrients, grass biomass, and bryophyte abundance (McDaniel & Ostertag, 2010; Rehm et al., 2019; Scowcroft et al., 2004; Yelenik, Rose, & Paxton, 2022), seem to favor greater seedling establishment under ʻōhiʻa than koa, which was supported by the Yelenik, Rose, and Paxton (2022) data. Conversely, the lack of a canopy effect in our current seed addition/grass removal study might have been due to our choice of grass removal/seed addition trees, because these were all without understory. Although we did this to better control for seeds entering the system, we also then lost the natural variability between the two canopy trees in factors correlated with seedling recruitment. While microhabitat differences between the species remain in terms of light levels and soil nutrients (Yelenik, Rose, & Paxton, 2022), these were apparently not great enough without added understory to cause a seed germination or seedling survival effect. The Yelenik, Rose, and Paxton (2022) data included more individual trees that may have better captured individual variation in physical structure and consequent microhabitat conditions, leading to a significant impact on naturally occurring seedlings.

The inconclusive findings of overstory trees on seedling recruitment, in combination with the fact that our seed addition experiment showed that seed rain at current rates is not enough to overcome the grass recruitment barrier, suggests that the effects of increasing understory on seedling recruitment are likely due to grass reduction. High understory densities might lower grass biomass by some combination of shading (McDaniel & Ostertag, 2010), smothering of grass with increased litterfall (Yelenik, Rehm, & D'Antonio, 2022), and/or competition for soil nutrients or water. Similar effects of understory have been shown in other forest ecosystems for lowering light at the seedling level (Messier et al., 1998; Wang et al., 2013). In fact, a global review of understory impacts on forest dynamics found that the understory influence on community succession is likely underappreciated (Royo & Carson, 2006).

MANAGEMENT IMPLICATIONS

Understanding the constraints and thresholds that limit natural forest regeneration can help to inform management strategies (Suding et al., 2004). Our work provides evidence that grass cover must be reduced to a certain threshold to facilitate understory regeneration, but it does not need to be eliminated. Grass reduction could be done via herbicide, in concert with either seed scattering or planting of desired species. Manual removal can also lower grass biomass temporarily. Past work from other Hawaiian restoration sites showed that this could lead to faster grass regrowth than herbicide, and results are mixed as to whether it can help facilitate native woody regeneration, particularly in kikuyu grass (McDaniel et al., 2011; Warren et al., 2019). Our work suggests that even an herbicide that only lowered grass cover by half would be effective in promoting seedling recruitment of woody plants in these sites. Caution should be taken that removing 100% of the grass biomass may lead to secondary invasions (D'Antonio et al., 2017; Pearson et al., 2016), as was seen in Australia when nonnative woody encroachment occurred in herbicide plots. Indeed, warbling white-eyes, the most numerous seed dispersers in the koa restoration forests, have a high fraction of the noxious weed *R. argutus* (Florida raspberry) in their diet (Yelenik, Rose, & Paxton, 2022). This suggests that they may facilitate its occurrence if grasses are completely removed.

Planting understory in higher densities than is currently done may help to lower invasive grass biomass via light reduction and thereby increase seed rain over time, without leading to secondary invasions through the use of herbicide that leaves open soil gaps for long periods of time (S. Yelenik, personal observation). This strategy may lead to faster subcanopy closure and naturally reduce grass biomass while increasing seed set in the absence of any herbicide use. Concentrating plantings in smaller nodes that are dispersed across the refuge—a "forest node" or "nucleation" approach (Corbin & Holl., 2012; Zahawi et al., 2013)—would be a way to spread limited plant stock farther across the landscape. In this case, natural regeneration and infilling between planted "woody nodes" in the grass matrix would then be an indicator of success.

AUTHOR CONTRIBUTIONS

Evan M. Rehm, Carla D'Antonio, and Stephanie Yelenik conceived, designed, and executed the study. Evan M. Rehm, Carla D'Antonio, and Stephanie Yelenik wrote the manuscript, and Evan M. Rehm and Stephanie Yelenik conducted the analyses.

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and the U.S. Geological Survey, and in part by the USDA Forest Service Rocky Mountain Research Station. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government. The findings and conclusions in this publication should not be construed to represent any official USDA determination or policy. This publication has been peer-reviewed and approved for publication consistent with U.S. Geological Survey Fundamental Science Practices (http://pubs.usgs.gov/circ/1367/). We acknowledge that our fieldwork took place in the ahupua'a of Honohina, in the moku of Hilo, on the mokupuni of Hawai'i, which are the ancestral and traditional lands of the Native Hawaiian people.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data for this publication are available from the U.S. Geological Survey in Yelenik, Rehm, & D'Antonio (2021) at https://doi.org/10.5066/P9MY5240 and in Yelenik et al. (2023) at https://doi.org/10.5066/P98OUTPW.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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