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RESEARCH ARTICLE

Co-designed Projects in Ecological Research and Practice

Elevation, canopy cover and grass cover structure patterns of seedling establishment in a subtropical post-fire restoration

Christopher Warneke[1] | **Lars A. Brudvig**[1] | **Makani Gregg**[2] | **Sierra McDaniel**[3] | **Stephanie Yelenik**[4]

[1]Department of Plant Biology and Program in Ecology, Evolution, and Behavior, Michigan State University, East Lansing, Michigan, USA

[2]Pacific Cooperative Studies Unit, Hawaiʻi Volcanoes National Park, Resources Management, Division, Hawaiʻi National Park, Hawaii, USA

[3]National Park Service, Hawaiʻi Volcanoes National Park, Resources Management Division, Hawaiʻi National Park, Hawaii, USA

[4]United States Geological Survey, Pacific Island Ecosystems Research Center, Hawaiʻi National Park, Hawaii, USA

Correspondence
Christopher Warneke
Email: crwarneke@gmail.com

Present address
Christopher Warneke, Department of Integrative Biology, University of Wisconsin-Madison, Madison, Wisconsin 53706, USA
Stephanie Yelenik, USDA Forest Service, Rocky Mountain Research Station, Reno, Nevada 89512, USA

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Abstract

1. Ecological restoration is beneficial to ecological communities in this era of large-scale landscape change and ecological disruption. However, restoration outcomes are notoriously variable, which makes fine-scale decision-making challenging. This is true for restoration efforts that follow large fires, which are increasingly common as the climate changes.
2. Post-fire restoration efforts, like tree planting and seeding have shown mixed success, though the causes of the variation in restoration outcomes remain unclear. Abiotic factors such as elevation and fire severity, as well as biotic factors, such as residual canopy cover and abundance of competitive understorey grasses, can vary across a burned area and may all influence the success of restoration efforts to re-establish trees following forest fires.
3. We examined the effect of these factors on the early seedling establishment of a tree species—māmane (*Sophora chrysophylla*)—in a subtropical montane woodland in Hawaiʻi. Following a human-caused wildfire, we sowed seeds of māmane as part of a restoration effort. We co-designed a project to examine māmane seedling establishment.
4. We found that elevation was of overriding importance, structuring total levels of plant establishment, with fewer seedlings establishing at higher elevations. Residual canopy cover was positively correlated with seedling establishment, while cover by invasive, competitive understorey grasses very weakly positively correlated with increased seedling establishment.
5. Our results point to specific factors structuring plant establishment following a large fire and suggest additional targeted restoration actions within this subtropical system. For example, if greater native woody recruitment is a management goal, then actions could include targeted seed placement at lower elevations where establishment is more likely, increased seeding densities at high elevation where recruitment rates are lower, and/or invasive grass removal prior to seeding.

Such actions may result in faster native ecosystem recovery, which is a goal of local land managers.

KEYWORDS
co-designed research, co-production, fire severity, Hawai'i, invasive grass, māmane, seed-based restoration, *Sophora chrysophylla*, translational ecology, wildfire

1 | INTRODUCTION

Large-scale changes in land use and ecosystem disturbance regimes are happening worldwide (Lewis & Maslin, 2015; Steffen et al., 2011). These changes lead to alterations to biodiversity with the associated consequences (Haddad et al., 2015; Pereira et al., 2010). A tool that is used to address the concerns of biodiversity decline is that of ecological restoration (Gann et al., 2019; United Nations, 2020). However, the outcomes of ecological restoration are notoriously unpredictable (Barnard et al., 2019; Brudvig et al., 2017). Understanding the reasons behind the variability of restoration outcomes is critical for moving the field of ecological restoration forward and enabling greater success of restoration actions (Brudvig, 2017).

Variability in restoration outcomes is especially prevalent following wildfire, for example with revegetation efforts via planting or reseeding (Bates et al., 2014; Brudvig et al., 2017; Engel & Abella, 2011). Wildfire, both natural and anthropogenic, is increasing in frequency and scale and is expected to continue increasing worldwide, due partially to the changing climate (Flannigan et al., 2000; Moritz et al., 2012). Fire, especially in ecosystems where it may have historically been infrequent, can change ecosystem composition and function (D'Antonio & Vitousek, 1992). Species diversity is often lost following large fires, which can change community functioning and ecosystem services, including for humans (such as changes to water quality) (D'Antonio et al., 2017; Smith et al., 2011). As a result of these effects on ecological communities and human wellbeing, restoration ecologists commonly attempt large and costly actions to try to mitigate disturbance by fire, often involving revegetation of the burned area via planting and reseeding of native species, and, in forested systems, of trees (Copeland et al., 2018; McDaniel et al., 2008; Peppin et al., 2010; Vallejo & Alloza, 2015). However, these efforts have varied success in terms of the re-establishment of desired vegetation (Bates et al., 2014; Munson et al., 2020). A better understanding of the context dependency underpinning revegetation success could allow restoration practitioners, who often have limited funds, personpower and time, to direct effort to areas more likely to have successful restoration outcomes or develop new techniques for problematic contexts (Brudvig & Catano, 2021; Gann et al., 2019).

One factor that leads to more frequent fire in systems where fire was infrequent historically is that of invasive grasses (D'Antonio et al., 2011; D'Antonio & Vitousek, 1992). These grasses may form self-reinforcing positive feedback loops with fire, in which fire area increases and return interval decreases as a result of increased fuel (provided by the grasses), which then benefits grasses relative to native plant species that may not be as well adapted to fire (Ellsworth et al., 2014; Mahood & Balch, 2019; Smith & Tunison, 1992). This feedback loop may result in species-poor alternative stable states where one of the major components is the cover of invasive grasses (D'Antonio et al., 2011; Hamilton et al., 2021; Smith & Tunison, 1992; Yelenik & D'Antonio, 2013). In addition to altering native biodiversity by changing fire regimes, invasive grasses may directly affect native plants through competition. Grasses are often strong competitors for resources in systems where fire was historically rare but has increased in prevalence since European colonization, as is the case in the upland forests of Hawai'i. In these systems where monoculture-forming grasses were historically absent, invasive grasses can consistently suppress natural regeneration of the native flora, even in the absence of fire (Smith & Tunison, 1992; Yelenik & D'Antonio, 2013). Indeed, past work has shown that invasive pasture grasses in the understorey of forests can create priority effects that stall succession to a more diverse forest system (Rehm et al., 2019; Yelenik, 2017). In sites where fire has occurred, these forests tend to re-establish as species-depauperate systems with a native monotypic canopy and invasive grass understorey (Hamilton et al., 2021; Hughes & Vitousek, 1993). A tool that may work to increase native diversity, lower grass dominance and break grass–fire cycles is that of seed-based restoration, where diverse seeds of native species are sown immediately after a fire (Copeland et al., 2018; McDaniel et al., 2008). Work, both in systems similar those that occur in Hawai'i, as well as more broadly, has shown that while this approach may help with maintenance of biodiversity, it does not always break the grass–fire cycle (McDaniel et al., 2008; Munson et al., 2020).

There are a myriad of interacting factors that may affect the success of restoration via revegetation following a fire, including residual canopy cover, fire severity, abiotic aspects of the soil, invasive plant species responses and others (Bowles et al., 2011; Díaz-Delgado et al., 2003; Kulpa et al., 2012). Factors such as landscape position and fire severity can impact how restoration and revegetation proceeds by affecting, for example, post-fire canopy cover, soil moisture levels, soil hydrophobicity and incident sunlight (Díaz-Delgado et al., 2003; Kulpa et al., 2012). Elevation, especially in topographically diverse systems, can change local habitat characteristics including temperatures, precipitation, vegetation types and thus the ability to restore vegetation via seed addition (Ainsworth & Kauffman, 2010; Bowles et al., 2011; D'Antonio et al., 2000; Davies et al., 2011). Fire severity may affect post-fire restoration outcomes by changing soil aggregate properties, hydrophobicity, organic matter, nutrients and the microbial community (Dooley & Treseder, 2012; Vallejo & Alloza, 2015). Other factors, such as competition with invasive species and residual canopy cover following fire, are likely to change patterns of revegetation in restoration settings and are often heterogeneous across burned landscapes, in part due to variability in fire severity (D'Antonio et al., 2000; Davies et al., 2011). Canopy cover may have positive or negative effects, depending on the system, and may positively correlate with the success of forest interior species but negatively correlate with the success of open-habitat species. Invasive species, such as nonnative grasses, may compete with desired native species in ways that reduce the germination, survival and growth of those native plants and thus negatively impact the resulting restoration outcome (D'Antonio & Vitousek, 1992; Davies et al., 2011; Smith & Tunison, 1992). Thus, many of these factors interact in ways that make predictions of post-fire regeneration and restoration success difficult. To resolve these context dependencies, tests are needed linking plant establishment success following wildfire to specific measured conditions, across numerous locations varying in these conditions.

To better understand the factors that lead to differences in revegetation following wildfire, we used a replicated system of 45 seed addition plots in a recently burned area on the Island of Hawai'i. In this system, fire was historically rare, but has increased due to the presence of a suite of invasive pasture grasses and increased anthropogenic ignition events. In the upland forests of Hawai'i, restoration action seeks to maintain and re-establish native, fire-tolerant vegetation following fire, while creating resistance to introduced species, with a particular focus on invasive grasses, and resilience to fire (McDaniel et al., 2008). However, restorations in these systems are not always successful. We co-designed a project between academic restoration ecologists and land manager restoration ecologists to together investigate a suite of factors that are hypothesized to affect restoration success to determine which were the most important in structuring the early plant establishment in field conditions. The measure of success that we focused on was seedling establishment, owing to the critical importance of this demographic event for subsequent vegetation re-establishment. Our question was: How do biotic factors (e.g. canopy cover, grass abundance) and abiotic factors (e.g. elevation, fire severity) affect seedling establishment across the landscape? We predicted highest rates of establishment when: (1) Canopy cover was high, reflecting the naturally forested state of our focal system, (2) invasive grass abundance was low, due to competitive effects of grasses, (3) elevation was high, mirroring the natural distribution of our focal species along the elevational gradient and (4) fire severity was low, owing to natural rarity of fire in our focal system.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted this study within Hawai'i Volcanoes National Park (HAVO) on the Island of Hawai'i, Hawai'i. An accidentally human-ignited fire took place in August 2018 and burned approximately 1500 hectares of land, mostly within the national park (on the southeast flank of Mauna Loa; Figure 1; Theune, 2018; West Hawaii Today Staff, 2018). This area contains mostly native upland forest and is dominated at lower elevations by koa (*Acacia koa* A. Gray), and at higher elevations by māmane (*Sophora chrysophylla* (Salisb.) Seem.)

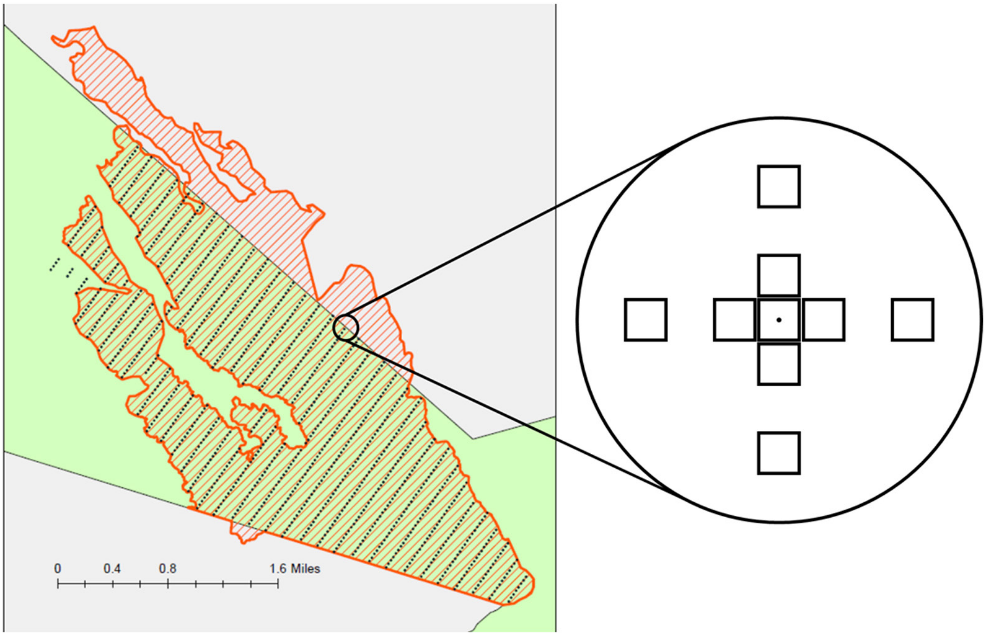

FIGURE 1 Plot and quadrat diagram. The black point in the circular plot represents the plot centre, with the quadrats arrayed from there. Quadrats are 1 m^2 and are to scale, within the circular plot (5 m radius). The red irregularly shaped polygon represents the burned area and the black points are the planned 1180 plots (spaced 50 m apart on each transect, which are themselves 200 m apart) designated for seeding by the Natural Resources Management team.

and ʻaʻaliʻi (*Dodonaea viscosa* (L.) Jacq.), with koa being less abundant. The study site is located on a mountain slope, in which elevation correlates with climate, with lower elevations being relatively warmer and wetter than higher elevations. The fire resulted in large-scale mortality of trees and understorey plants, as is typical in fires in this system (Ainsworth & Kauffman, 2010). The heavy mortality of native species, in conjunction with the abundance of invasive grasses, led the National Park Service to engage in a restoration effort to re-establish the native plant community, with goals of promoting more fire-tolerant native species, which in turn might help reduce the abundance of invasive grasses (McDaniel et al., 2008). The most problematic invasive grasses in our study plots were *Microlaena stipoides* (Labill.) R. Br. (meadow ricegrass, a rhizomatous perennial present in 90% of plots) and *Paspalum dilatatum* Poir. (dallis grass, a clump-forming perennial present in 40% of plots). The mat-forming perennial *Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone (kikuyu grass) is a major threat in these habitats but was largely absent from our sampled plots (present only in 9% of plots). These invasive grasses are known to be detrimental to forest recovery (McDaniel et al., 2008; Yelenik, 2017).

2.2 | Seed sowing

Between November 2018 and March 2019, within the burned area, members of the HAVO Natural Resources Management team and from the University of Hawaiʻi Mānoa, Pacific Cooperative Studies Unit seeded ~700 plots (of a planned 1180 plots) with seeds of native species, including māmane, to promote forest regrowth (Figure 1). Our research team consisted of members of the Natural Resources Management team as well as governmental and academic restoration ecologists that have worked together to study the outcomes of this restoration effort with a goal of improving future restoration efforts. The species that were seeded (including māmane; see Supporting Information for complete list) were chosen as a part of an overarching management effort to shift the community composition in these habitats to native species that are fire tolerant, focusing on native species that have some resilience to fire via resprouting and/or having seeds that can withstand fire (Loh et al., 2009). We report results for māmane here because it was the only species sown in all plots across all elevations; additionally, on the timespan of this project, māmane had relatively high establishment, allowing for more statistically rigorous comparisons than if we were to use any other species. Seeded plots were circular (5 m radius) and located 50 m apart along transects, with transects being 200 m apart, from 1340 to 1710 m a.s.l. in elevation. Likely because of the variability in intensity within the burn area, grass cover varied from zero grass cover in high-intensity burn areas to essentially full cover in low-intensity burn areas. Because of this variation in burn intensity and grass cover, plots with >50% cover of invasive grasses were not selected for restoration, nor for our work here, as high grass covers are expected to decrease native species establishment (i.e. they would require additional forms of management before sowing could take place, and resources did not allow for that). Although this restriction of plot selection to plots with <50% grass cover does influence our capacity for inference in high grass plots, such plots are expected to have poor native seedling survival (Yelenik, 2017). In preparation for seeding, plots were raked to disturb the soil surface. Seeds were sown along raking lines within the plot and loosely covered with soil. Māmane was seeded at a rate of 49.2 g/plot, which is approximately 730 seeds/plot or roughly 9.3 seeds/m^2 (see the Table S1 for calculation of seeding rate).

Predation of māmane seeds is exceedingly unlikely once seeds have been sown. Māmane seeds contain quinolizidine alkaloids that are toxic to vertebrates and may deter insects that lack adaptations to these compounds (Banko et al., 2002). At least one introduced potential seed predator insect was unable to complete its lifecycle on māmane seed (Medeiros et al., 2008). Additionally, the native seed predators the Palila (*Loxioides bailleui* Oustalet, 1877; an endemic bird species, which does not occur in our study area; Hess et al., 2014) and several Hawaiian endemic moths in the genus *Cydia* Hübner, 1825, all prey on seeds pre-dispersal, and do not consume seeds after dispersal has occurred (Brenner et al., 2002; Hess et al., 2014). Depending on elevation, a subset of the māmane seeds were scarified prior to seeding to increase the rate and evenness of germination. In plots below 1500 m a.s.l., where fast-growing invasive grasses are more prevalent, all māmane seeds were scarified to facilitate māmane germination in the short, post-fire, grass-free window. In plots at higher elevations, where invasive grasses are less abundant, half of the māmane seeds were scarified and the other half were not to increase the length of time over which māmane might germinate, a practice similar to that seen in other systems that allows for bet-hedging of germination and establishment success by spreading germination over multiple years (Madsen et al., 2016). For our analyses, we corrected for these differences in the amount of scarified seeds, as described in the *Analysis* section, below. Scarification, when done, occurred in a solution of 100% sulfuric acid for 1 h, and seeds were then rinsed to remove the acid solution (Scowcroft, 1978).

2.3 | Data collection

In late October to early November 2019 (7–11 months following seeding and 14–15 months after fire), we randomly selected 15 plots, within each of the three elevational bands ($n = 45$ total plots; Table S2). The fire burned land across a range of elevations from 1170 to 1710 m a.s.l. The three elevational bands were low elevation (1338–1400 m a.s.l.), middle elevation (1427–1487 m a.s.l.) and upper elevation (1578–1652 m a.s.l.). The elevational bands were chosen to capture the breadth of elevational change that was present in the burned area.

Within each plot, we used a subsample of nine 1 m × 1 m quadrats (Figure 1). Within each quadrat, we recorded the number of māmane seedlings, grass abundance (as a per cent cover) and the per cent cover of bare soil (a proxy for microsite availability). The cover of grass and of bare soil was recorded to the nearest whole per cent for values greater than 1%, to the nearest 0.1% for values between 0.1 and 1% and to the nearest 0.01 for values between 0 and 0.1%.

Additionally, at the level of each plot, we took data on canopy cover (taken in June/July 2019) and fire severity. We measured canopy cover using densiometers (Robert E. Lemmon Forest Densiometers, Rapid City, South Dakota). For each plot, we took four readings (one for each of the cardinal directions) and summed them to obtain a reading for the plot. Each reading consisted of a count of the number of vertices of the densiometer that were covered by the canopy, and followed the subsetting methods of Strickler (1959). We measured fire severity using char height (USDI National Park Service, 2003; Van Wagner, 1973), which is the estimated average height, in metres, that char is left on the trees in or immediately adjacent to the plot. We realize that fire severity is a complex variable to measure and that other proxies for this measure exist (Keeley, 2009); however, this measure adequately provided reliable estimates of the relative differences in fire severity across plots and is, thus, the measure we used (USDI National Park Service, 2003).

2.4 | Analysis

We ran two generalized linear mixed effects models; in both of these, the response was the number of seedlings, and the fixed effects were canopy cover, grass cover, bare ground, fire severity and elevation, and the random effect was plot. In early model selection, we had run all the pairwise interactions with elevation, but when these interactions were included, only elevation was significant. We therefore decided to remove the nonsignificant interaction terms, focusing only on main effects. We modelled seedling count following a negative binomial distribution, as is typical for overdispersed count data using the lme4 package, version 1.1–23 (Bates et al., 2015). Because only half of māmane seeds that were sown in the upper elevation band were scarified and it is unlikely that any non-scarified seeds germinated on the timescale of this project (Scowcroft, 1981), we halved the number of seedlings in the lower and middle elevation bands, to enable comparability between the elevational bands. The difference between the two models was that in one, elevation was categorical (as originally collected) and in the other, elevation was continuous. The overall results were qualitatively the same between the models, in terms of which variables were significant and the direction of the effect, and so we present the results of the model using continuous elevation, below. We checked all models for collinearity using the function check_collinearity within the performance package, version 0.4.5 (Lüdecke et al., 2020). Collinearity was not a problem in our models (all variance inflation factors <2.6).

To see how our predictor variables varied across elevation, we also ran generalized linear models with elevation (continuous, in m a.s.l.) as a predictor and each of canopy cover, bare ground, grass cover and fire severity as response variables. We ran each of these models at the level of the plot ($n = 45$), with no random effects. We ran all four of these models following a gamma distribution, with a negligible offset of 1×10^{-14}, so that there were not zeros in the data. Additionally, we calculated Pearson's r for each of these four relationships, using the data at the plot level for canopy cover and fire severity and the data at the quadrat level for grass cover and bare ground.

All analyses were performed in R, version 3.6.3 (R Core Team, 2021) through the interface of RStudio version 1.2.5033 (RStudio, 2021).

3 | RESULTS

Elevation was significantly negatively correlated with recruitment ($p = 0.0035$; Pearson's $r = -0.217$), indicating fewer seedlings at higher elevations (Figure 2). Recruitment was also structured by canopy cover, which positively correlated with the number of seedlings ($p = 0.0062$; Pearson's $r = 0.214$; Figure 2) and grass cover, which counterintuitively showed a positive correlation between grass cover and the number of seedlings ($p = 0.038$; Pearson's $r = 0.005$; Figure 2). Bare ground did not affect the number of seedlings ($p = 0.51$) nor did fire severity ($p = 0.31$).

Canopy cover ($p < 0.0001$; Pearson's $r = -0.63$) and grass cover ($p < 0.0001$; Pearson's $r = -0.46$) decreased with elevation. Char height, our measure of fire severity, increased with elevation ($p < 0.0001$, Pearson's $r = 0.49$). There was no relationship between bare ground and elevation ($p = 0.35$, Pearson's $r = 0.098$; Figure 3).

4 | DISCUSSION

Following a large-scale post-wildfire restoration seeding, elevation was a critical factor behind patterns of seedling establishment, with fewer seedlings at higher elevations. We additionally found that seedling establishment increased with canopy cover and, unexpectedly, with invasive grass cover, with these variables and our measure of fire severity related to elevation. These relationships between elevation on other factors that influence plant recruitment may necessitate different restoration actions at different elevations (Davies et al., 2011; Yelenik & D'Antonio, 2013).

Elevation was a structuring factor in our study, both for seedling establishment as well as other environmental variables, some of which were also important for seedling establishment. In montane systems, such as ours, elevation is of overriding importance in structuring plant communities and their dynamics (Ainsworth & Kauffman, 2010). Elevation additionally influences other biotic and abiotic factors that affect seedling establishment patterns because it covaries with a host of factors, including precipitation, temperature, plant competitive interactions and others (D'Antonio et al., 2000; Davies et al., 2011). In our study, elevation also structured canopy tree species composition, with lower elevation plots with a relatively higher abundance of koa and higher elevation plots with a relatively higher abundance of māmane and ʻaʻaliʻi. It is possible that these differences in the relative composition of the tree canopy may help to explain part of our

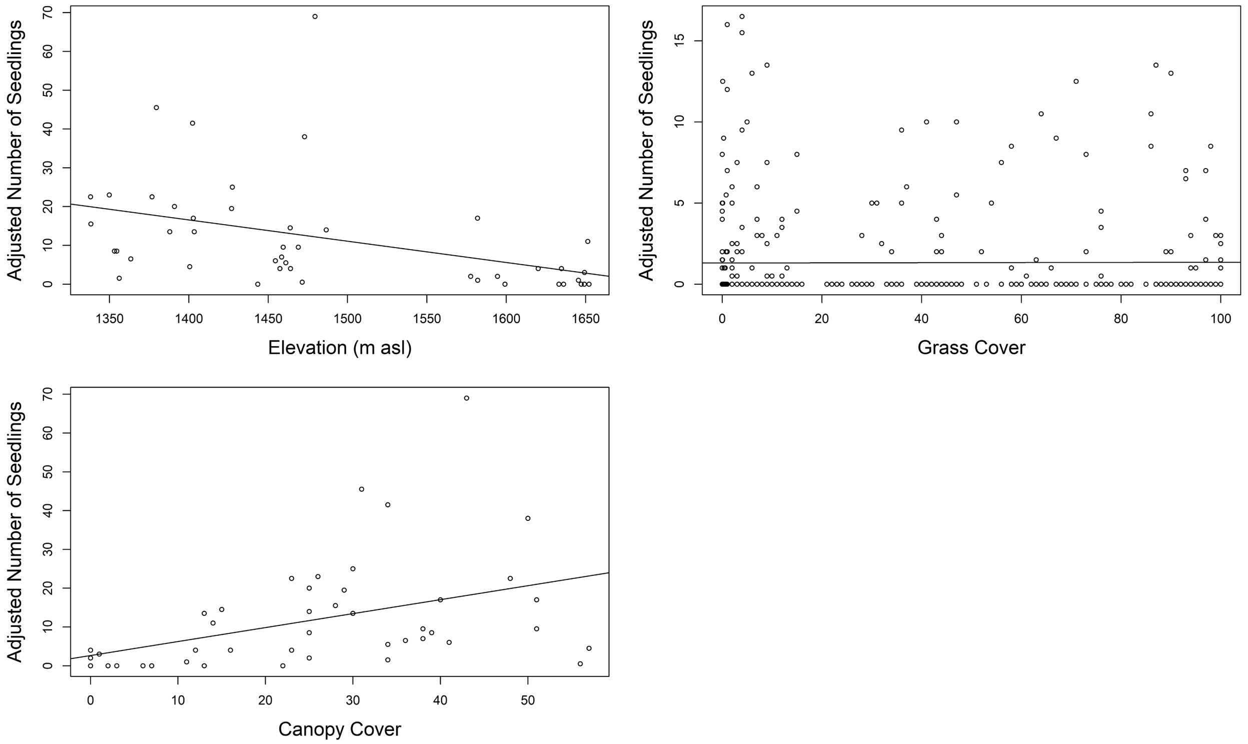

FIGURE 2 The relationship between the number of māmane seedlings and elevation, canopy cover and grass cover. The data shown here are the adjusted number of seedlings, obtained by halving the number of seedlings at the two lower elevational bands. The data presented here for elevation and canopy cover are sums of the number of seedlings at the plot level ($n=45$), while grass cover is at the quadrat level ($n=405$). The trendlines are for visual comparison only.

elevation finding, independent of other factors related to elevation and/or canopy cover, although the mechanism(s) for such an effect remain unclear. Koa supports denser canopies, though these differences are accounted for by our canopy cover data. Both species are nitrogen fixing, though koa has higher growth rates overall. A recent study illustrated greater māmane performance in soils originating from under conspecific trees (Warneke et al., 2023)—a finding not congruent with our results, where māmane recruited at higher rates at lower elevations where koa is more dominant. Although other potential mechanisms exist, it is also possible that both canopy tree composition and māmane recruitment are structured by similar underlying elevational factors, such as moisture and temperature regimes.

Cover by invasive grasses affected plant establishment, where higher grass cover was weakly, but significantly correlated with number of seedlings (Pearson's $r=0.005$). Grass cover is known to be a major negative driver of restoration success in similar Hawaiian systems (Yelenik, 2017), so the very weak positive correlation was unexpected. There may be several reasons for this pattern. First, grass cover could be interacting with other factors, some of which we did not measure, to influence seedling establishment (Ainsworth & Kauffman, 2010; D'Antonio et al., 2000). The National Park Service uses vegetation consumed as a metric of fire intensity and it is possible that high-intensity fire (and thus low grass cover) led to, for example, hydrophobic soils (Certini, 2005), or to low canopy cover that hindered seed germination and survival via mechanisms outlined below (Dobrowski et al., 2015; Rodman et al., 2020). It is also possible that higher moisture availability at lower elevations (Giambelluca et al., 2013) facilitates establishment of both māmane and of invasive grass, which may result in patterns similar to those that we observed (i.e. higher grass cover and seedling recruitment). Another reason could be a temporal delay (Crouzeilles et al., 2016; Matthews & Spyreas, 2010). We collected our data 7–11 months following seeding and 14–15 months after the fire. It is possible that seedling establishment on this timescale is less structured by grasses, which only achieved a maximum of 60% cover at the time of sampling, which is fairly low for this productive system. A negative effect of grass cover may become more clear over time (Grman et al., 2020; Stricker et al., 2015; Yelenik & D'Antonio, 2013), especially given recent findings pointing to threshold effects of invasive grasses on native woody seedlings in Hawai'i (Rehm et al., 2023). Given the nitrogen-fixing status of māmane, it is unlikely that this species alone would lower grass biomass via competitive interactions, especially given its known facilitative effects on invasive species (August-Schmidt et al., 2015). If the positive relationships between grass cover and seeded plant establishment persist, breaking the grass–fire cycle with seed-based restoration alone is likely to be challenging, and may not be possible under some circumstances.

Additionally, we found evidence that establishment increased with higher canopy cover. This may be due to a facilitative relationship, as occurs in moderately to strongly harsh environments (Callaway et al., 2002; Holmgren & Scheffer, 2010; Yelenik et al., 2015). Specifically, canopy trees may have fostered seedling survival by shading seedlings from harsh sun, lowering soil

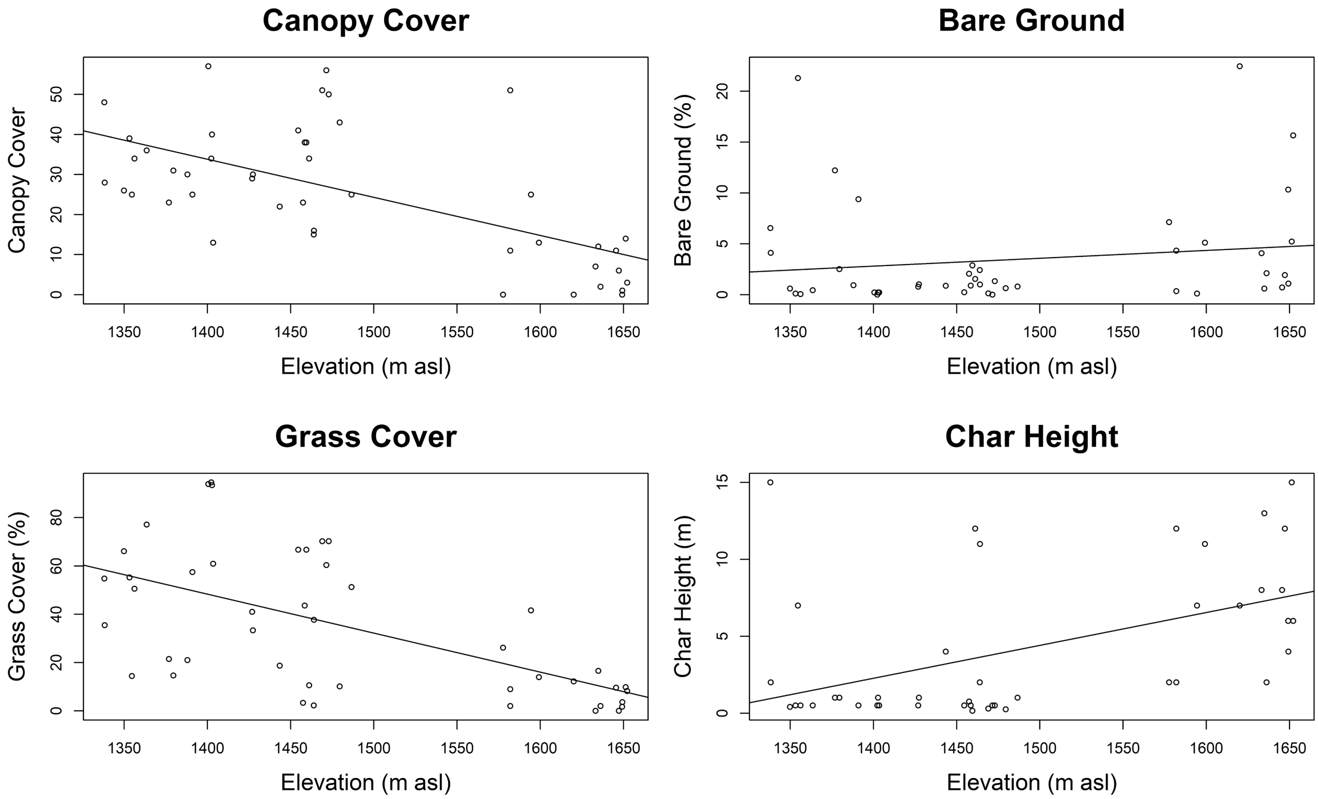

FIGURE 3 The relationships between elevation and each of canopy cover, bare ground, grass cover and fire severity (as measured through char height). All relationships are statistically significant, except for bare ground.

evaporation and/or through the addition of soil organic matter and nutrients (e.g. Dobrowski et al., 2015; Rodman et al., 2020). These potential facilitative interactions may be more consequential than grass competition within these abiotically harsh post-fire areas (Badano et al., 2015). Using effective proxies for plant establishment success may help managers make resource-saving decisions by focusing effort in locations where success may be higher. In abiotically harsher systems, such as our upper elevation plots, using the presence of living canopy trees as a guide may be helpful (Gómez-Aparicio et al., 2004). Determining these, and similar, factors will require knowledge of the system and is an argument for an adaptive management approach, where further management actions are determined based on the results of earlier actions.

The seed-sowing strategies employed in the setup of our study plots likely influenced our findings in some ways. The scarification of only half of the māmane seeds in the upper elevation band resulted in our need to recalibrate our data in order to effectively compare the elevations. However, after recalibrating the data, we found the same results, which is to say that elevation was still a significant factor in structuring seedling establishment patterns. This shows that, even after adjusting for the number of seeds sown, fewer māmane establish at higher elevations, relative to lower elevations. This difference may be indicative of the local environment being harsher at upper elevations, thus the choice to scarify only half of the seeds as a bet-hedging technique for the harsh environment is likely an effective method for ensuring restoration success in these areas (Madsen et al., 2016). Additionally, the sowing of seeds in the raking lines, rather than uniformly, which was done to expedite plot preparation and allow more plots to be seeded in less time, resulted in a clustered pattern of seedlings. This clumped pattern of the seedlings may have made our results more variable (because seedlings not located within our sampled quadrats were not counted), and thus our ability to determine the driving factors of plant establishment more challenging. Such clustering may also have long-term effects on seedling survival due to potentially increased microscale intraspecific competition within clusters (Murrell, 2009). Alternatively, there is evidence that māmane seedlings perform best in soil that has been conditioned by conspecifics (Warneke et al., 2023), and this may thus facilitate seedling success. Lastly, the selection of plots with <50% grass cover for restoration restricted our ability to examine the effects on seedling establishment in plots with very high grass covers. It is possible that the expected effects of grass cover may be observed at a given threshold of grass cover, and we were simply unable to determine this due to the sowing of seeds only in plots with <50% grass cover at the project outset.

4.1 | The importance of co-design and co-production

Our work clearly demonstrates the utility of collaboration and co-production between ecologists working in natural resource management and ecologists working in academia and governmental agencies. By having discussions and co-designing this experiment from the beginning, our team was able to produce data and address questions of interest to both natural resource management and basic ecology (Funk et al., 2020; Gornish et al., 2021). These questions could not have been addressed without involvement from all parties. This was only possible because of a close and maintained working relationship between HAVO, the Pacific Cooperative Studies Unit and the USGS Pacific Island Ecosystems Research Center (PIERC). Within weeks of the fire, HAVO Natural Resources staff reached out to PIERC staff and instigated a field trip to discuss the fire incident, planned fire effects sampling and potential restoration efforts. Due to past research (Loh et al., 2007, 2009), HAVO was already prepared with in-house seed collections of desired post-fire restoration species for reseeding and planting efforts. Once HAVO secured BAER (Burned Area Emergency Response) funds for restoration work, HAVO staff relayed plans to PIERC staff and both parties worked to change certain project designs to ask specific management questions. The project we report here arose from these and related conversations. HAVO also provided PIERC with plants, and teams exchanged work days to accomplish both experimental and management goals. In other words, the relationship provided place-based knowledge and knowledge sharing, capacity and in-kind support that otherwise would not have occurred.

The close relationship between these agencies with different missions enables and has enabled effective co-production of research that is mutually beneficial to all parties involved (Hallett et al., 2017; Lawson et al., 2017; Norström et al., 2020). The success of this particular relationship has resulted in both on-the-ground management and useful publications (e.g. Gill et al., 2018; Hamilton et al., 2021; Warneke et al., 2023; Yelenik et al., 2020). Furthermore, the partnership between government scientists and academic scientists, in our case through the INTERN program of the National Science Foundation (NSF), provided both critical funding and personpower. Training the next generation of ecological scientists in the importance of co-produced work is an integral component of ensuring the production of useful, robust, applied science (Brunson & Baker, 2016; Schwartz et al., 2017) and is often unavailable in traditional academic degree programs. The NSF INTERN, NSF Graduate Research Internship Program (GRIP) and the Joint Fire Science Program's Graduate Research Innovation (GRIN) programs have allowed trainee graduate students to form working relationships and network with government partners and gain experience and skills in co-production. This experience benefits the trainees, the agencies and helps build capacity in the field (Schwartz et al., 2017). Co-produced work, like that demonstrated here, also helps to stretch the often-limited funds associated with restoration activities to help achieve the goals of all parties. Furthermore, by working closely together, ecologists with a focus on resource management and those with an academic focus can both rapidly disseminate information that can be mutually beneficial to each other's respective missions (Lawson et al., 2017).

5 | CONCLUSIONS

Our results offer several recommendations for restoration practice. Due to the positive relationship with canopy cover that we observe, it may be beneficial to plant under canopy cover, when possible, in this system. Additionally, increasing the seeding rate at higher elevations may help to increase the number of surviving seedlings at those elevations, given the generally lower seedling success at higher elevations. Furthermore, despite the weak correlation found in this study, removing grass when feasible and seeding into areas with lower grass cover may increase the number of established seedlings over time. This is due to the known dynamics of grass cover on long-term restoration success in this system (Yelenik, 2017). Further monitoring of these plots in the future could help to evaluate the importance of grass reductions at this study site.

Our results help to resolve context dependencies in plant re-establishment during post-fire restoration, illustrating roles of elevation, canopy cover and invasive grass abundance. This work furthers understanding of how biotic and abiotic pressures influence restoration outcomes, an area of active inquiry (Ainsworth & Kauffman, 2010; Davies et al., 2011; Munson et al., 2011). The diversity of factors that influence restoration outcomes continues to be a challenge for the field of restoration ecology and is a major barrier in helping ecological restoration to fulfil its aims in service to humanity and the world (Brudvig, 2017). Our results here help address this challenge by clarifying the nuanced relationships between the drivers of early seedling establishment success in a post-fire restoration setting. In turn, these findings point to specific locations where restoration efforts are likely to be most successful and suggests the need for additional restoration interventions in other locations.

AUTHOR CONTRIBUTIONS

Sierra McDaniel and Makani Gregg secured post-fire restoration funding, selected target species, collected seeds, designed seed plot distribution and implemented seed additions. All authors contributed to the study design. Christopher Warneke collected data, did analyses and wrote the initial draft of the manuscript. All authors critiqued and revised the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data not found in the Supplementary Material can be accessed at https://doi.org/10.5066/P9FEN91Q (Yelenik & Warneke, 2023).

ORCID

Christopher Warneke https://orcid.org/0000-0003-2530-4273
Lars A. Brudvig https://orcid.org/0000-0002-3857-2165
Stephanie Yelenik https://orcid.org/0000-0002-9011-0769

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SUPPORTING INFORMATION

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

Table S1. Seed weight table.

Table S2. Coordinates and elevation for our 45 study plots. The elevation for each plot was determined using the Bulk Point Query tool at the United States Geological Survey's The National Map project (USGS, 2019).

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