Article

Understanding Grass Invasion, Fire Severity, and *Acacia koa* Regeneration for Forest Restoration in Hawai'i Volcanoes National Park

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Abstract: With invasive grasses increasing wildfire occurrence worldwide, a better understanding of the relationships between native plants, fire, and invasive grass is needed to help restoration plans facilitate ecosystem resilience. Invasive grasses are particularly problematic for altering fire regimes in the tropics, yet in Hawai'i, restoration sites are often planted with monocultures of the native tree *Acacia koa*, which can promote grass growth via nitrogen fixation. This, combined with the difficulty of estimating pre-fire grass cover under thick canopies, complicates attempts to restore Hawaiian ecosystems. We studied the 2018 Keauhou Ranch Fire in Hawai'i to investigate three questions: (1) at what level of precision can pre-fire grass cover be accurately estimated from oblique aerial photos? (2) how are post-fire *A. koa* regeneration densities affected by fire severity? and (3) how are post-fire *A. koa* regeneration densities affected by pre-fire grass cover and its interaction with fire severity? We collected burn severity and post-fire regeneration data from 30 transects stratified across mid-elevation woodland, montane woodland, and montane shrubland communities. We evaluated visual estimates of pre-fire grass cover from oblique aerial imagery with quantitative in situ data from 60 unburned transects of the same cover types. Pre-fire estimates of grass cover categories were 67% accurate in montane woodland (*n* = 9) and 100% accurate in montane shrubland (*n* = 11), but only 20% accurate in mid-elevation woodland (*n* = 10). In montane woodlands with low pre-fire tree densities, *A. koa* regeneration densities were higher with increased fire severity, but this trend reversed when pre-fire tree densities were high. We detected no effect of pre-fire grass cover, nor its interaction with fire severity, on *A. koa* regeneration density. This indicates that restoration through the planting of *A. koa* may be successful in promoting fire-resilient *A. koa* forest, although there are potential issues to consider regarding the effects that *A. koa*'s grass promotion may have on other species within the ecosystem.

Keywords: fire; *Acacia koa*; *Ehrharta stipoides*; *Setaria parviflora*; *Cenchrus clandestinus*; *Andropogon glomeratus*; invasive; Hawai'i

1. Introduction

The potential for wildfire ignition "based on flammability and exposure to ignition vectors" [1] has been increasing in fire-prone regions globally throughout the past century [2], and the world is seeing larger, more frequent wildfires as a result [3], necessitating restoration plans that incorporate fire resiliency. There are multiple causes of the global increase in wildfires, including climate change [4], changes in land use patterns [1,5], and shifting fuel dynamics within ecosystems, which occur when an ecosystem's vegetation changes in a way that affects its fire potential [6]. Shifts in fuel dynamics may be precipitated seasonally with senescence or over multiple years via structural changes as vegetation

ages [7,8]. Shifts can also be caused by human alterations of an ecosystem's structure such as logging, development, fire suppression [1,9–11], or when an ecosystem is invaded by a plant species such as non-native, invasive grasses [6,12,13].

Invasive grasses can disrupt soil nutrient dynamics [14,15], plant water dynamics [16], and soil carbon cycling [17]. Many are suited to post-disturbance environments and propagate easily after wildfire, and some of the most successful invasive grasses have seeds that are stimulated to germinate after exposure to heat and smoke [18,19]. Additionally, many invasive grasses tend to have low moisture levels and high fuel biomass and flammability [6,12,13]. Invasive species that are fire-tolerant can crowd out native species that are slower to establish in a post-fire landscape, creating a positive feedback loop in which an increase in the abundance of invasive species leads to more frequent wildfire, which in turn leads to a further increase in the abundance of invasive species [20]. Such positive feedback increases the resilience of the ecosystem's invaded state [21], and makes the restoration of diverse, native landscapes without invasive grasses difficult [22,23].

The Hawaiian Islands offer an example of this phenomenon, as native forests there are being encroached upon by highly flammable invasive grasses such as *Ehrharta stipoides* (meadow ricegrass), *Megathyrsus maximus* (Guinea grass), and *Andropogon glomeratus* (bushy bluestem) [12,24,25]. These grasses were introduced to the Hawaiian Islands to provide forage for cattle and quickly began to reproduce, becoming widespread by the 1960s [24,26]. In the absence of grass invasion, Hawaiian forests and woodlands have historically had subcanopies dominated by ferns, shrubs, and sub-trees, with little to no native grass present [24,26]. Because invading grasses change the fuel composition of Hawaiian forests, propagate quickly in burned areas, and prevent the reestablishment of less flammable native species, they increase fire potential and have led to wildfires that are more frequent and intense than historical fire patterns [24,25].

Paleontological evidence indicates that pre-settlement Hawaiʻi experienced occasional wildfires caused by volcanic activity and lightning strikes [27]. While there is some debate over the degree to which Polynesian settlers used fire to alter landscapes in Hawaiʻi [28], sedimentological evidence does indicate that their arrival caused a significant increase in fire frequency [27,29,30]. Early Hawaiians employed fire as a tool to increase the abundance of *Heteropogon contortus* (pili grass), which they used for thatching [30]. European colonization further increased fire frequency as agriculture expanded and non-native grasses were introduced for cattle forage [27,30]. From 1904 to 1959, the total area burned per year statewide increased over fourfold, and it is experiencing unprecedented highs in the present day [31]. From 2005 to 2011, there were on average 1007 fires per year across all the islands, burning an average of 8427 ha per year [31]. Because many native plant species in Hawaiʻi are vulnerable to the effects of frequent [32] or intense [30] fire, the shifting Hawaiian wildfire regime has contributed to their decline, which in turn has negatively affected wildlife habitat quality and ecosystem function [30].

Efforts to re-establish native species composition in grass-invaded sites in Hawaiʻi often include planting or otherwise facilitating the native koa tree *Acacia koa*, which can reduce grass cover through shading [33,34]. *A. koa* is considered a good candidate for restoration of Hawaiian forests because it has high survival rates, grows quickly relative to other native canopy dominant trees, and holds economic, ecological, and cultural value [33,35]. Additionally, in the absence of invasive grass, *A. koa* quickly regenerates after disturbance, including fire, through resprouting and seedling establishment [36].

However, the overrepresentation of *A. koa* at restoration sites may have negative ecological consequences. *A. koa* is a nitrogen fixer, which leads to localized increase in invasive grass under its canopy relative to under the canopies of common non-fixing native trees such as *Metrosideros polymorpha* (ʻōhiʻa) [37]. This increased grass cover hinders the development of native understories, particularly in *A. koa* monocultures [37]. Because the National Park Service (NPS) and other management organizations aim to restore biodiversity in Hawaiʻi, suppression of native understory may be counterproductive, and restoration alternatives to *A. koa* are being considered. Additionally, as invasive grass cover

expands, grass-fueled fires will become more frequent and more likely to diminish *A. koa* seed banks, because frequent fires can prevent *A. koa* stands from reaching seeding age before being burned [36], a phenomenon referred to as immaturity risk [38]. It is unknown how a higher frequency of grass-fueled fires may affect post-fire *A. koa* establishment in areas with increasing grass cover. Increased grass cover may suppress post-fire regeneration of *A. koa* due to competition for resources other than nitrogen [39].

If grass cover negatively affects post-fire *A. koa* regeneration, *A. koa*'s grass facilitation could be highly problematic for the long-term success of *A. koa* restoration in areas that experience wildfires [36]. Literature is sparse on the effects of high-severity fire on *A. koa* regeneration, although there is evidence that *A. koa* is able to establish naturally and aggressively after high-severity fire [40]. It is not known whether there is a threshold at which grass cover has substantial negative effects on *A. koa* regeneration through its potential influence on fire severity. We aimed to test this at sites with varying levels of pre-fire grass cover by determining the combined effects of grass cover and fire severity on *A. koa* regeneration densities one year after fire.

Assessing grass cover is key to understanding its effects on ecosystems and can be done in person or remotely. However, it is difficult to assess grass cover from remote sensing data in forested ecosystems when the forest floor is obscured by the canopy, as is often the case in Hawai'i. This presents a challenge to determining the fire risk and management needs of forested landscapes without spending time and resources on in-person surveys. We aimed to test whether oblique-angle aerial images could fill this knowledge gap. Oblique aerial images are shot at an angle that allows the viewer to see further under the canopy than one can using traditional top-down images, and this could potentially allow for greater ability to assess grass cover.

The objectives of this study were to quantify how grass cover, fire severity, and the interaction of the two affect *A. koa* regeneration, and to discover whether one can obtain accurate grass cover estimations from oblique-angle aerial photography. The future resilience of *A. koa* to the increasing threat of grass-fueled wildfire depends on how it responds to various levels of grass cover and fire severity. Understanding this response and knowing whether oblique-angle aerial photography is a viable option for grass cover measurement will allow land managers to make informed choices about how they assess fire hazard and restoration priorities on their land.

We chose to use the landscape burned in the 2018 Keauhou Ranch Fire as our study area. The Keauhou Ranch Fire burned an estimated 1203 hectares of land in Hawai'i Volcanoes National Park (HAVO) and 308 hectares of the surrounding state and public lands on the Island of Hawai'i [41]. The fire affected numerous ecotypes, including *A. koa* forests with varying levels of grass invasion. Ongoing restoration efforts in Hawai'i seek to restore forest habitat by planting native species and limiting invasive grass cover. However, for restoration efforts to be successful, land managers would benefit from knowledge of how invasive grass cover varies across the landscape and how it influences both fire effects and native plant response to fire. In an effort to achieve this knowledge, we investigated a method for estimating grass cover from oblique aerial photos, and analyzed the relationships between fire severity, grass cover, and the dominant native tree, *Acacia koa*.

We asked the following:

1. At what level of precision can categories of pre-fire grass cover be accurately (≥60% accuracy) estimated from oblique aerial photos?
2. How do post-fire *A. koa* regeneration densities vary with fire severity?
3. How do post-fire *A. koa* regeneration densities vary with pre-fire grass cover and its interaction with fire severity?

2. Materials and Methods

2.1. Study Area

The study area was within the mid-elevation woodland, montane woodland, and montane shrubland zones of HAVO [42,43], which has been designated as a National Park since 1916 and contains a broad range of ecosystems with many endemic flora and fauna. Our sites ranged in elevation from 1006 to 2195 m. The study area included a 39.59 km^2 area along the Mauna Loa Road on the southeastern slope of Mauna Loa, 12.95 km^2 of which burned in the 2018 Keauhou Ranch Fire. It also included a 52.89 km^2 area in the Kahuku Unit on the southwestern slope of Mauna Loa (Figure 1). Within both regions (Mauna Loa Road and Kahuku) of the study area, the three cover types—woodland, montane woodland, and montane shrubland zones—occurred [43] (Table 1).
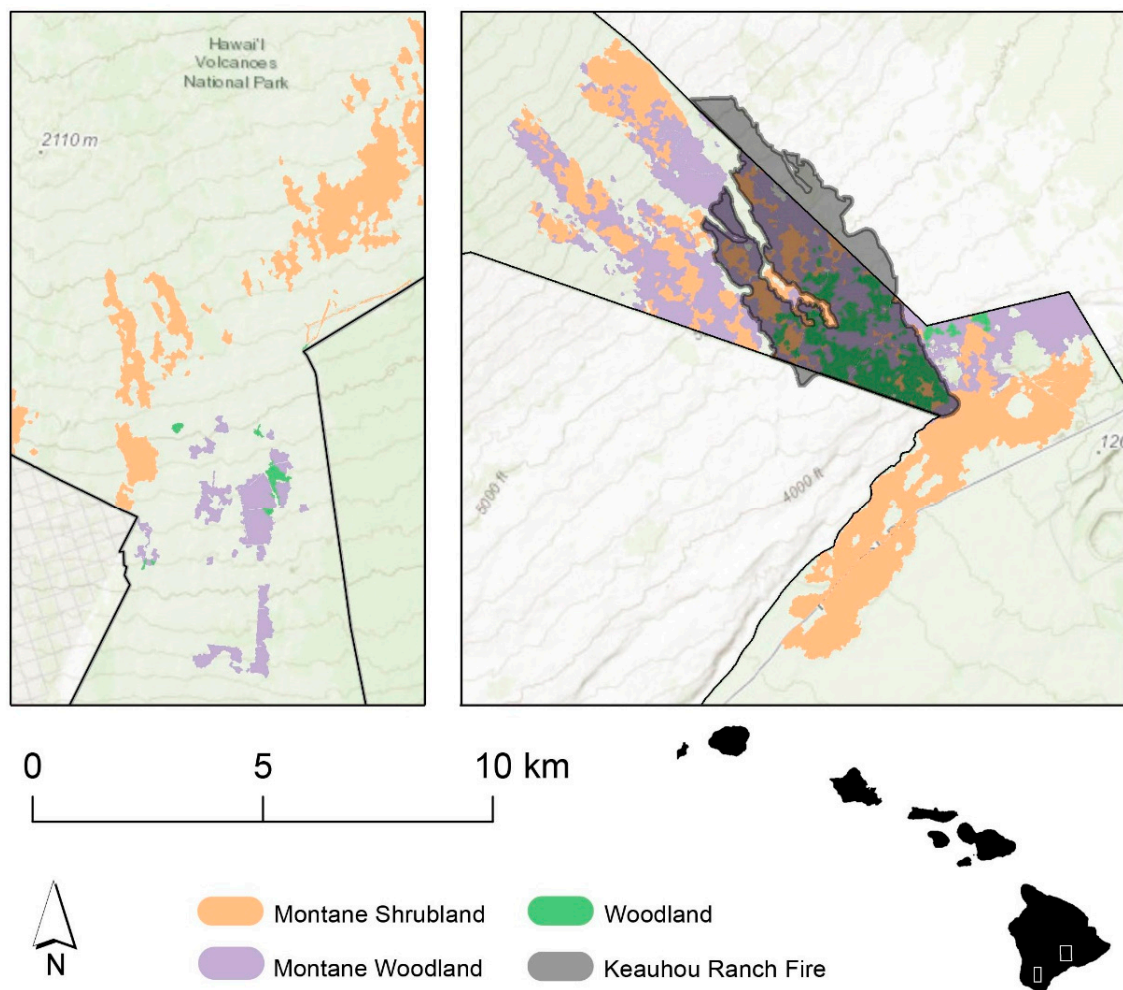

Figure 1. Map of the study area: the Mauna Loa Road area (**right**) and the Kahuku Unit (**left**) of Hawai'i Volcanoes National Park (HAVO), on the Island of Hawai'i. The grey perimeter represents the Keauhou Ranch Fire, which burned in 2018 [44]. The black perimeter represents the boundaries of HAVO [42].

Table 1. Vegetation assemblage, elevation, moisture regime, and vegetation overstory and understory information for each cover type, referenced from Green et al. (2015) [43].

Cover Type	Assemblage	Elevation	Moisture Regime	Vegetation Overstory	Vegetation Understory
Mid-elevation woodland	*A. koa*-dominated	1200–2100 m	Mesic	Often dense *A. koa*	Herbaceous layer dominated by exotic *Ehrharta stipoides*, exotic *Setaria parviflora* (marsh bristlegrass), or exotic *Cenchrus clandestinus* (Kikuyu grass). Sparse *Leptecophylla tameiameiae* (pūkiawe) and/or *Dodonaea viscosa* ('a'ali'i).
Montane woodland	*A. koa*-dominated	1350–2100 m	Mesic	Scattered to medium-density *A. koa* with scattered *Sophora chrysophylla* (māmane)	Dominant *Leptecophylla tameiameiae* and *Dodonaea viscosa*, herbaceous layer of exotic *Ehrharta stipoides*
	Māmane-dominated	1400–2400 m	Dry	Sparse *Sophora chrysophylla* and sometimes sparse *Myoporum sandwicense* (naio)	Dominant *Leptecophylla tameiameiae* and *Dodonaea viscosa*, herbaceous layer of exotic *Ehrharta stipoides*
Montane shrubland	Pūkiawe- and 'a'ali'i-dominated	1000–2300 m	Dry to mesic	Scattered *Sophora chrysophylla*	Occasional *Vaccinium reticulatum* ('ōhelo 'ai); sparse to well-developed layer of exotic *Schizachyrium condensatum* (bush beardgrass) and exotic *Andropogon virginicus* (broom sedge) at more mesic sites
	Pūkiawe-dominated	1500–2000 m	Dry	Scattered *Sophora chrysophylla* and *Dodonaea viscosa*	*Deschampsia nubigena* (alpine hairgrass), scattered exotic herbaceous species

The study area, especially the mid-elevation woodland section, was subject to land clearing and ungulate effects in the 20th century, which lowered biodiversity and created an artificially simplified vegetation community that the area has been naturally regenerating from since ungulates were removed. Cattle were removed in 1948; goats and pigs were removed in the 1970s and 1980s. There are currently no ungulates in the study area.

Persistent non-native grass cover and a lack of native plant seed sources have both been major barriers to full recovery of the mid-elevation woodland zone. There has not been any large-scale *A. koa* planting in the study area.

2.2. Aerial Photo Interpretation

2.2.1. Field Methods

From September 2019–February 2020, we collected in situ measurements of percent grass cover along 100 m transects ($n = 60$) that lay outside the area that burned in 2018 using the point-intercept method [45]. The locations of these transects were randomly selected in ArcGIS, stratified by cover type (mid-elevation woodland, montane woodland, and shrubland). We collected data from unburned areas that were similar and close to the areas that burned, but because almost all woodland in the Mauna Loa Road area was burned, we also collected data from unburned patches of woodland in the Mauna Loa Road area as well as from the same elevation range in the Kahuku Unit of the park (Figure 1). Data from 30 of these transects were set aside as validation data, while data from the remaining 30 sites were used as training data to calibrate the estimation of grass cover from

oblique-angle aerial imagery taken in 2014 [46]. All aerial images were taken using three true-color bands capturing visible light. Because these sites had not been substantially altered by fire or human intervention since 2014, it was likely that they still reflected the vegetation composition and structure from the year of the fire. Cover types were equally represented among training and validation data.

2.2.2. Data Analysis

Visible light aerial photos were georeferenced by Pictometry International. Although exact zenith angles were not reported, all images were taken at low oblique angles (below the horizon line, typically near 45°). On each aerial photo, we overlaid a 100 m transect line that mirrored the actual transect line from which we took in situ measurements in 2019–2020.

To calibrate our grass cover estimations, we labeled 30 training sites with the corresponding in situ grass cover percentages. We studied the images and grass cover percentages of the training sites and trained ourselves to recognize context clues that signified the amount of grass cover along a transect, such as the amount of grass present directly on a transect, the amount of grass present in the area around the transect, nearby openings in the canopy, and the degree to which a site had rocky substrate or well-developed soil. The use of visual and context clues has been shown to be a viable method of aerial photography analysis in past studies [47,48]. We used two image interpreters (Hamilton and Gill) in our grass cover estimations.

After training, we visually interpreted the percentage of grass cover along the transects of the 30 remaining validation data sites. We estimated grass cover to the nearest 5% and averaged estimates from the two image interpreters together so that we would have a single estimated value per site. We compared these estimates to the in situ grass cover percentage for each site, which had not been looked at before estimation. We then determined the accuracy achieved when we generalized the 5% estimates to varying levels of precision. We generalized them to ten levels of precision (0–9%, 10–19%, 20–29%, 30–39%, 40–49%, 50–59%, 60–69%, 70–79%, 80–89%, and 90–100% grass cover; Table A1), five levels (0–19%, 20–39%, 40–59%, 60–79%, and 80–100% grass cover; Table A2), four levels (0–24%, 25–49%, 50%–74%, and 75–100% grass cover; Table A3), and three levels of precision (0–33%, 34–66%, and 67–100% grass cover; Table A4).

For comparison, we randomly generated percentages in increments of 5% using the RAND Function in Microsoft Excel (version 16.50) and performed a *z*-test to determine whether the accuracy of the image-based grass cover estimates at each level of precision was significantly ($p < 0.05$) greater than by chance (Table 2). We also ran a one-way ANOVA to determine whether there was a relationship between pre-fire grass cover and post-fire grass cover to further (anecdotally) validate grass cover estimates, as areas with high post-fire invasive grass cover might coincide with areas that had high pre-fire invasive grass cover as a result of resprouting and pre-existing soil seedbank [18,19].

Table 2. Grass cover estimates were more accurate than randomly generated estimates at 10-, 5-, 4-, and 3-class levels of precision.

Level of Precision (Number of Classes)	Average Accuracy of Random Values	Overall Accuracy of Grass Cover Estimations	Standard Error of Estimations	*z* Value	*p* Value
10	10%	47%	0.002	232.393	<0.001
5	20%	53%	0.002	142.799	<0.001
4	24%	67%	0.003	168.221	<0.001
3	39%	63%	0.003	88.972	<0.001

To quantify bias, we calculated the average of the difference between the in situ grass percentages and the image interpreters' estimations. We also calculated the average difference between the image interpreters' estimations to determine variability.

2.3. Fire Severity Effects on Post-Fire A. koa Regeneration

2.3.1. Field Methods

We randomly generated 100 m burned transects in ArcGIS (*n* = 27) stratified by burn severity (high, medium, and low) and cover type (mid-elevation woodland, montane woodland, and montane shrubland). We determined burn severity categories using a U.S. Forest Service Burned Area Reflectance Classification (BARC) map [49] of the Keauhou Ranch Fire, and cover type using spatial vegetation cover data produced by Green et al. [43] in 2015. Each transect was oriented in a random direction. Like the unburned transects (Section 2.2.1), the burned transects were sampled one year after fire.

In October 2019, we collected in situ data from each burned transect to assess fire severity and post-fire vegetation. At 1-m intervals along each transect, we took point-intercept measurements of the plant species present [45]. We recorded whether each occurrence of a species was alive or dead. We used a hypsometer to record scorch height and char height on the nearest tree or shrub every 5 m along the transect. We counted all trees and shrubs within 1 m of either side of the transect (2 m × 100 m plots). Live trees and shrubs, including post-fire recruitment, were identified by species.

2.3.2. Data Analysis

We tested for a relationship between burn severity and *A. koa* regeneration density using a mixed-effect linear model fit by restricted maximum likelihood (REML, R [50] lmerTest package [51]). We conducted post hoc *t*-tests in R (version 4.0.2) using Satterthwaite's method. All formulae used are found in Table A5.

We set post-fire *A. koa* regeneration density as a function of minimum scorch height. Minimum scorch height is the lowest scorch height recorded along an entire transect, and is a demonstrated indicator of fire severity [52]. We selected it from among other collinear fire severity metrics for several reasons. First, minimum scorch height is a continuous variable, which some of our models required. Second, it is measured from the ground up, which allows for recording of fine-scale, vertically oriented effects that may be missed by top-down satellite data such as BARC fire severity classification. Minimum scorch height also avoided any error from surrounding features that would have influenced the BARC measurements, which are taken from 1 to 3 pixels of satellite data, each of which represents 30×30 m^2 on the ground. Third, minimum scorch height values were less skewed than char values, which were zero-inflated. Finally, minimum scorch height captured subtle within-site variability and patchiness in a way that average scorch height did not; average scorch height values could be skewed by outliers and thus give an inaccurate picture of the true condition of a site, while minimum scorch height accurately portrays a threshold level of fire effects that were experienced throughout a plot. We chose not to relativize scorch height values as a percentage of canopy height because of the large difference in canopy heights between woodland and shrubland cover types, which overrode the variability in apparent flame lengths when scorch height was relativized. We measured scorch height using a meter stick or a hypsometer, depending on whether the scorch height extended past our reach.

Because we wanted to control for the influence of differences in post-fire *A. koa* seed availability, we chose to use surviving *A. koa* dominance, a categorical measurement of what percentage of a site's post-fire canopy was composed of *A. koa* trees, as a random effect in all of our models. Surviving *A. koa* dominance was calculated by dividing the number of surviving *A. koa* trees by the number of total surviving trees at each site, and then categorizing the values so that the variable could be used as a random effect. Categories were "*A. koa* dominated" (>50% *A. koa*, *n* = 14), "dominated by other species" (<50% *A. koa*, *n* = 6), and "no local canopy seedbank" (there were no surviving trees at a site, *n* = 7).

2.4. Pre-Fire Grass Cover's Interaction with Fire Severity, and Its Effects on A. koa Regeneration
Data Analysis

Informed by the precision and accuracy rates determined in addressing Q1 (Section 2.2), we classified the burned sites by estimating pre-fire grass cover using four levels of classification. Following the procedure used to address Q2 (Section 2.3), we used a linear mixed-effects model to estimate post-fire *A. koa* regeneration density from pre-fire grass cover and other variables, testing as well for significant ($p < 0.05$) interaction between pre-fire grass cover and fire severity (R, lmerTest package [50,51]). *A. koa* regeneration density was set as a function of minimum scorch and estimates of pre-fire grass cover. Surviving *A. koa* dominance was again included as a random effect in all models (Table A5).

We also tested whether there was a relationship between post-fire grass cover and post-fire *A. koa* regeneration density, with the hypothesis that increased grass recovery might suppress *A. koa* recruitment, using a one-way ANOVA. We additionally tested whether there was a relationship between pre-fire grass cover and fire severity, isolated from post-fire *A. koa* regeneration density, using a one-way ANOVA.

3. Results

3.1. Accuracy of Aerial Photo Interpretation

We achieved greater than 60% overall accuracy (67%) in grass cover estimations at a four-category level of precision (Table 3) across all cover types together. Comparisons of classified data to reference data for the other tested levels of precision (3, 5, and 10) can be found in Appendix A (Tables A1–A4). Accuracy was 20% in mid-elevation woodland, 67% in montane woodland, and 100% in montane shrubland (Table 3). There was no trend in whether estimated grass cover tended to be underestimated or overestimated. When an estimation was incorrect, 78% of the time it was only separated from the true value by one class. Grass cover estimates were significantly more accurate than random ($z = 168.221$, $p < 0.001$; Table 2). Randomly generated estimates were 20% accurate. There was a significant positive relationship between pre-fire grass cover estimates and post-fire presence of grass cover ($df = 1$, $F = 16.7$, $p = 0.000397$, Appendix B), which anecdotally supports the overall accuracy of the grass cover estimates: high levels of pre-fire grass can imply high levels of grass seed in the soil seedbank, which could lead to higher post-fire grass establishment.

Table 3. Accuracy rates of grass cover estimations at four different levels of precision.

Number of Classes	3	4	5	10
Overall accuracy	63%	67%	53%	47%
Mid-elevation woodland	0%	20%	0%	0%
Montane woodland	89%	67%	56%	33%
Montane shrubland	100%	100%	100%	100%

Differences in average grass and canopy cover in the three cover types exacerbated different accuracy rates between them. In montane woodland, grass cover was consistently less than 50%. It was often possible to see the forest floor because of breaks in the canopy, which allowed us to make accurate predictions (Table 3). In montane shrublands, which tended to have open canopies, the ground was highly visible, enabling us to predict grass cover with high accuracy (Table 3). In situ measurements of grass cover at these sites were consistently low (0–24%), as were predictions from visual interpretation of imagery. This lack of variability hindered our ability to analyze interactions between grass cover and fire severity or *A. koa* regeneration within the montane shrubland cover type. The mid-elevation woodland accuracy rate was low (Table 3) because of the thick canopy cover at the mid-elevation woodland sites, which often made it difficult to view the ground. Comparisons of classified data to reference data for each individual cover type can be found in Appendix A (Tables A6–A8).

A comparison between the in situ grass percentages and both image interpreter's grass percentage estimations is displayed in Table 4.

Table 4. We subtracted the average of each image interpreter's grass cover percentage estimations from the averages of the in situ grass percentage values to obtain each interpreter's average error.

Image Interpreter	Mid-Elevation Woodland Error	Montane Woodland Error	Montane Shrubland
Hamilton	−4.8%	8.4%	2.4%
Gill	−4.3%	−2.7%	−4.3%

The average difference between the two image interpreters' estimations was −0.5% in mid-elevation woodland, 11.1% in montane woodland, and 6.8% in montane woodland.

3.2. Fire Severity and Post-Fire A. koa Regeneration

Minimum scorch height and post-fire *A. koa* regeneration density were positively related ($p = 0.006$, $F_{23} = 9.115$) when all cover types were grouped together (Table 5). Transects with greater burn severity tended to have more regenerating *A. koa* (Figure 2). Minimum scorch height and pre-fire tree density were also positively related except when pre-fire tree density was high (significant interaction, $p < 0.05$, $F_{23} = 4.396$) (Table 5, Figure 2). Transects with greater *A. koa* density before the fire tended to have greater post-fire regeneration, but this was not statistically significant ($p = 0.073$, Table 5). Pre-fire tree density was unrelated to fire severity in the individual cover types, including when they were grouped ($p > 0.05$; Table 5).

Table 5. *A. koa* regeneration density exhibited a significant, positive relationship with minimum scorch height, except when tree density was particularly high (greater than 70 trees per site, Figure 2). *A. koa* regeneration density displayed only a marginally significant, positive relationship ($p = 0.073$) with pre-fire tree density.

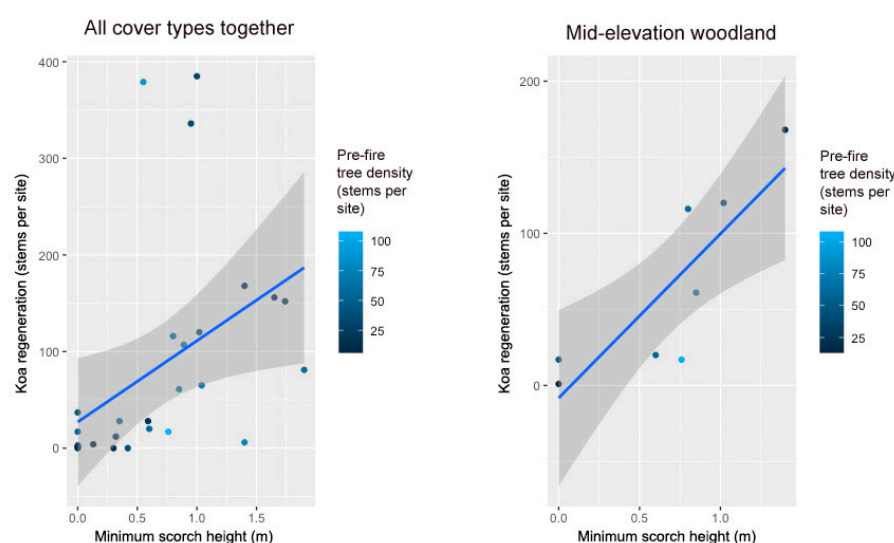| Factor	Coefficient	Standard Error	*df*	*F* Value	*p* Value
Minimum scorch	198.666	65.803	23	9.115	0.006
Pre-fire tree density	2.610	1.390	23	3.527	*0.073*
Minimum scorch × pre-fire tree density	−3.447	1.644	23	4.396	0.047

Figure 2. When all cover types were grouped together, post-fire *A. koa* regeneration increased with minimum scorch height. However, at sites with highest pre-fire tree densities, this trend reversed. In mid-elevation woodlands, post-fire *A. koa* regeneration densities exhibited a significant, positive relationship with minimum scorch height and only a marginally significant, positive relationship ($p = 0.091$) with pre-fire tree density.

In the montane shrubland and montane woodland cover types, *A. koa* regeneration density was not affected by minimum scorch height or any other of the tested variables (Table A9, Figure 3). In mid-elevation woodlands, post-fire *A. koa* regeneration densities exhibited a significant, positive relationship with minimum scorch height ($p = 0.005$, $F_5 = 22.734$) and a marginally significant, positive relationship ($p = 0.091$, $F_5 = 4.369$) with pre-fire tree density (Table 6, Figure 2).

Table 6. In mid-elevation woodland, *A. koa* regeneration density exhibited a significant, positive relationship with minimum scorch height and a marginally significant negative relationship with pre-fire tree density at the $p = 0.09$ level.

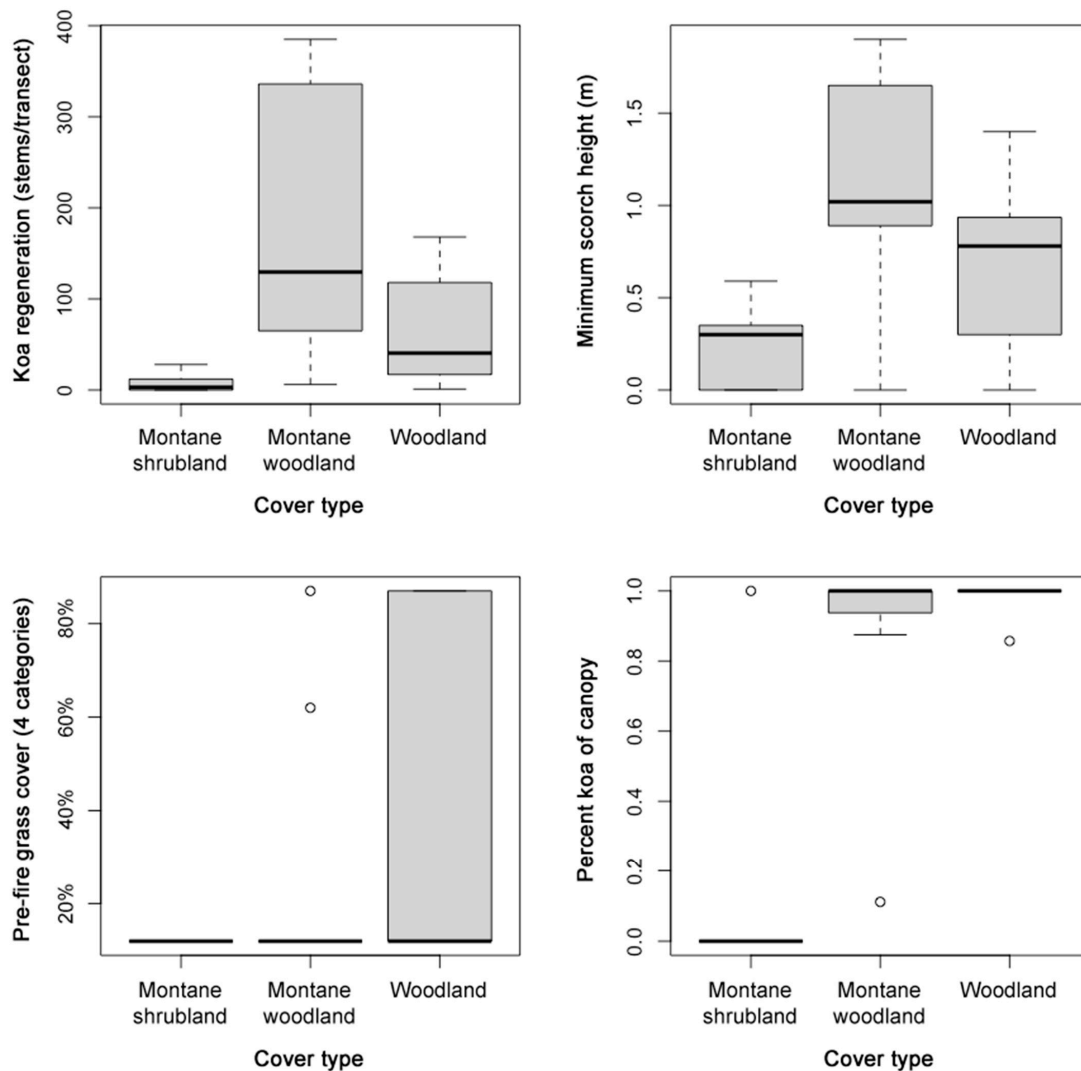| Model	Coefficient	Standard Error	*df*	*F* Value	*p* Value
Minimum scorch	111.144	23.311	5.000	22.734	0.005
Pre-fire tree density	−0.766	0.367	5.000	4.369	*0.091*

Figure 3. Measurements of in situ conditions at burned sites by cover type. The top two panels represent post-fire variables: *A. koa* regeneration and minimum scorch height. The bottom two panels represent pre-fire variable: grass cover estimates derived from aerial imagery interpretation, and percent *A. koa* of canopy. The accuracy of the grass cover estimates varied considerably by cover type. Grass cover was estimated categorically, but is displayed as a percentage here. The midline is the median value, and the upper and lower limits of each box are the 75th and 25th percentile, respectively. The points represent outliers.

3.3. Pre-Fire Grass Cover, Fire Severity, and A. koa Regeneration

We could only analyze the relationship between post-fire *A. koa* regeneration and pre-fire grass cover's interaction with minimum scorch height in montane woodland sites, as we did not have reliable pre-fire grass cover estimates for mid-elevation woodland sites and the montane shrubland sites had no variability in grass cover.

At the four-category level of precision in grass cover estimates, there was no significant relationship between pre-fire grass cover and *A. koa* regeneration, and no significant relationship between *A. koa* regeneration and the interaction of pre-fire grass cover and minimum scorch height (Table 7, Figure 3). Put another way, the amount of pre-fire grass cover at a site and the severity of the fire did not appear to interact in a way that influences post-fire *A. koa* regeneration. We additionally did not find a significant relationship between post-fire grass cover and post-fire *A. koa* regeneration density (Present grass cover, $df = 1$, $F = 0.041$, $p = 0.841$, Appendix B).

Table 7. Using four categories of pre-fire grass cover, there was no significant relationship between *A. koa* regeneration, minimum scorch height, and pre-fire grass cover in the montane woodland cover type.

Model	Coefficient	Standard Error	df	*F* Value	*p* Value
Minimum scorch	−131.076	197.967	5	0.438	0.537
Grass cover	−15.730	23.234	5	0.458	0.528
Pre-fire tree density	−0.288	2.719	5	0.011	0.920
Minimum scorch × grass cover	8.813	14.096	5	0.391	0.559

We also did not detect a significant relationship between minimum scorch height and pre-fire grass cover when analyzed separately from *A. koa* regeneration in montane woodland (minimum scorch, $df = 1$, $F = 1.877$, $p = 0.208$, Appendix B).

4. Discussion

Our goal was to understand better the role of fire on *A. koa* regeneration in Hawai'i. As a part of this, we also estimated pre-fire grass cover, as grasses are well known to alter fire spread and in some cases can lead to lower native woody abundance post-fire [20,24,53]. We accurately estimated pre-fire grass cover from aerial imagery, though this may depend on habitat type and canopy cover. Pre-fire grass cover, however, was not found to be related to post-fire *A. koa* regeneration. In contrast, burn severity and pre-fire tree cover were important factors in one of the three habitat types studies: the mid-elevation woodland habitat.

4.1. Aerial Photo Interpretation

We found that by estimating from aerial photos using our training and validation protocol, land managers can assess grass cover in montane shrubland and montane woodland landscapes with reasonable confidence, and in a shorter amount of time than in situ measurements in remote sites. A greater understanding of grass cover in these landscapes enables more targeted restoration efforts. For example, sites with high invasive grass cover could be prioritized for management actions such as supplemental planting of native woody species, which can lower grass biomass and possibly reduce the ability of fine fuels to carry fire into forest sites [40,54,55]. Improved grass cover data also allows for historical vegetation data to be compared to contemporary aerial photos to investigate how fire can affect successional processes and forest composition. However, a better method is needed for assessing grass cover in heavily canopied mid-elevation woodland areas. In situ measurements showed that mid-elevation woodland sites had highly variable levels of grass, ranging from 8% to 85% of ground cover along our transects, with an average of 48% cover. Being unable to assess grass cover remotely at these sites creates blind spots that hinder efforts to detect and control invasive grass spread, complicate large-scale spatial

analyses of grass cover, and decrease land managers' ability to target restoration and fire hazard management plans effectively.

It would be illuminating to replicate the present study using a different form of remote sensing to assess grass cover, such as light detection and ranging (lidar). High-resolution airborne lidar can detect invasive grass in open tropical savanna woodland habitat [56], but whether it can be used to detect invasive grass in denser tropical woodland is unknown. It may convey greater precision and accuracy than aerial imagery when assessing montane woodland cover types, where there is more visible ground than in mid-elevation woodland. It also might give greater precision within the montane shrubland cover type, potentially enabling observers to record more variation in grass cover within that cover type and allowing analysis of the relationships between invasive grass cover and other variables, including those relating to fire such as post-fire grass cover, native woody regeneration, and grass-fire cycles.

A limitation in this study was our inability to distinguish between invasive grasses and native grasses in our aerial photos. This does not pose a problem for site assessment in the mid-elevation woodland and montane woodland cover types, which we found to have low proportions of native grass to invasive grass during our in situ data collection. We found the montane shrubland cover type to contain a higher proportion of native grass than the other cover types did, so an inability to distinguish between native and invasive grasses might hinder the ability of land managers to gather meaningful information on site needs in montane shrubland. However, because montane shrubland sites consistently displayed low levels of grass cover overall (<10% cover), they would not be high-priority sites for grass control, and this limitation may not be relevant to management.

4.2. Fire Severity Effects on Post-Fire A. koa Regeneration

We found a positive relationship between fire severity (as measured by minimum scorch height) and *A. koa* regeneration in mid-elevation woodland cover types. This pattern might be due to the fact that *A. koa* benefits from canopy openness and clearing of debris from the forest floor [36,57,58], which can be brought about by fire. In addition, *A. koa* seedbanks are able to survive wildfires, and vegetatively resprout from live root stock after fire, while seeds of other species may be consumed, leading to increased post-fire *A. koa* recruitment [39,59]. The majority of the *A. koa* we observed regenerating at our sites was regenerating from seed.

If increased light availability as a result of high fire severity is a contributor to increased *A. koa* regeneration [57], it may be tempered by cover type. *A. koa* was not abundant in montane shrublands despite high light availability, and there was no correlation between scorch height and post-fire *A. koa* regeneration in montane woodland. These two cover types experience lower temperatures and precipitation than the mid-elevation woodland cover type does. In addition, the montane shrubland cover type has less soil present than the other cover types (observed during field work), which, like its climate, tends to support lower productivity than the other cover types and could suppress regenerating *A. koa*. Montane woodland and mid-elevation woodland sites displayed similar canopy closure and stand density, so their differing levels of seed presence in the soil may be what led to differences in *A. koa*'s response to fire between them.

If *A. koa* regeneration has a positive relationship with fire severity, as in the mid-elevation woodland cover type, then invasive grasses may also be indirectly promoted via facilitation by *A. koa*. *A koa*'s nitrogen-fixing capabilities locally increase soil nitrogen, and this, in combination with higher incident light under the canopy than in more diverse forest, may help facilitate grass abundance [33,37]. Invasive grasses in Hawai'i are well known to stall native seedling germination and survival [15,33,60], leading to homogenous landscapes with seemingly stable states of *A. koa* and grass [21,40]. This would hinder the NPS's goal of increasing biodiversity in Hawai'i Volcanoes National Park [61]. The planned ongoing research of the U.S. Geological Survey (USGS) and the NPS into optimal restoration strategies and restoration treatment success in Hawaiian landscapes, in which

various combinations of native species are being planted into restoration sites, may be helpful in determining if planting a broader range of species leads to reduced invasive grass establishment compared to restoration efforts where primarily *A. koa* is planted. Sites with high burn severity could be targeted for direct seeding of non-*A. koa* native species to increase biodiversity.

In our study area, there were sites that had burned in both 1975 and 2018. *A. koa* regeneration and resprouting was abundant following both fires [62]. However, shorter wildfire intervals may affect *A. koa* regeneration differently. Trauernicht et al. (2018) [40] showed that *A. koa* seedbanks in the soil deplete themselves extensively after a wildfire event; the seedbanks regenerate aggressively and the regenerating trees self-thin, lowering the overall amount of seed in the soil. This depletion may be in the process of occurring after the Keauhou Ranch Fire, especially given the high rates of *A. koa* regeneration in the woodland sites (Table 8).

Table 8. Average *A. koa* regeneration was highest in montane woodland sites and lowest in montane shrubland sites.

Factor	Cover Type	Average (Stems/Transect)	Standard Error	Range
Regenerating *A. koa* stem density	Montane shrubland	8.444	3.902	28
	Montane woodland	170.40	45.397	379
	Mid-elevation woodland	65.000	21.950	167

If wildfire intervals in Hawai'i continue to shorten [31], *A. koa* stands regenerating from fire may be killed by another fire before they are able to reach reproductive maturity, as *A. koa* generally take five years to start bearing seeds [63]. If so, mid-elevation woodland restoration sites would benefit from outplanting of native species that are fire-tolerant and/or reach reproductive maturity quickly (<2 years), such as *Dodonaea viscosa*, *Santalum freycinetianum* ('iliahi), and *Santalum paniculatum* ('iliahi) [63,64]. Plants that are outplanted as juveniles will reach sexual maturity faster than those that are direct seeded, which would further protect mid-elevation woodland sites from seedbank depletion due to wildfire. Creating green fuel breaks of native vegetation around these sites could raise local humidity, shade out local grass cover, and increase landscape resistance to fire disturbance while simultaneously increasing landscape resilience after fire disturbances through the planting of fast-growing native species that are quick to reproduce. Additionally, diverse assemblages of native species planted at these sites might help suppress grass by taking up resources that the grass would otherwise benefit from. Green fuel breaks have been shown to be effective in other systems [65,66], and could help protect not only *A. koa* seedbanks but also other native plants from grass invasion and wildfires. In the Keauhou Ranch Fire, areas with understories that had been restored with biodiverse native species did not carry fire as well as the surrounding simplified *A. koa*–grass forest [62].

4.3. Pre-Fire Grass Cover, Fire Severity, and A. koa Regeneration

Other researchers have found a link between grass invasion and fire severity in Hawai'i [23,25]. We suspect we did not detect significance because of limitations in our dataset; there are environmental variables such as soil moisture that we did not measure and that could have influenced our results. We also could not definitively assess pre-fire forest composition, as many of the burned trees at sites were unidentifiable.

If there is no relationship between *A. koa* regeneration and the interaction between fire severity and grass cover in montane woodland sites, as our study indicates, then land managers wishing to promote *A. koa* can continue to plant it in sites with high grass cover without concern of *A. koa* regeneration being suppressed by grasses after fire. However, the sample size of this analysis was small ($n = 10$). Similar to the analysis we performed on grass cover's relationship with fire, there may be factors this analysis did not take into account, such as soil moisture, temperature, species composition, and humidity, which could all affect fire, grass, and *A. koa* regeneration trends.

5. Conclusions

In this study, we determined that grass cover can be accurately estimated from visual interpretation of oblique-angle aerial photos in Hawaiian montane shrubland and montane woodland ecosystems using four categories of precision. Other methods, such as lidar, may be helpful in areas with denser canopies.

We found that fire intensity, as indicated by minimum scorch height, has a positive effect on post-fire *A. koa* regeneration densities in mid-elevation woodlands when pre-fire tree density is low, though this trend reversed when pre-fire tree density was high (>70 trees per transect). Our findings imply that, when fire intervals are long enough to allow a sufficient soil seedbank to develop, *A. koa* is capable of regenerating at high density even after severe fire in low- to medium-density stands (<70 trees per transect). Further research would allow determination of the cause of the negative relationship between minimum scorch height and *A. koa* regeneration in high-density stands, and determination of how densely *A. koa* regenerates when fire intervals are less than 43 years, the shortest interval contained in our study area.

We did not detect a relationship between *A. koa* regeneration and the interaction between pre-fire grass cover and fire severity. This finding only applies to the montane woodland cover type because we could not use the grass cover estimations from the other two cover types in our analysis. If there truly is no relationship between grass cover, fire severity, and *A. koa* regeneration, then *A. koa* in grassy montane woodland areas are not at risk of grass suppressing their post-fire regeneration. Further research would be needed to determine whether this lack of a relationship holds true at larger sample sizes and across multiple cover types, and with other environmental variables considered.

Although *A. koa* regenerates quickly after fire [36,40] and does not appear to be sensitive to potential changes in fire behavior caused by invasive grass, the establishment of *A. koa* alone is not sufficient to maintain ecological diversity to the NPS's standards, especially in areas where post-fire grass cover is high and suppresses native understory. Many threatened and endangered plant species of Hawai'i Volcanoes National Park are not fire adapted and cannot be planted into grassy areas; thus, creating landscapes that are low in grass cover and protected from wildfire may help with conservation efforts of these species. The planting of other native species alongside *A. koa*, which is the NPS's current practice in HAVO, would help achieve this goal in Hawai'i.

Appendix A

Table A1. Classified data, which represent predicted grass cover from visual interpretation, versus reference data, which represent in situ grass cover across all cover types, when using 10 levels of precision. Each value in the table represents a number of transects. The italicized diagonal values represent how many transects were interpreted accurately per grass cover category. The column total represents the number of transects of field-based data that fell within each cover class. Row totals are the number of transects of predicted data that fell within each cover class.

| | | Reference Data | | | | | | | | | | |
		0–9%	10–19%	20–29%	30–39%	40–49%	50–59%	60–69%	70–79%	80–89%	90–99%	Row Total
Classified Data	0–9%	*14*	1	0	1	1	0	0	0	0	0	17
	10–19%	1	*0*	0	0	1	0	0	0	0	0	2
	20–29%	2	0	*0*	0	0	0	1	0	0	0	3
	30–39%	0	0	0	*0*	0	0	0	0	0	0	0
	40–49%	1	0	1	0	*0*	0	0	0	0	0	2
	50–59%	0	0	0	1	0	*0*	0	1	1	0	3
	60–69%	0	0	0	0	0	0	*0*	0	0	0	0
	70–79%	0	0	0	0	2	0	0	*0*	0	0	2
	80–89%	0	0	0	1	0	0	0	0	*0*	0	1
	90–99%	0	0	0	0	0	0	0	0	0	*0*	0
	Column Total	18	1	1	3	4	0	1	1	1	0	30

Table A2. Classified data versus reference data across all cover types when using 5 levels of precision. Each value in the table represents a number of transects. The italicized diagonal values represent how many transects were interpreted accurately per grass cover category. The column total represents the number of transects of field-based data that fell within each cover class. Row totals are the number of transects of predicted data that fell within each cover class.

| | | Reference Data | | | | | |
		0–19%	20–39%	40–59%	60–79%	80–99%	Row Total
Classified Data	0–19%	*16*	1	2	0	0	19
	20–39%	2	*0*	0	1	0	3
	40–59%	1	2	*0*	1	1	5
	60–79%	0	0	2	*0*	0	2
	80–99%	0	1	0	0	*0*	1
	Column Total	19	4	4	2	1	30

Table A3. Classified data versus reference data across all cover types when using 4 levels of precision. Each value in the table represents a number of transects. The italicized diagonal values represent how many transects were interpreted accurately per grass cover category. The column total represents the number of transects of field-based data that fell within each cover class. Row totals are the number of transects of predicted data that fell within each cover class.

| | | Reference Data | | | |
		0–24%	25–49%	50–74%	75–99%	Row Total
Classified Data	0–24%	*18*	3	1	0	22
	25-49%	1	*1*	0	0	2
	50-74%	0	3	*1*	1	5
	75-99%	0	1	*0*	*0*	1
	Column Total	19	8	2	1	30

Table A4. Classified data versus reference data across all cover types when using 3 levels of precision. Each value in the table represents a number of transects. The italicized diagonal values represent how many transects were interpreted accurately per grass cover category. The column total represents the number of transects of field-based data that fell within each cover class. Row totals are the number of transects of predicted data that fell within each cover class.

		Reference Data			
		0–33%	34–66%	67–99%	Row Total
Classified Data	0–33%	*19*	2	1	22
	33–66%	3	*0*	2	5
	67–99%	0	3	*0*	3
	Column Total	22	5	3	30

Table A5. R formulae for the calculations carried out for each research question, and their corresponding tables and R packages. The * symbol represents an interaction between two variables.

Table	Formula	Corresponding Research Question	Package
3	Keauhou_Burned_2019$ Grass4Categories ~ Keauhou_Burned_2019$PostFireGrass	2	Base
4	MidElevationWoodland$KoaRegen ~ (1 \| MidElevationWoodland$ KoaDominance) + MidElevationWoodland$MinScorch + MidElevationWoodland$ PreFireTreeDensity	2	lmerTest
5	MontaneWoodland$KoaRegen ~ (1 \| MontaneWoodland$KoaDominance) + MontaneWoodland$MinScorch * MontaneWoodland$Grass4Categories + MontaneWoodland$ PreFireTreeDensity	3	lmerTest
6	Keauhou_Burned_2019$PostFireGrass ~ Keauhou_Burned_2019$KoaRegen	3	Base

Table A6. Classified data versus reference data in the montane woodland cover type at 4 levels of precision. Each value in the table represents a number of transects. The italicized diagonal values represent how many transects were interpreted accurately per grass cover category. The column total represents the number of transects of field-based data that fell within each cover class. Row totals are the number of transects of predicted data that fell within each cover class.

		Reference Data				
		0–24%	25–49%	50–74%	75–99%	Row Total
Classified Data	0–24%	*6*	2	0	0	8
	25–49%	1	*0*	0	0	1
	50–74%	0	0	*0*	0	0
	75–99%	0	0	0	*0*	0
	Column Total	7	2	0	0	9

Table A7. Classified data versus reference data in the mid-elevation woodland cover type at 4 levels of precision. Each value in the table represents a number of transects. The italicized diagonal values represent how many transects were interpreted accurately per grass cover category. The column total represents the number of transects of field-based data that fell within each cover class. Row totals are the number of transects of predicted data that fell within each cover class.

		Reference Data				
		0–24%	25–49%	50–74%	75–99%	Row Total
Classified Data	0–24%	*0*	1	1	0	2
	25–49%	1	*1*	0	0	2
	50–74%	0	3	*1*	1	5
	75–99%	0	1	0	*0*	1
	Column Total	1	6	2	1	10

Table A8. Classified data versus reference data in the montane shrubland cover type at 4 levels of precision. Each value in the table represents a number of transects. The italicized diagonal values represent how many transects were interpreted accurately per grass cover category. The column total represents the number of transects of field-based data that fell within each cover class. Row totals are the number of transects of predicted data that fell within each cover class.

		Reference Data				
		0–24%	25–49%	50–74%	75–99%	Row Total
Classified Data	0–24%	*11*	0	0	0	11
	25–49%	0	*0*	0	0	0
	50–74%	0	0	*0*	0	0
	75–99%	0	0	0	*0*	0
	Column Total	11	0	0	0	11

Table A9. All of the fire severity metric variables we tested against *A. koa* regeneration density in the montane shrubland and montane woodland cover types.

Variable	Definition
Average scorch height	The average height (m) of scorch on trees and shrubs at a site
Maximum scorch height	The maximum height (m) of scorch on trees and shrubs at a site
Minimum scorch height as percent of canopy height	The minimum height (m) of scorch on trees and shrubs at a site
Maximum scorch height as percent of canopy height	The maximum scorch height of a site expressed as a percentage of the site's average canopy height
Average scorch height as percent of canopy height	The average scorch height of a site expressed as a percentage of the site's average canopy height
Average char height	The average height (m) of char on trees and shrubs at a site
Maximum char height	The maximum height (m) of char on trees and shrubs at a site
Minimum char height	The minimum height (m) of char on trees and shrubs at a site
Minimum char height as percent of canopy height	The minimum char height of a site expressed as a percentage of the site's average canopy height
Maximum char height as percent of canopy height	The maximum char height of a site expressed as a percentage of the site's average canopy height
Average char height as percent of canopy height	The average char height of a site expressed as a percentage of the site's average canopy height
Percent mortality	The percentage of trees and shrubs at a site that were killed by fire
Percent stem mortality	The percentage of trees and shrubs at a site that experienced stem morality as a result of wildfire

Appendix B

(1) R formula modeling the relationship between pre-fire grass cover estimates and post-fire grass cover using R's lmerTest package [49,50].

Keauhou_Burned_2019$KoaRegen ~ (1 | Keauhou_Burned_2019$KoaDominance) +
Keauhou_Burned_2019$MinScorch*Keauhou_Burned_2019$PreFireTreeDensity

(2) R formula modeling the relationship between post-fire grass cover and post-fire A. koa regeneration density using R's base package [49].

Keauhou_Burned_2019$PresentGrass ~ Keauhou_Burned_2019$KoaRegen

(3) R formula modeling the relationship between minimum scorch height and pre-fire grass cover when analyzed separately from *A. koa* regeneration in montane woodland [49].

MontaneWoodland$Grass4Categories ~ MontaneWoodland$MinScorch

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