sustainability

MDPI

Article

Shifting Limitations to Restoration across Dryland Ecosystems in Hawai‘i

Erin J. Questad [1,*], Amanda Uowolo [2], Samuel Brooks [2,3] and Susan Cordell [2]

[1] Biological Sciences Department, California State Polytechnic University, Pomona, CA 91768, USA
[2] Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, HI 96720, USA; amanda.l.uowolo@usda.gov (A.U.); sebrooks@blm.gov (S.B.); susan.cordell@usda.gov (S.C.)
[3] Bureau of Land Management, Colton, OR 97017, USA
* Correspondence: ejquestad@cpp.edu

Abstract: Hawaiian dryland ecosystems are important for global biodiversity conservation and contain numerous species threatened with extinction. Over the past century, wildfire frequency and size have increased dramatically because of invasion by fire-promoting non-native invasive species, greatly threatening these ecosystems. Native species restoration is a tool that can disrupt the cycle of increased fire and invasion in lowland dry forest communities, but restoration prescriptions have not been studied systematically in other dryland plant communities. We examined the restoration of three Hawaiian dryland plant communities (a high-productivity *Diospyros sandwicensis* and *Metrosideros polymorpha* lowland dry forest (HP), a moderate-productivity *Myoporum sandwicense* and *Sophora chrysophylla* dry forest/woodland (MP), and a low-productivity *Dodonaea viscosa* shrubland (LP)), using a community-assembly framework to understand the abiotic and biotic constraints to species establishment and growth in each community. Because active restoration methods are often needed, at both high and low levels of productivity, we also examined restoration treatments and outcomes across the three sites, which spanned a gradient of rainfall and substrate age. At each site, we used the same factorial field experiment with three factors: habitat quality (high or low), weed control (yes or no), and species addition (none, seeding, or outplanting). Outplants (cohort 1) and seeds were added in the winter of 2009–2010, and outplants were added again in March 2011 (cohort 2). Dispersal limitation was apparent at the LP and HP sites, but was not observed in the MP site, which had, overall, greater native diversity and abundance. Outplant survival was greater in high-quality habitats at the HP site, likely due to reduced abiotic stress. Invasive species were found in greater abundance in certain types of microsites at the LP and MP sites, suggesting that shade or topography can be used to plan restoration and weed-control activities. Overall, active restoration methods improved restoration outcomes at the high- and low-productivity sites, and less so at the moderately productive site. Weed removal and outplanting were effective restoration prescriptions at the LP and HP sites, and habitat quality could also be used to increase survival at the HP site. Active restoration could be a lower priority for moderately invaded, moderate-productivity communities, which have the capability to maintain a native ecosystem state.

Keywords: productivity; dry forest; tropical dryland; invasive species; outplant; seed; community assembly

check for updates

Citation: Questad, E.J.; Uowolo, A.; Brooks, S.; Cordell, S. Shifting Limitations to Restoration across Dryland Ecosystems in Hawai‘i . *Sustainability* **2022**, *14*, 5421. https://doi.org/10.3390/su14095421

Academic Editors: Julio Campo, Christian P. Giardina and Rodolfo Dirzo

Received: 12 November 2021
Accepted: 21 April 2022
Published: 30 April 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Dryland ecosystems in Hawai‘i are critically important for the conservation of biodiversity and species at risk of extinction. There are more endangered species per square mile on these islands than any other place in the US, and most of these species, and the ecosystems in which they live, are found nowhere else in the world. Hawai‘i is home to nearly one-third of all federally listed threatened and endangered species and almost half of all listed plants. The total number of listed plant species in Hawai‘i has increased by

40% over the last few decades, and over 100 of these species have fewer than 20 known individuals [1]. Over 90% of the original Hawaiian dry forests have been destroyed [2,3], and over 25% of the officially listed endangered plant taxa in the Hawaiian flora are from dry forest or dry-scrub ecosystems [4].

Altered fire regimes are one of the most immediate threats to remnant dry forests and shrublands in the tropics. In Hawai'i, for example, fires were generally infrequent and limited in size prior to human-induced changes in native ecosystems [1]. Over the past century, however, wildfire frequency and size have increased dramatically, as a result of invasion by fire-promoting non-native invasive grasses [5,6]. These grasses increase fine fuel loads and alter fuel structure in ways that increase the likelihood of fire ignition and spread [7,8]. Furthermore, fire effects and post-fire environmental conditions promote the recruitment of these grasses and inhibit the recruitment of native woody species. These changes in community structure and composition result in fuel and microclimate conditions that increase the likelihood of subsequent fire [9]. In this way, non-native grass invasion initiates a grass/fire cycle that converts native forest to non-native invasive-dominated grassland [10]. This cycle is now considered the primary agent of forest-to-grassland conversion in dry and mesic plant communities in Hawai'i and elsewhere in the tropics [11–15].

Disrupting this cycle of fire and forest loss is of the utmost importance to the conservation of biodiversity in this region. Native ecosystem rehabilitation and restoration can control invasive species and, therefore, fire danger, as the shade created by native woody plants reduces the biomass of light-adapted grasses [16]. Restoration is also an attractive option for fine-fuel control, because other fuel reduction methods (i.e., prescribed burning, controlled grazing, and large-scale herbicide applications) are not likely to be ecologically or economically feasible in Hawai'i. While natural fires historically did occur in some Hawaiian plant communities [17], most native species recover slowly, if at all, after fire, and are not capable of surviving repeated fires [5]. For these reasons, prescribed burning is likely to only temporarily reduce fuels while exacerbating problems with loss of native species and invasion of non-natives. Although intense grazing can reduce fuel loads locally [18], grazing causes substantial damage to native vegetation [19,20], contributes to loss of forest cover [18] and has been shown to be ineffective at reducing fire frequency and severity at landscape scales. Finally, large-scale herbicide application is expensive and likely to be difficult to implement safely in landscapes containing substantial numbers of endangered native species. Thus, revegetation with native species may be one of the best approaches to simultaneously accomplish the goals of reducing fire risk from invasive grasses and reestablishing functioning native plant communities on disturbed sites.

The restoration of invaded ecosystems, such as Hawaiian drylands, can be improved by examining abiotic and biotic constraints to species establishment and growth, using a community-assembly framework [21–28]. Restoration is improved by understanding which processes filter species from the regional species pool to produce the co-existing members of local communities. In Hawaiian lowland dry forests, biotic filters include propagule limitation of native species, non-native ungulate grazing and browsing, and competition with invasive plant species; abiotic filters include frequent fire, drought, and other environmental stresses [29–35]. However, less is known about how filters affect the restoration of other Hawaiian dryland plant communities, such as higher elevation woodlands and shrublands, which are also critical for conserving biodiversity [36,37].

In addition, restoration methods needed to rehabilitate invaded ecosystems should vary across sites with differing levels of productivity, defined as the availability of water, nutrients, and other resources (Figure 1) [38]. Active restoration methods are often needed at both high and low productivity due to high competition with invasive species at high productivity and low establishment due to environmental stress at low productivity [38]. Restoration is expected to be more spontaneous at moderate productivity. Here, we examine restoration treatments and outcomes at three Hawaiian dryland sites, spanning a gradient of rainfall and substrate age. Our primary goal was to test whether restoration

prescriptions that are effective in lowland dry forests are also effective across the three dryland communities, or whether restoration prescriptions should vary across different dryland ecosystems. We established the same restoration field experiment simultaneously across three dryland communities, which applied treatments to address the major barriers to restoration (i.e., invasion of non-native grasses; lack of native species seed and/or propagules, and absence of suitable microhabitat for native species). We hypothesized that active restoration in the form of invasive plant removal would have its greatest impact at the highest-productivity site, active restoration in the form of planting seedlings of native species and finding suitable microhabitats would have its greatest impact in the lowest-productivity site, and the moderate-productivity site could be restored more passively.

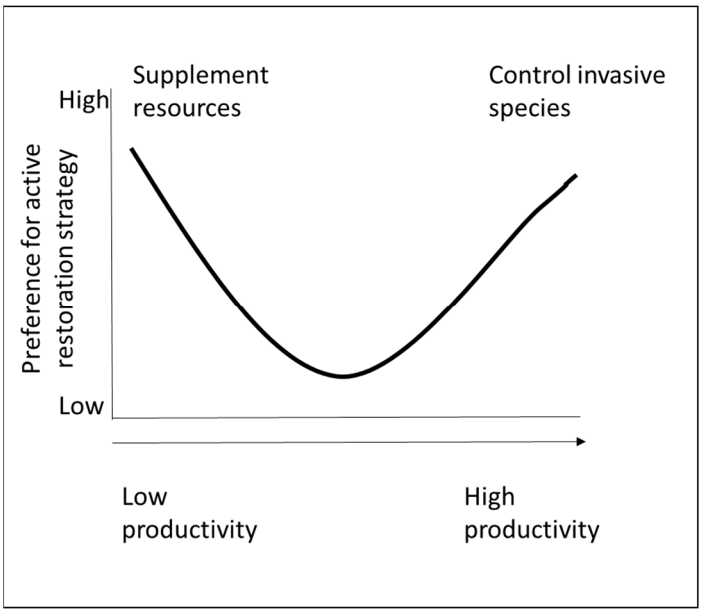


Figure 1. Preference for an active restoration strategy as a function of productivity after [38].

2. Materials and Methods

2.1. Study Sites

We identified native dryland communities that represent a large proportion of dryland ecosystems across Hawai‘i, and that are critical for restoration due to their degree of grass invasion and strategic location for fire suppression. The following three community types were selected: Lowland dry forest high productivity (HP) dominated by *Diospyros sandwicensis* (lama) and *Metrosideros polymorpha* (*‘ōhi‘a lehua*), Myoporum-Sophora dry forest/woodland moderate productivity (MP) dominated by *Myoporum sandwicense* (naio) and *Sophora chrysophylla* (māmane), and *Dodonaea viscosa* (a‘ali‘i)-dominated shrubland low productivity (LP). Two of these communities were within the Pōhakuloa Training Area (PTA) and one was found at Pu‘u Wa‘awa‘a (PWW; Figure S1).

Pu‘u Wa‘awa‘a is a state forest reserve located on the western or leeward side of the Island of Hawai‘i on the northern flank of Hualālai volcano (Figure S1). Lavas of Hualālai are primarily Holocene in age, and the study area occurred on a 1500–3000-year-old ‘A‘ā flow [39]. The study site was at approximately 600 m elevation with a mean annual temperature around 20 °C and 480 mm annual precipitation on average (Table S1). Botanical records for Pu‘u Wa‘awa‘a date back almost 100 years. Native plant communities in this zone are among the most diverse in Hawai‘i, containing many rare and endangered species [40,41]. These woodlands have been greatly damaged by fire and feral animals during the past 150 years [41]. The lowland dry forest (LDF) site occurred within PWW with *D. sandwicensis* and *M. polymorpha* as the dominant tree species. Other less common trees include *Psydrax odorata* (alahe‘e), *Erythrina sandwicensis* (wiliwili), *Reynoldsia sandwicensis* (‘ohe makai), and *Colubrina oppositifolia* (kauila). *Pennisetum setaceum* (fountain grass) was

the dominant invasive species at the site. Due to the higher rainfall of this region, this site was considered to be high productivity.

The Pōhakuloa Training Area, is the U.S. Army's largest training area in the Hawaiian archipelago located on the Island of Hawai'i, encompassing 44,045 ha in the saddle between Mauna Loa and Mauna Kea volcanoes (Figure S1). Because of PTA's position largely above the inversion layer, its rainfall is considerably lower than the LDF zone at lower elevations. The average annual precipitation across the installation is 370 mm with the highest rainfall accruing in the winter months. The annual mean temperature is about 16 °C. Vegetative cover varies from barren lava to dense shrub and forest ecosystems but is collectively classified as Subalpine Dryland [42]. The vegetation found in a given area is largely a function of the age of the lava flow on which it grows, as nutrient availability varies predictively with substrate age and type [43,44]. This area is biologically rich encompassing 24 vegetation communities. Twenty-two rare plant species have been documented with eleven of those listed as federally endangered and nine as species of concern [45]. Numerous rare and endangered fauna are also found at PTA. Critical habitat and areas of special concern in terms of their botanical composition and or habitat value for rare species have been designated at PTA [46]. The MP dry forest/woodland site occurred within PTA at Kipuka Alala at 1600 m elevation on a 3000–5000-year-old pāhoehoe substrate from Mauna Loa. The LP *Dodonaea viscosa* shrubland site occurred within PTA at Kipuka Kalāwamauna at 1622 m on a 14–65 thousand-year-old a'a substrate from Mauna Kea [47–49]. Average rainfall in the four years prior to this study at the MP and LP was 404 mm and 297 mm, respectively (Table S1). Common invasive species at both sites include *P. setaceum* and *Senecio madagascariensis* (fireweed). *Delairea odorata* (cape ivy) also occurs at the MP site.

The three sites represent a gradient of productivity based on rainfall and substrate age, as nutrient availability, especially phosphorous, declines as substrates age [43,44]. The HP site has the highest rainfall and youngest substrate; the MP site has intermediate rainfall and an intermediate substrate age; the LP site has lower rainfall and the oldest substrate (Table S1). During the present study, rainfall was exceptionally low due to historic drought conditions (Table S1). Aboveground carbon stocks, an indicator of primary production, were estimated to be 1090 Mg C ha^{-1} for the HP site and 1 Mg C ha^{-1} for the MP site [50]. Carbon stocks for the LP site were not estimated but are expected to be lower than the MP site due to a lack of tree canopy cover.

2.2. Experimental Design and Data Collection

We used a factorial field experiment with three factors: habitat quality (high or low), weed control (yes or no), and species addition (none, seeding, or outplanting). Within each community type, we established six 15 x 25 m blocks with similar elevation and substrates in fenced ungulate exclosures. Three of these blocks represented high-quality habitat patches and three represented low-quality/degraded habitat. We used remote sensing data and imagery analysis to locate high-quality and degraded habitat areas. For the HP and MP sites, we used LiDAR data to find high-quality areas with dense tree canopy cover (upper 25th percentile of canopy cover for each ecosystem), and we located low-quality blocks in nearby open areas. Areas under trees were considered higher quality due to shade that reduces solar stress and inhibits invasive grass growth as well as lower wind speeds which can be desiccating to young seedlings. Due to the low stature of vegetation in the LP, we used analysis of microtopography to locate high- and low-quality areas. Higher-quality areas were protected from desiccating winds and were in topographic depressions where soil accumulates more quickly and moisture is retained for longer periods [36].

Each block was divided into six 4.5 x 4.5 m plots with a buffer of at least 5 m in between. Experimental weed control and species addition treatments were applied in a fully factorial combination to the six plots in each block. In 2009, the plots receiving weed control had all invasive species removed by spraying 2% glyphosate herbicide, followed by mechanical weed trimming and hand clearing two weeks later. Plots were monitored regularly for the duration of the study and weeded as necessary.

Our first outplanting (cohort 1) of native species occurred in November and December 2009 (Table S2). Outplants were grown from seed collected from each site in a growing medium of one part cinder and three parts Sunshine Media Mix #3 (Sun Gro Horticulture Distribution Inc., Agawam, MA, USA) at the Institute of Pacific Islands Forestry nursery (Hilo, HI, USA). Outplants were grown for three to six months, depending on the species, and were hardened in the field at each site for at least two weeks before outplanting. The size of plants varied but was approximately 20 cm tall on average. The outplants were planted in a random order in a seven-by-seven grid, equally spaced within each plot. The species selected for each site represented common species occurring in nearby intact plant communities. As is typical with large-scale restoration projects, the number of individuals of each species varied depending on propagation success of the species (Table S2). While this led to an unequal number of each species planted it reflects a standard practice in restoration used to maximize the total number of seedlings added to a site. Seeds of all species were hand broadcast to seeded plots in January 2010. The number of seeds added per species varied depending on seed viability, determined with tetrazolium testing and germination trials; therefore, more seeds were added for species with lower viability to equalize germination potential (Table S2). Due to low survival of cohort 1 outplants a second outplanting (cohort 2) of 20 *D. viscosa* seedlings per plot occurred in March 2011. This species was selected due to its common abundance at all three sites. Plants were grown by Future Forests Nursery (Kailua-Kona, HI, USA) from seeds collected at each site. Plants were planted evenly spaced in each plot, and evenly spaced with any existing outplants from cohort 1.

The effectiveness of restoration treatments was measured as survival of outplants; increases in native species cover, richness, and diversity, and decreases in invasive species cover. Outplants in cohort 1 were surveyed for survival in Spring 2010 during April, Fall 2010 during August, and Spring 2011 in February. Outplants in cohort 1 and 2 were surveyed in Fall 2011 in October, and Spring 2012 in February and March. Species cover estimates were collected from three 4.5 m parallel transects in each plot, point sampled every 50 cm with a 1.9 cm diameter pole. The percent cover of each species was calculated as the number of points it occurred at in the plot divided by the total number of sampling points. Only understory species were sampled and large canopy trees were excluded. We calculated total native and invasive cover by summing the percent cover of all species in each category, native species richness (S) as the number of native species recorded, and native species diversity as the inverse Simpson's index (1/D).

2.3. Statistical Analysis

Due to low survival of cohort 1 at all sites (Table 1) survival data from only the Spring 2010 census were analyzed. For the HP site, survival of each outplant from cohort 1 was analyzed with a generalized linear mixed effects model with a binomial distribution. The model had fixed factors for species identity, habitat quality, weed control, and species addition, and random factors for plot and block. All two-way interaction terms were included in the model. Due to very low survival, the species *M. polymorpha* was excluded from the analysis. Due to even lower survival of cohort 1 at the LP and MP sites, survival of each species (presence/absence within a plot) was analyzed with a generalized linear mixed effect model with a binomial distribution using the same fixed and random effects and interaction terms as for the HP site.

Survival of cohort 2 was calculated as the proportion of *D. viscosa* outplants surviving in each plot and was analyzed separately for each site. Survival was analyzed with a linear mixed effects model with fixed effects for sampling date, habitat quality, weed control, and species addition, and random factors for plot and block. All two-way interaction terms were included in the model.

Total invasive cover, total native cover, S, 1/D, and E were analyzed separately for each site with a linear mixed effect model. The model included fixed factors for date, habitat quality, weed control, and species addition, and random factors for plot and block,

as well as all two-way interaction terms. All analyses were conducted using R and the lme4 package [51,52]. Least square means were calculated for pairwise comparisons between levels of fixed factors and interaction terms using the package emmeans [53].

3. Results

3.1. Outplant Survival

Survival of the first cohort of seedlings was low, especially in the MP and LP sites (Table 1). At the HP site, cohort 1 survival of *Chenopodium oahuense* was greatest among the species (Table S3, Figure 2), and survival of all species declined over time (Figure S2a). There was a trend of greater survival in high-quality habitats, and survival of *C. oahuense*, *S. fallax*, *S. chrysophylla*, and *O. anthyllidifolia* was 1.35, 1.55, 2.96, and 1.94-times higher in high-quality habitats, respectively; however, the difference was significant only for *S. chrysophylla* (Table S3, Figure 2). When cohort 1 survival data were analyzed for the MP and LP sites, no significant treatment effects were found at either site ($p > 0.05$). By the final survey in 2012, survival of cohort 2 ranged from 15% to 100% among plots, with all plots having three or more of the twenty planted individuals surviving. Survival of cohort 2 declined over time at all three sites and was lowest overall at the HP site (Table 2, significant date factor; Figure S2b). There were no other significant treatment effects on survival of cohort 2 at any site.

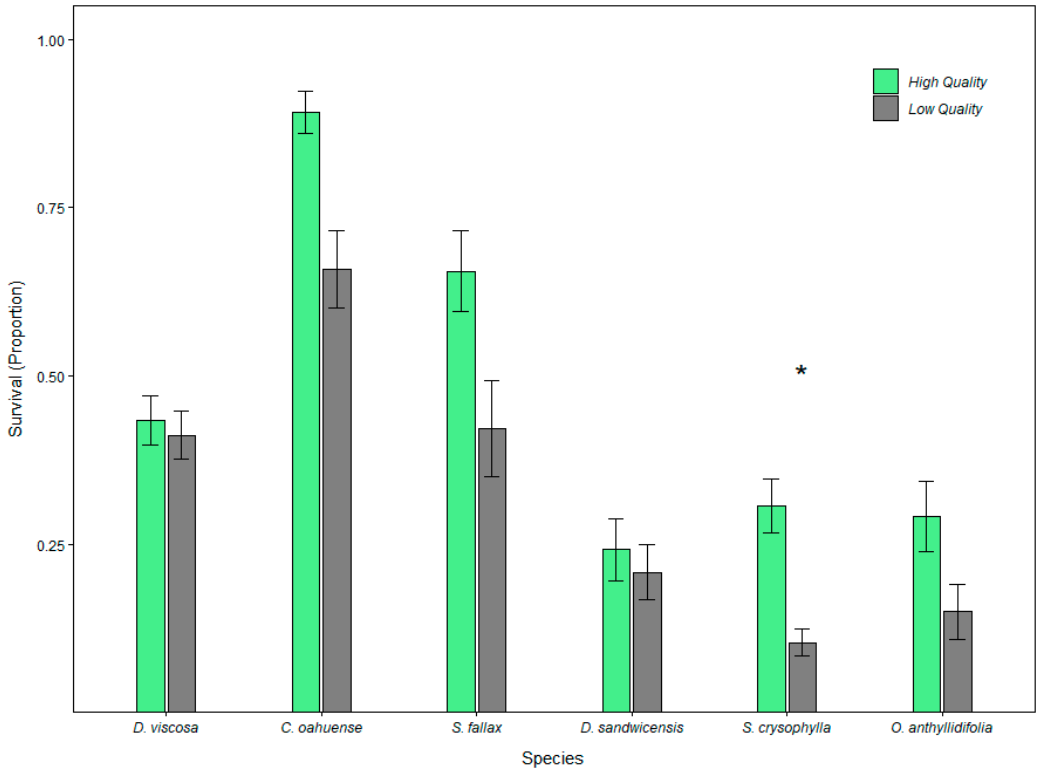


Figure 2. Survival of cohort 1 outplants at the HP site expressed as proportion of individuals surviving in each plot. Mean and standard error for each species across high-quality and low-quality plots. Data are presented as proportions for visual comparison, but were analyzed with a mixed effects model with a binomial distribution (* $p = 0.05$).

Table 1. The number of plots (out of 12 maximum) at each site with cohort 1 individuals surviving.

Species	Spring 2010			Spring 2011		
	LP	MP	HP	LP	MP	HP
Dodonaea viscosa	4	9	12	1	0	12
Chenopodium oahuense	10	6	12	0	0	12
Bidens menziesii	5	5	N/A	0	0	N/A
Dubautia linearis	3	5	N/A	0	0	N/A
Sida fallax	8	3	11	0	0	9
Sophora chrysophylla	3	7	12	0	0	10
Metrosideros polymorpha	1	0	0	0	0	0
Diospyros sandwicensis	N/A	N/A	10	N/A	N/A	6
Osteomeles anthyllidifolia	N/A	N/A	7	N/A	N/A	6

Table 2. Linear model results (F values) for survival analysis at the LDF site.

	LDF Cohort 1			LDF Cohort 2		
	Num df	Den df	F	Num df	Den df	F
Habitat Quality	1	8	2.03	1	8	1.82
Weed Control	1	8	0.24	1	8	2.98
Species	5	301	83.57 ***	N/A	N/A	N/A
Date	4	301	6.90 ***	1	9	28.17 ***
Habitat Quality: Weed Control	1	8	1.98	1	8	0.02
Habitat Quality: Date	4	301	0.20	1	9	2.67
Habitat Quality: Species	5	301	3.75 **	N/A	N/A	N/A
Weed Control: Species	5	301	2.22	N/A	N/A	N/A
Weed Control: Date	4	301	0.04	1	9	4.17
Species: Date	24	301	0.29	N/A	N/A	N/A

Significance codes: *** <0.001 ** <0.01–0.06.

3.2. Percent Cover

Non-native cover was highest in 2011 in the HP and MP sites and was highest in 2012 in the LP site (Table 3 significant year factor). Weed control reduced non-native species cover at all sites (Table 3 significant weed control factor; Figure 3C). The MP site had the greatest increase in non-native cover over time (Figure 3A). Interestingly, the interaction of habitat quality with the weed control treatment was different between the MP and LP sites (Table 3, Figure 4). In plots without weed control in the MP site, non-native species cover was 1.5-times greater in high-quality, compared to low-quality, treatments; however, in the LP site, it was 1.8-times greater in low-quality, compared to high-quality, treatments (Figure 4, Table 3 significant habitat quality x weed control interaction). There were also differences in which invasive species were abundant in each site; *S. madagascariensis* was the most abundant invasive species in the MP site, whereas *P. setaceum* was the most abundant species in the LP and HP sites (Table S4). In the plots without weed control in the LP site, non-native species cover was 53% in the no-species-addition treatment and 58% in the seed-addition treatment, and it was reduced to 41% in the outplanting treatment (Table 3 significant weed control x species addition interaction; Figure S3).

Table 3. Linear model results (F values) for analyses of native and non-native cover.

	Num df	Den df	Native Cover			Non-Native Cover		
			LP	MP	HP	LP	MP	HP
Habitat Quality	1	4	2.76	6.03	2.82	16.34 *	1.43	1.17
Weed Control	1	22	3.11	2.35	0.003	244.51 ***	66.36 ***	287.62 ***
Species Addition	2	22	0.81	3.53 *	7.06 **	3.42	0.07	0.87
Year	2	62	7.54 **	2.22	32.89 ***	22.45 ***	33.08 ***	3.28 *
Habitat Quality: Weed Control	1	22	1.22	2.86	1.52	24.64 ***	4.69 *	2.36
Habitat Quality: Year	2	62	3.02-	0.51	1.59	1.23	1.37	0.01
Habitat Quality: Species Addition	2	22	0.08	0.47	0.09	1.30	1.35	0.58
Weed Control: Species Addition	2	22	0.20	2.92	0.72	3.87 *	1.54	0.16
Weed Control: Year	2	62	1.06	0.96	3.53 *	4.47 *	1.37	0.33
Species Addition: Year	4	62	0.65	0.38	19.63 ***	0.87	1.19	1.72

Significance codes: *** <0.001 ** <0.01 * <0.05–0.06.

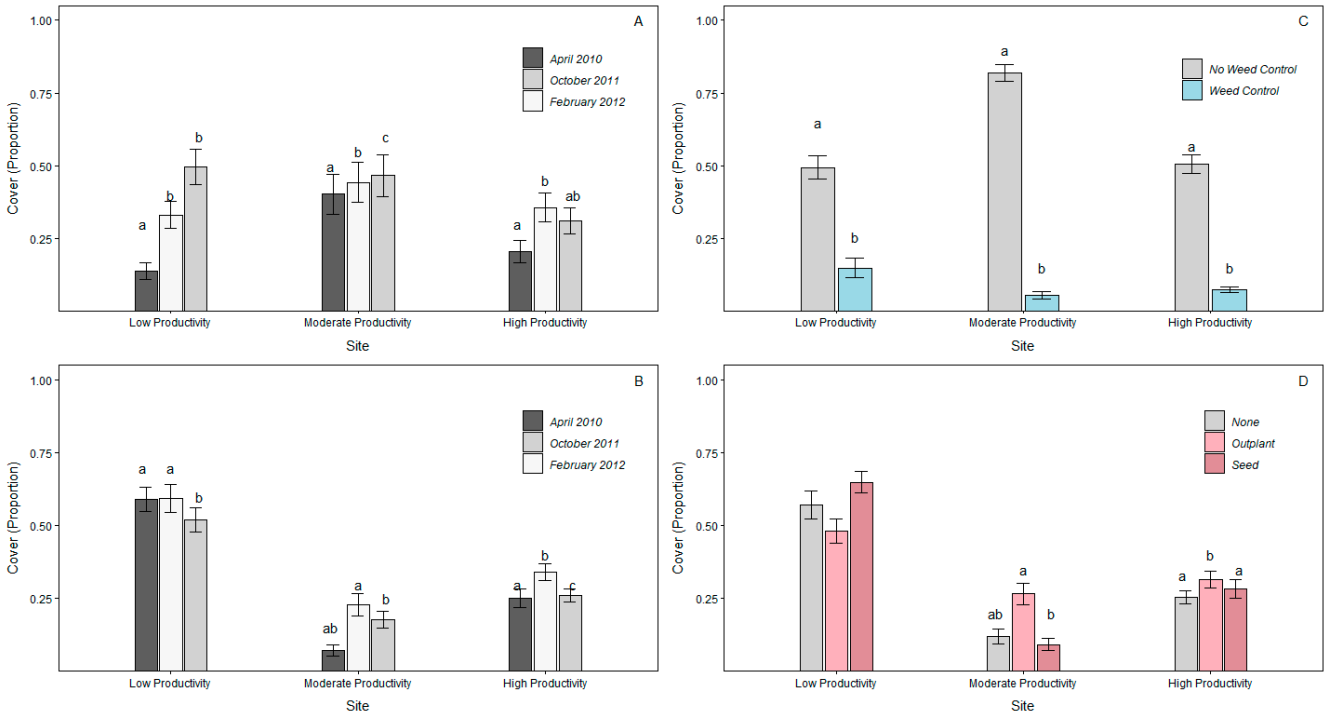


Figure 3. Cover at each site of (**A**) non-native species over sampling dates, (**B**) native species over sampling dates, (**C**) non-native species by weed control treatment, and (**D**) native species by species-addition treatment. Mean and standard error of cover expressed as a proportion. Letters indicate significant differences among factor levels within each site ($p < 0.05$).

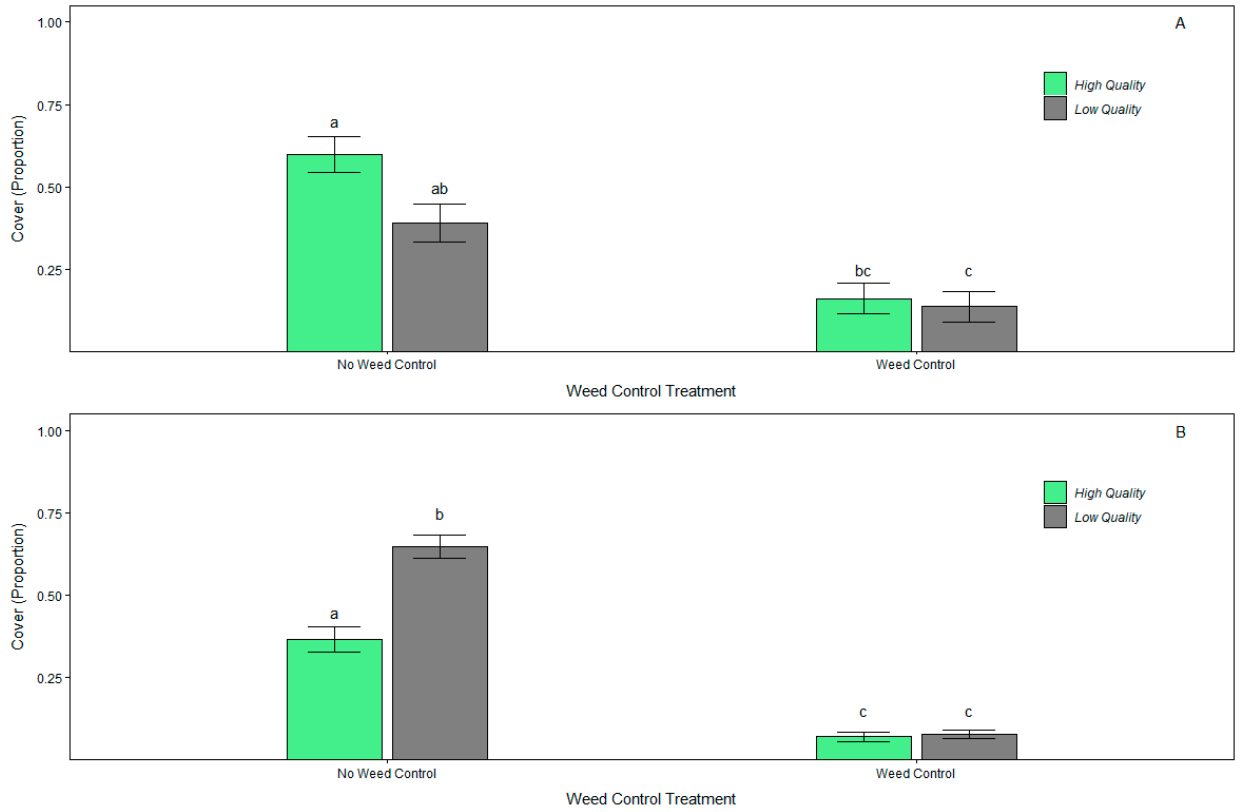


Figure 4. Non-native cover by weed control and habitat quality treatments in the (**A**) MP site and (**B**) LP site. Mean and standard error of cover expressed as a proportion. Without weed control, non-native cover was higher in low-quality habitats at the LP site but was higher in high-quality habitats at the MP site. Letters indicate significant differences among factor levels within each site ($p < 0.05$).

Native cover was lowest in the HP site and highest in the MP site, and it increased over time in the HP and LP sites and stayed the same in the MP site (Table 3 significant year factor, Figure 3B). In the MP site, the seed-addition treatment had slightly higher native cover than the other treatments; however, this was likely due to the native cover conditions at the start of the experiment (Table 3, Figure 3D). The influence of the experimental treatments on native cover was most evident in the HP site, where native cover was approximately three-times greater in outplanted treatments compared to no-addition treatments, in 2011 and 2012 (Table 3 significant species addition x year interaction, Figure 3D). Plots receiving weed control in the HP site had low native cover in 2010, but in 2011, the native cover was greater than unweeded plots; however, by 2012, native cover was equal among weed control treatments (Table 3 significant weed control x year interaction, Figure S4).

3.3. Native Richness and Diversity

Native species richness ranged from zero to six species per plot. Richness and diversity were lowest at the HP site and highest at the MP site (Figure S5). Outplanting significantly increased richness and diversity at the HP and LP sites, but not the MP site (Tables S5 and S6 significant species addition x year interaction; Figure 5). While there were some significant treatment effects on richness and diversity at the MP site, they were difficult to interpret in the context of this study.

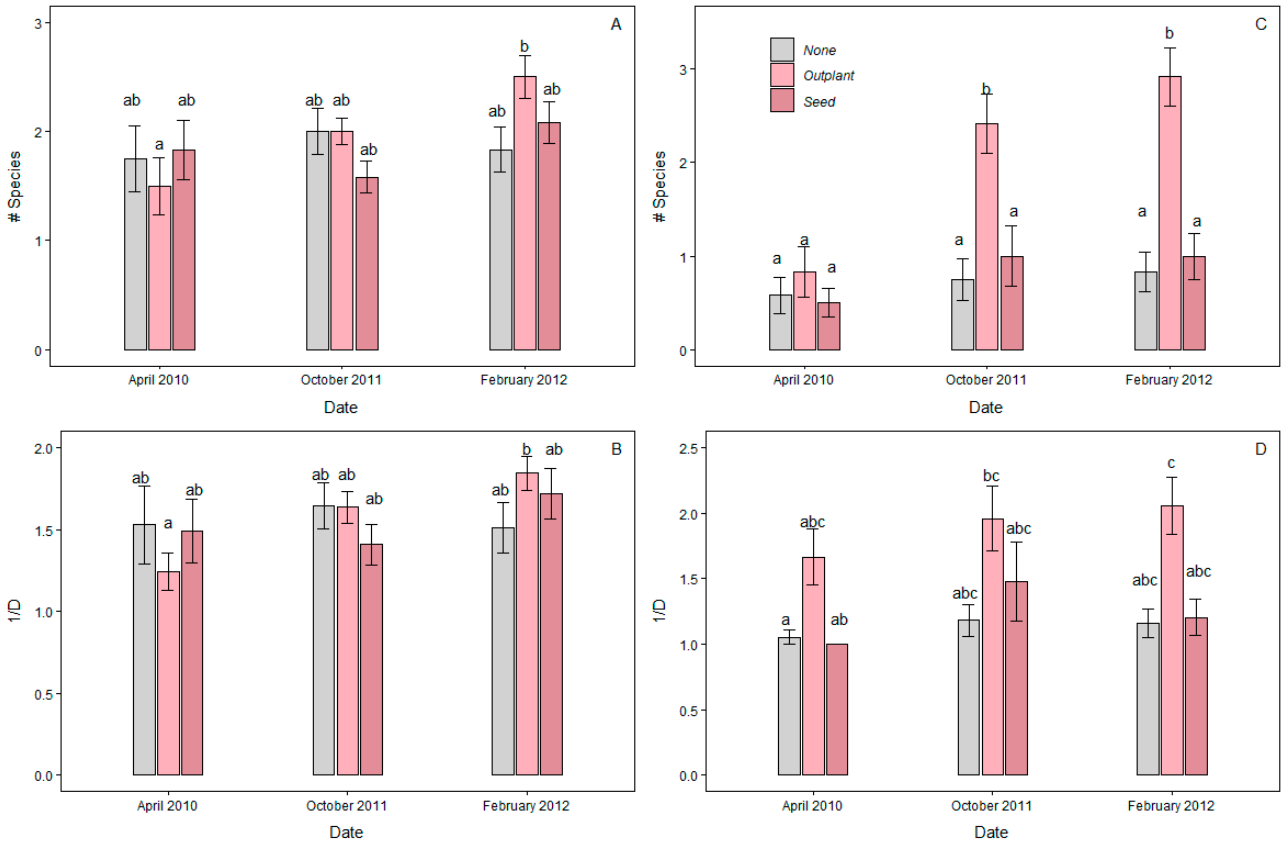


Figure 5. LP (**A**,**B**) and HP (**C**,**D**) richness and diversity by species addition. In the LP site, the outplanting treatment on the final sampling date had the highest species richness. In the HP site, the outplanting treatment on the last two sampling dates had the highest richness. HP native diversity was greatest in the outplanting treatment over all sampling dates. Letters indicate significant differences among factor levels ($p < 0.05$).

4. Discussion

Removing or controlling invasive species is often the first step in the restoration of invaded ecosystems and its effectiveness has been demonstrated previously in LDF restoration at other sites [29,30,33,34,54–56]. Our weed control treatment was successful in reducing non-native species at all sites but had the greatest impact at the LDF/HP site, where the difference in invasive cover between weeded and non-weeded treatments was greatest. Therefore, if the goal of restoration is to reduce the abundance of invasive species and fine fuels, weed control would be successful across dryland communities; however, we found that if the goal is to increase native biodiversity, more intensive restoration is needed.

The restoration prescriptions that were the most effective at increasing native biodiversity varied across sites (Table 4). As predicted (Figure 1), outplanting, the most expensive and labor-intensive treatment, had positive impacts on restoration, at both the low- and high-productivity sites and had more modest effects at the MP site. At the LP and HP sites, outplanting increased native species richness and diversity, although the increase in richness due to outplanting was modest, ranging from approximately 0.67 to 2.1 species more than sites receiving no outplanting or seed addition (Figure 5 final sampling date). At the LP site, outplanting also reduced non-native cover, and at the MP and HP sites, it increased native cover but only by a small amount.

Table 4. Site-specific pathways conceptualizing relevance to future management based on restoration metric, treatments applied, and initial site conditions. Restoration success is considered as outplant survival, a decrease in non-native cover, or an increase in native cover, species richness, or species diversity. A (+) symbol indicates a significantly positive response between the treatment and the desired outcome; a (++) symbol indicates a very large, significant positive response; a (–) symbol indicates a significant negative response. Responses for the seed-addition treatment were not significant and are not included in the table.

		Low LP	**Moderate MP**	**High HP**	**Initial Productivity**
Metric	**Treatment**				
Outplant Survival	Habitat quality			+	
	Weed removal				
Non-native cover	Habitat quality	+	–		
	Weed removal	++	++	++	
	Outplanting	+			
Native cover	Habitat quality				
	Weed removal				
	Outplanting			+	
Native richness	Habitat quality				
	Weed removal				
	Outplanting	+		++	
Native diversity	Habitat quality		*		
	Weed removal		*		
	Outplanting	+		++	

* Unresolved and needs further study.

The larger increase in native richness with outplanting at the HP site is likely due to the greater survival of cohort 1, which included several species, compared to cohort 2, which included only *D. viscosa*. There was no benefit of outplanting on richness or diversity in the MP site, likely because this site had higher native richness and abundance than the other sites before restoration. Further research testing the establishment of a variety of species with a variety of functional traits would improve our understanding of which species are the most useful for restoration activities in different dryland communities.

Seeding has been used with moderate success in prior LDF restoration experiments but had no effect on restoration at any of our study sites [29,30]. This result could be explained by the extreme drought conditions that occurred during the study. In the year that seeding occurred, rainfall was 44, 68, and 105 mm at the LP, MP, and HP sites, respectively (Table S1). These values are 15–22% of the typical average rainfall and are among the lowest levels ever recorded at these sites. Seeding has been shown to be effective at increasing native cover in less stressful conditions [30]; therefore, seeding could be an effective restoration treatment in wetter years, but more study is needed to understand its impact across dryland ecosystems. However, the positive impact of outplanting but lack of effect of seeding suggests that there are biotic and abiotic filters during community assembly of these communities. First, the biotic filter of propagule limitation of native species was expanded by both treatments. The lack of impact of seeding suggests that addressing this filter alone was not sufficient and that other filters, such as seedling desiccation stress or granivory, also limit the establishment of native plants in these communities.

It was interesting that cohort 1 had the highest survival at the HP site and extremely low survival at the other two sites, whereas cohort 2 had the lowest survival at the HP sites compared to the other two (Figure 3). The low survival of cohort 1 at the drier sites can be explained by the extreme drought conditions during the study. However, the lower survival of cohort 2 at the HP site is harder to explain. One possibility is our use of volunteers to

aid with planting at this site, but not the other sites due to the limited access of civilians in the Army training area. Volunteers were trained and supervised by research staff, but it is possible that survival was lower if volunteers were not as careful as paid employees during planting activities. The use of volunteers in restoration planting is ubiquitous and cost effective, but few studies have reported associated survival results, indicating an area that needs more study [57–59].

Outplanting in high-quality habitats led to greater survival rates for several species at the HP site (Figure 2), but we did not find strong associations between habitat quality and restoration outcomes at the other sites. It is possible that the drought conditions during the study reduced any fine-scale abiotic differences between high- and low-quality habitats as we defined them. These differences could be more apparent during years with more typical rainfall. Therefore, it is important to continue studies of various microsite conditions and how they affect plant establishment across years with varying conditions.

However, we did find that without restoration, invasive species cover was higher in high-quality habitats at the LP site but was higher in low-quality habitats at the MP site. This result occurred due to how we defined habitat quality at each site and due to the identity of the dominant invasive species. At the LP site, *P. setaceum* was the most abundant invasive species, and its occurrence was greater in more extreme topographic microsites. This species is a C4 grass that is adapted to warmer temperatures and grows on steep hillsides; therefore, it may be able to take advantage of space in these more stressful areas, where native growth is reduced [36]. The dominant invader at the MP site was *S. madagascariensis*, a low-statured forb occurring in open areas. This species was less abundant in high-quality sites, under the canopy of existing trees, where it potentially was light-limited. Therefore, our designation of shadier microsites as "high quality" is somewhat species-specific, especially when applied to invasive species that are adapted to high-light environments. However, this result supports the pattern also found in LDF restoration, where competition with invasive species is reduced in shadier microsites with greater soil moisture [33]. Therefore, restoration could be planned strategically in shadier sites if competition with invasive species is a concern.

In summary, several important abiotic and biotic filters were identified by replicating this study among three dryland plant communities. Native dispersal limitation was apparent at the LP and HP sites but was not observed in the MP site, which had overall greater native diversity and abundance. Outplant survival was greater in high-quality habitats at the HP site, likely due to reduced abiotic stress. Invasive species were found in greater abundance in certain types of microsites at the LP and MP sites, suggesting that shade or topography can be used to plan restoration and weed control activities. Overall, active restoration methods improved outcomes at the high- and low-productivity sites, and less so at the moderately productive site. Weed removal and outplanting were effective restoration prescriptions at the LP and HP sites, and habitat quality could also be used to increase survival at the HP site. Active restoration could be a lower priority for moderately invaded, moderate-productivity communities, which have the capability to maintain a native ecosystem state.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/su14095421/s1, Table S1. Annual rainfall totals for each site during the years of the study and the average of the four years prior to the study, Table S2. Number of cohort 1 outplants and seeds added to each plot at each site, Table S3. Generalized linear model results for cohort 1 at the HP site, Table S4. Mean abundance of common understory species in each site, Table S5. Linear model results for analyses of species richness, Table S6. Linear model results for analyses of native diversity, Figure S1. Map of research sites on the Island of Hawai'i, Figure S2. Outplant survival over time for cohort 1 and cohort 2, Figure S3. LP non-native cover by weed control and species-addition treatments, Figure S4. HP native cover by weed control and date, Figure S5. Richness (A) and diversity (B) by date among sites.

Author Contributions: Conceptualization, S.C. and E.J.Q.; methodology, S.B., A.U., E.J.Q. and S.C.; investigation, S.B., A.U. and E.J.Q.; data curation, S.B., A.U. and E.J.Q.; writing—original draft preparation, E.J.Q.; writing—review and editing, S.B., A.U., E.J.Q. and S.C.; funding acquisition, S.C. and E.J.Q. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Department of Defense Strategic Environmental Research and Development Program and the Environmental Security Technology Certification Program for funding (Projects RC-1645 and RC-201203).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to data concerning sensitive species.

Acknowledgments: Thank you to M. Selvig, M. Biggs, R. Moseley, H. K. Hinds, J. Diep, and C. Perry for fieldwork assistance and K. Kinney for mapping support. We also thank staff at Pōhakuloa Military Training area, the USDA Forest Service, Institute of Pacific Islands Forestry, and the State of Hawaii, Division of Forestry and Wildlife for logistics and field support. We gratefully acknowledge Commanders W. Richardson, R. C. Niles, and E. P. Shwedo for support at PTA and E. Parsons for support at PWW.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Loope, L.L. Hawaii and the pacific islands. *Status Trends Nation's Biol. Resour.* **1998**, *2*, 747–774.
2. Bruegmann, M.M. Hawaii's dry forests. *Endanger. Species Bull.* **1996**, *21*, 26–27.
3. Mehrhoff, L. Rare Plants in Hawaii: A Status Report. *Plant Conserv.* **1993**, *7*, 1–2.
4. Barton, K.E.; Westerband, A.; Ostertag, R.; Stacy, E.; Winter, K.; Drake, D.R.; Fortini, L.B.; Litton, C.M.; Cordell, S.; Krushelnycky, P.; et al. Hawai'i forest review: Synthesizing the ecology, evolution, and conservation of a model system. *Perspect. Plant Ecol. Evol. Syst.* **2021**, *52*, 125631. [CrossRef]
5. Smith, C.; Tunison, J. *Fire and Alien Plants in Hawaii: Research and Management Implications for Native Ecosystems*; University of Hawaii at Manoa Department of Botany: Honolulu, HI, USA, 1992; pp. 394–408.
6. Trauernicht, C.; Pickett, E.; Giardina, C.P.; Litton, C.M.; Cordell, S.; Beavers, A. The Contemporary Scale and Context of Wildfire in Hawaii. *Pac. Sci.* **2015**, *69*, 427–444. [CrossRef]
7. Fujioka, F.M.; Fujii, D.M. *Physical Characteristics of Selected Fine Fuels in Hawaii—Some Refinements on Surface Area—To Volume Calculations*; USDA Forest Service Pacific Southwest Forest and Range Experiment Station: Berkeley, CA, USA, 1980; pp. 1–8.
8. Hughes, R.F.; Vitousek, P.M.; Tunison, T. Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology* **1991**, *72*, 743–746. [CrossRef]
9. Freifelder, R.R.; Vitousek, P.M.; D'Antonio, C.M. Microclimate change and effect on fire following forest-grass conversion in seasonally dry tropical woodland. *Biotropica* **1998**, *30*, 286–297. [CrossRef]
10. D'Antonio, C.M.; Vitousek, P.M. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **1992**, *23*, 63–87. [CrossRef]
11. Mack, M.C.; D'Antonio, C.M. Impacts of biological invasions on disturbance regimes. *Tree* **1998**, *13*, 195–198. [CrossRef]
12. Angelo, C.L.; Daehler, C.C. Upward expansion of fire-adapted grasses along a warming tropical elevation gradient. *Ecography* **2013**, *36*, 551–559. [CrossRef]
13. Bowman, D.M.; MacDermott, H.J.; Nichols, S.C.; Murphy, B.P. A grass–Fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecol. Evol.* **2014**, *421*, 4185–4194. [CrossRef]
14. Goldammer, J.G. *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges*; Springer Science & Business Media: Berlin/Heidelberg, Germany, 2012; Volume 84.
15. Loope, L.L.; Hughes, R.F.; Meyer, J.-Y. Plant invasions in protected areas of tropical Pacific Islands, with special reference to Hawaii. In *Plant Invasions in Protected Areas*; Springer: Berlin/Heidelberg, Germany, 2013; pp. 313–348.
16. Funk, J.L.; McDaniel, S. Altering Light Availability to Restore Invaded Forest: The Predictive Role of Plant Traits. *Restor. Ecol.* **2010**, *18*, 865–872. [CrossRef]
17. Mueller-Dombois, D. Vegetation dynamics in a coastal grassland of Hawaii. *Vegetatio* **1981**, *46*, 131–140. [CrossRef]
18. Blackmore, M.; Vitousek, P.M. Cattle grazing, forest loss, and fuel loading in a dry forest ecosystem at Pu'u Wa'aWa'a Ranch, Hawai'i. *Biotropica* **2000**, *32*, 625–632. [CrossRef]
19. Scowcroft, P.G.; Giffin, J.G. Feral herbivores suppress mamane and other browse species on Mauna Kea. *J. Range Manag.* **1983**, *36*, 638–645. [CrossRef]

20. Zhu, T.R.; Litton, C.M.; Giardina, C.P.; Trauernicht, C. Moisture availability and ecological restoration limit fine fuels and modeled wildfire intensity following nonnative ungulate removal in Hawaii. *J. Appl. Ecol.* **2021**, *58*, 2207–2219. [CrossRef]
21. Fargione, J.; Brown, C.S.; Tilman, D. Community assembly and invasion: An experimental test of neutral versus niches processes. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, 8916–8920. [CrossRef]
22. Weiher, E.; Freund, D.; Bunton, T.; Stefanski, A.; Lee, T.; Bentivenga, S. Advances, challenges and a developing synthesis of ecological community assembly theory. *Philos. T. R. Soc. B* **2011**, *366*, 2403–2413. [CrossRef]
23. Young, T.P.; Chase, J.M.; Huddleston, R.T. Community succession and assembly: Comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecol. Restor.* **2001**, *19*, 5–18. [CrossRef]
24. Young, T.P.; Petersen, D.A.; Clary, J.J. The ecology of restoration: Historical links, emerging issues and unexplored realms. *Ecol. Lett.* **2005**, *8*, 1–12. [CrossRef]
25. Funk, J.L.; Cleland, E.E.; Suding, K.N.; Zavaleta, E.S. Restoration through reassembly: Plant traits and invasion resistance. *Trends Ecol. Evol.* **2008**, *23*, 695–703. [CrossRef] [PubMed]
26. Hobbs, R.J.; Jentsch, A.; Temperton, V.M. Restoration as a Process of Assembly and Succession Mediated by Disturbance. In *Linking Restoration and Ecological Succession*; Walker, L.R., Walker, J., Hobbs, R.J., Eds.; Springer: New York, NY, USA, 2007. [CrossRef]
27. Temperton, V.M.; Hobbs, R.J.; Nuttle, T.; Halle, S. *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*; Island Press: Washington, DC, USA, 2004.
28. Weiher, E.; Keddy, P. *Ecological Assembly Rules: Perspectives, Advances, Retreats*; Cambridge University Press: Cambridge, UK, 1999.
29. Cabin, R.J.; Weller, S.G.; Lorence, D.H.; Cordell, S.; Hadway, L.J. Effects of microsite, water, weeding, and direct seeding on the regeneration of native and alien species within a Hawaiian dry forest preserve. *Biol. Conserv.* **2002**, *104*, 181–190. [CrossRef]
30. Cabin, R.J.; Weller, S.G.; Lorence, D.H.; Cordell, S.; Hadway, L.J.; Montgomery, R.; Goo, D.; Urakami, A. Effects of light, alien grass, and native species additions on Hawaiian dry forest restoration. *Ecol. Appl.* **2002**, *12*, 1595–1610. [CrossRef]
31. Cabin, R.J.; Weller, S.G.; Lorence, D.H.; Flynn, T.W.; Sakai, A.K.; Sandquist, D.; Hadway, L.J. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conserv. Biol.* **2000**, *14*, 439–453. [CrossRef]
32. Thaxton, J.M.; Cole, T.C.; Cordell, S.; Cabin, R.J.; Sandquist, D.R.; Litton, C.M. Native species regeneration following ungulate exclusion and nonnative grass removal in a remnant Hawaiian dry forest. *Pac. Sci.* **2010**, *64*, 533–544. [CrossRef]
33. Thaxton, J.M.; Cordell, S.; Cabin, R.J.; Sandquist, D.R. Non-native grass removal and shade increase soil moisture and seedling performance during Hawaiian dry forest restoration. *Restor. Ecol.* **2012**, *20*, 475–482. [CrossRef]
34. Ammondt, S.A.; Litton, C.M.; Ellsworth, L.M.; Leary, J. Restoration of native plant commnities in a Hawaiian dry lowland ecoystem dominated by the invasive grass *Megathyrsus macimum*. *Appl. Veg. Sci.* **2013**, *1*, 29–39. [CrossRef]
35. Questad, E.J.; Thaxton, J.M.; Cordell, S. Patterns and consequences of re-invasion into a Hawaiian dry forest restoration. *Biol. Invasions* **2012**, *14*, 2573–2586. [CrossRef]
36. Questad, E.J.; Kellner, J.R.; Kinney, K.; Cordell, S.; Asner, G.P.; Thaxton, J.; Diep, J.; Uowolo, A.; Brooks, S.; Inman-Narahari, N.; et al. Mapping habitat suitability for at-risk plant species and its implications for restoration and reintroduction. *Ecol. Appl.* **2014**, *24*, 385–395. [CrossRef]
37. Kellner, J.R.; Asner, G.P.; Kinney, K.M.; Loarie, S.R.; Knapp, D.E.; Kennedy-Bowdoin, T.; Questad, E.J.; Cordell, S.; Thaxton, J.M. Remote analysis of biological invasion and the impact of enemy release. *Ecol. Appl.* **2011**, *21*, 2094–2104. [CrossRef]
38. Prach, K.; Hobbs, R.J. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restor. Ecol.* **2008**, *16*, 363–366. [CrossRef]
39. Moore, J.; Clague, D. Volcano growth and evolution of the island of Hawaii. *Geol. Soc. Am. Bull.* **1992**, *104*, 1471–1484. [CrossRef]
40. Rock, J.F. *The Indigenous Trees of the Hawaiian Islands*, Reprinted in 1974 ed.; Pacific Tropical Botanical Garden: Lawai, HI, USA; Charles F. Tuttle: Rutland, VT, USA, 1913.
41. Giffin, J.G. *Puu Waawaa Biological Assessment, Puu Waawaa, North Kona, Hawaii*; State of Hawaii, Department of Land and Natural Resources, Division of Forestry and Wildlife: Hilo, HI, USA, 2003; p. 92.
42. Bern, C. *Land Condition-Trend Analysis Summary of Vegetation Monitoring, Pohakuloa Training Area, Hawaii, 1893–1993*; Center for Ecological Management of Military Lands, Colorado State University: Fort Collins, CO, USA, 1995; p. 102.
43. Vitousek, P.M.; Aplet, G.; Turner, D.; Lockwood, J.J. The Mauna-Loa Environmental Matrix—Foliar and Soil Nutrients. *Oecologia* **1992**, *89*, 372–382. [CrossRef]
44. Aplet, G.H.; Hughes, R.F.; Vitousek, P.M. Ecosystem development on Hawaiian lava flows: Biomass and species composition. *J. Veg. Sci.* **1998**, *9*, 17–26. [CrossRef]
45. U.S. Army Garrison Hawaii. *Pōhakuloa Integrated Natural Resources Management Plan*; Center for Environmental Management of Military Lands, Colorado State University: Fort Collins, CO, USA, 2010.
46. Stout, G. Associates. In *Integrated Natural Resources Management Plan*; Center for Ecological Management of Military Lands, Colorado State University: Fort Collins, CO, USA, 2002; p. 290.
47. Trusdell, F.A.; Wolfe, E.W.; Morris, J. Digital Database of the Geologic Map of the Island of Hawai'i: U.S.; Geological Survey Data: 2005. Available online: https://pubs.usgs.gov/ds/2005/144/ (accessed on 20 April 2022).

48. Rhodes, J.; Lockwood, J. Mauna Loa Revealed: Structure, Composition, History, and Hazards.; American Geophysical Union: 1995. Available online: https://www.researchgate.net/publication/281245937_Mauna_Loa_Revealed_Structure_Composition_History_and_Hazards (accessed on 20 April 2022).
49. Giambelluca, T.W.; Nullet, M.A.; Schroeder, T.A. *Rainfall Atlas of Hawaii*; State of Hawaii, Department of Land and Natural Resources, Division of Water and Land Development: Honolulu, HI, USA, 1986.
50. Asner, G.P.; Sousan, S.; Knapp, D.E.; Selmants, P.C.; Martin, R.E.; Hughes, R.F.; Giardina, C.P. Rapid forest carbon assessments of oceanic islands—a case study of the Hawaiian archipelago. *Carbon Balance Manag.* **2016**, *11*, 13. [CrossRef]
51. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020.
52. Bates, D.; Machler, M.; Bolker, B.M.; Walker, S.C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [CrossRef]
53. Lenth, R.V. Emmeans: Estimated Marginal Means, Aka Least-Squares Means. 2021. Available online: https://cran.r-project.org/web/packages/emmeans/emmeans.pdf (accessed on 20 April 2022).
54. Mack, M.C.; D'Antonio, C.M. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecol. Appl.* **2003**, *13*, 154–166. [CrossRef]
55. Cordell, S.; Ostertag, R.; Michaud, J.; Warman, L. Quandaries of a decade-long restoration experiment trying to reduce invasive species: Beat them, join them, give up, or start over? *Restor. Ecol.* **2016**, *24*, 139–144. [CrossRef]
56. Cordell, S.; McClellan, M.; Carter, Y.Y.; Hadway, L.J. Towards restoration of Hawaiian tropical dry forests: The Kaupulehu outplanting programme. *Pac. Conserv. Biol.* **2008**, *14*, 279–284. [CrossRef]
57. Hnatiuk, S.; Rayner, I.; Brookhouse, M.; Freudenberger, D. Survival of native seedlings planted by volunteers: The Lower Cotter, ACT case study. *Ecol. Manag. Restor.* **2020**, *21*, 151–154. [CrossRef]
58. Brancalion, P.H.S.; Holl, K.D. Guidance for successful tree planting initiatives. *J. Appl. Ecol.* **2020**, *57*, 2349–2361. [CrossRef]
59. Holl, K.D.; Brancalion, P.H.S. Tree planting is not a simple solution. *Science* **2020**, *368*, 580–581. [CrossRef] [PubMed]