Sustainability **2013**, *5*, 1317-1339; doi:10.3390/su5031317

OPEN ACCESS

sustainability

ISSN 2071-1050

www.mdpi.com/journal/sustainability

Article

Restoring Native Forest Understory: The Influence of Ferns and Light in a Hawaiian Experiment

Rachelle K. Gould [1,*], Harold Mooney [2], Laura Nelson [3], Robert Shallenberger [4] and Gretchen C. Daily [2]

[1] Emmett Interdisciplinary Program in Environment and Resources, Stanford University, 473 Via Ortega, Stanford, CA 94305, USA

[2] Department of Biology, Stanford University, 371 Serra Mall, Stanford, CA 94305, USA; E-Mails: hmooney@stanford.edu (H.M.); E-Mail:gdaily@stanford.edu (G.C.D.)

[3] P.O. Box 514, Holualoa, HI 96725, USA; E-Mail: alohapalola@yahoo.com

[4] P.O. Box 6779, Kamuela, HI 96743, USA; E-Mail: rshall@hawaii.rr.com

* Author to whom correspondence should be addressed; E-Mail: rgould@stanford.edu; Tel.: +1-650-723-6117; Fax: +1-650-725-4139.

Received: 12 January 2013; in revised form: 7 February 2013 / Accepted: 15 February 2013 / Published: 20 March 2013

Abstract: Ecological restoration is an increasingly important component of sustainable land management. We explore potential facilitative relationships for enhancing the cost-effectiveness of restoring native forest understory, focusing on two factors: (1) overstory shade and (2) possible facilitation by a fern (*Dryopteris wallichiana*), one of few native colonists of pasture in our montane Hawaiʻi study system. We planted 720 understory tree seedlings and over 4000 seeds of six species under six planting treatments: a full factorial combination of low, medium and high light, situating plantings in either the presence or absence of a mature fern. After three years, 75% of outplanted seedlings survived. Seedling survivorship was significantly higher in the presence of a fern (79% *vs.* 71% without a fern) and in medium and low light conditions (81% *vs.* 64% in high light). Relative height was highest at low to medium light levels. After 2.2 years, 2.8% of the planted seeds germinated. We observed no significant differences in seed germination relative to light level or fern presence. Analyzing several approaches, we found nursery germination of seeds followed by outplanting ca. 20% less costly than direct seeding in the field. This study opens new questions about facilitation mechanisms that have the potential to increase the extent and effectiveness of restoration efforts.

Keywords: ʻalalā (Hawaiian Crow; *Corvus hawaiiensis*); biodiversity conservation; economic costs of restoration; interspecific facilitation; land-use change; pasture; private lands; tropical forest restoration

1. Introduction

Ecological restoration of various habitats plays an increasing role in ecosystem management, supported with billions of dollars annually around the world [1–3]. China alone has invested over USD 100 billion in restoring tens of millions of hectares of forest over the past two decades, for purposes of flood mitigation, landscape stabilization (especially in earthquake-prone areas), sandstorm control, carbon sequestration, and biodiversity conservation [4,5]. Ecosystem service motivations for restoration are becoming widespread [6–9]. There is thus a critical need to find practical, scalable, and economically efficient techniques and approaches for recreating desired ecosystems.

The range of restoration techniques is limited by a suite of barriers. While some heavily modified systems may recover ecosystem structure with no assistance once active human disturbance has ceased [10], most efforts are impeded by such obstacles as: competition from non-native flora and fauna (including predation on seeds and seedlings) [11,12]; loss of ecosystem components (e.g., seed sources, seed dispersers, pollinators, specific plant species [13–15]); unfavorable physical conditions (e.g., light levels, edaphic characteristics, microclimate [16–18]); and high up-front financial costs [19,20]. Given these diverse challenges, aligning restoration approaches with successional processes is one approach to enhancing success [21,22]. For example, many studies show that tree plantations, whether native or non-native, can serve as "nurse crops" for the establishment of native forest species, with light attenuation as one of their main benefits [23,24].

Ecological restoration has the potential not only to benefit from successional theory but also to inform it [25]. Many theories of forest succession posit that light levels and the related shade tolerance of different species are key drivers of forest change trajectories. Studies of succession rarely focus on species-specific links between light availability, growth, and mortality [26,27]. Studies of reforestation in tropical environments, however, have revealed species-specific differences in responses to light and other micro-environmental characteristics [28,29], and thus recommend that management be approached from a species level rather than from a community level [30]. Similarly, even though understory dynamics may play an important role in succession, successional theory pays little or no attention to the role of understory [31]. Yet, interspecific interactions, most of them involving the understory, may have significant effects on restoration outcomes; restoration action could take much better advantage of potential facilitative effects [32,33] and simultaneously increase understanding of the role of facilitation in succession.

Here we explore understory plant restoration, seeking approaches for practical application at scales of tens to hundreds of hectares, or more. We focus on mesic forest on the western, leeward flank of the Mauna Loa volcano on Hawaiʻi Island, partly motivated by planned reintroduction of the Hawaiian Crow (*Corvus hawaiiensis*, ʻalalā) and possibly the Hawaiian Thrush (*Myadestes obscures*, ʻōmaʻo), frugivorous birds dependent on now-absent understory vegetation. While modification of native forest

began about 1500 years ago with the arrival of the first humans [34], prior to 1800 this region supported native forest above ca. 800 m asl. Over the past 200 years, forest was transformed by logging (of sandalwood (*Santalum paniculatum*) and then koa (*Acacia koa*)) and cattle ranching, as well as introduction of numerous non-native plants, ungulates, and other organisms [35,36]. Today, pressures on native forest remain high, from these sources as well as residential development and climate change [37,38].

In this system, three of the most important perceived obstacles to restoration are high light, introduced grasses, and high costs. We explore the role that polypod ferns, under a variety of light levels, might play in mitigating these obstacles. Most of the scant literature on ferns and succession documents the negative competitive effect of native ferns on establishment and survival of other native plants [39–41]. The fern species discussed in these articles often spread asexually (rhizomally), forming dense mats on the forest floor. By contrast, here we explore the potential role of a native fern that lives as separate individuals.

We hypothesize that the presence of a fern may facilitate seed germination and seedling growth by providing low shade, and possibly enhancing moisture near the seedling by acting as a water funnel and/or fog capture screen (see Figure 1). The fern may also partially shade out vigorous non-native grasses. Apart from facilitating germination or survival of seedlings, ferns also may simply indicate micro-sites more suitable to plant growth, thus serving as management aids by targeting favorable locations for outplanting. In this experiment, we conducted both tree seedling outplanting and direct seeding to quantify success and cost of the two approaches, varying fern presence and light conditions (the latter as determined by canopy cover). We address three questions crucial in this system and more broadly: (1) Does the presence of a native understory fern, *Dryopteris wallichiana*, aid the survival and/or growth of outplanted seedlings or the germination of planted seeds? (2) How much shade (canopy cover) is required for seedling survival or seed germination? and (3) What are the costs of various restoration techniques (considering seed collection, propagation, site preparation, planting, and survivorship)?

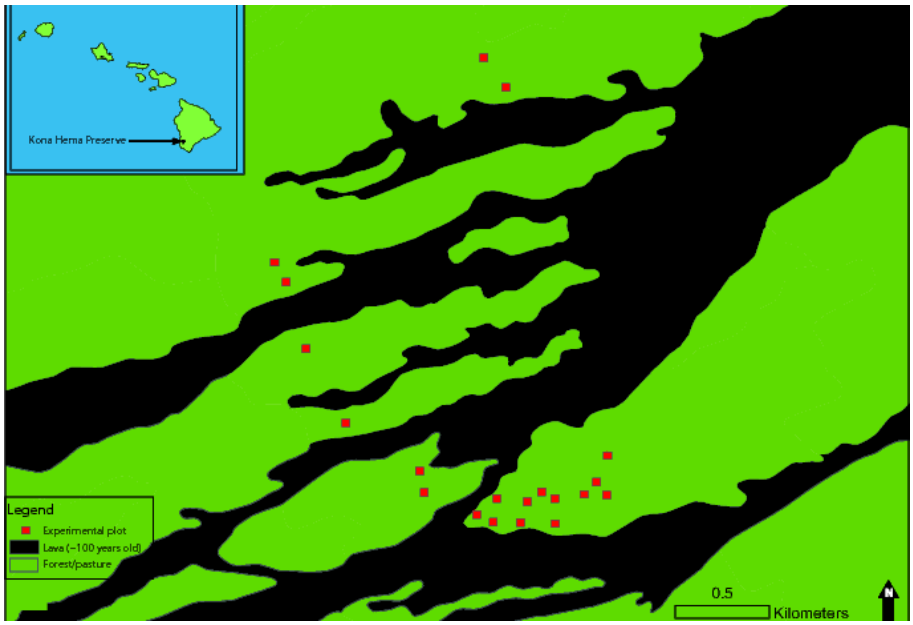
Figure 1. *Dryopteris wallichiana*, called the "shuttlecock" fern in English because of its shape.

2. Methods

2.1. Study Site

We worked at Kona Hema Preserve in the South Kona district on the leeward side of Hawai'i Island (Figure 2). The area was grazed from ca. 1916 until 1998, when a pig-proof fence was constructed and cattle, pigs, and other ungulates were removed; since 2003 it has been ungulate-free apart from temporary incursions. Kona Hema is a 3,185 ha parcel that extends from ca. 915 m to 1750 m elevation. Average rainfall is ca. 900 mm per year, with fairly consistent rainfall year-round punctuated by summer and winter storms [42]. Rainfall is concentrated in an elevation band of ca. 900–1200 m asl, and is lower above and below this band [42]. The substrate at Kona Hema is a 1500–3000 year old lava flow, overlain in parts by fingers of 1916 and 1926 flows (see Figure 2).

Figure 2. Salient features of the Kona Hema Preserve. The twenty 50 m × 50 m outplanting sites are indicated as red squares. The dark lines running east-west are lava flows <100 years old.



We situated our experiment at elevations between 1250 and 1450 m, where the primary land cover now comprises introduced pasture grasses, a native overstory of young *Acacia koa* (koa, mostly 5–25 years old) and *Metrosideros polymorpha* (ʻōhiʻa), and an understory almost devoid of fruiting plant species. We worked on the 1500-3000 year old substrate (and not on the 1916 and 1926 flows, which have little soil and remain very sparsely populated, mostly by scattered *M. polymorpha* and *Sadleria cyatheioides* (ʻamaʻumaʻu).

The two dominant non-native grasses are *Pennisetum clandestinum* (kikuyu) and *Microlaena stipoides* (meadow rice). *P. clandestinum*, the dominant cover in much pasture-land with low levels of shade, is a C4 grass that forms dense rhizomatous mats in the absence of ungulate grazing; it is difficult to clear, rebounds quickly, and impedes regeneration of other species [43]. *M. stipoides* is a C3 grass that begins to dominate as levels of shade increase. Relative to *P. clandestinum*, *M. stipoides* is relatively easy to clear and less vigorous in growth.

2.2. Outplanting and Direct Seeding Experiments

2.2.1. Choice of Facilitator Species

Dryopteris wallichiana (Figure 1), a pantropical polypod fern, is one of the most successful native colonizers of non-native grasslands in our study system. We selected *D. wallichiana* as a potential nurse plant in the experiment for several reasons: it is a notable component of forest structure prior to major human disturbance [43]; it survives along the spectrum from full sun to full shade; and it is one of the only native plants in Hawaiʻi that can outcompete non-native grasses. *D. wallichiana* appears to reproduce primarily sexually; individuals are often found at great distances from one another, allowing for wide spacing of experimental plantings. In addition, in some locations, we have observed disproportionate regeneration of understory seedlings within 10–50 cm of this fern than at other locations in the forest.

2.2.2. Outplanting and Direct Seeding Species

We used six understory species for outplanting and direct seeding, selected with a primary goal of creating habitat for *C. hawaiiensis*. Kona Hema is a possible site for reintroducing this island endemic, reported as extinct in the wild since 2002 [44]. Some plant species preferred by *C. hawaiiensis* were ruled out (for the time being) because of difficulty in propagation or extremely slow growth. We added one species not known to be preferred [45,46] (*A. stellata*) because it is thought to have been once abundant at Kona Hema; is especially easy to propagate and reestablish; has high cultural value; and is consumed by other frugivorous birds such as *M. obscures*. The six focal species, along with salient characteristics, are listed in Table 1.

Table 1. Species used in outplantings and direct seeding experiments. Taxonomic and life history information from Wagner [43].

Hawaiian name	Latin name	Family	Habit	Seed size	Seed recalcitrant / orthodox?
hō'awa	*Pittosporum hawaiianse*	Pittosporaceae	Understory tree	Medium (1 mm < x < 8 mm)	orthodox
kōlea	*Myrsine lessertiana*	Myrsinaceae	Understory tree	Medium (1 mm < x < 8 mm)	recalcitrant
maile	*Alyxia stellata*	Apocynaceae	Liana	Large (>8 mm)	orthodox
māmaki	*Pipturus albidus*	Urticaceae	Shrub / small tree	Small (<1 mm)	orthodox
naio	*Myoporum sandwichense*	Scrophulariaceae	Understory tree	Large (>8 mm)	orthodox
pilo	*Coprosma Montana*	Rubiaceae	Understory tree	Medium (1 mm < x < 8 mm)	orthodox

2.2.3. Study Design

Plantings were done in 20 experimental plots, each 50 m × 50 m square, in areas dominated by *P. clandestinum* at higher light levels and by a mixture of *M. stipoides* and *P. clandestinum* at lower light levels. These areas reflect general conditions common both in this region and in many deforested tropical regions globally. Locations of the plots are indicated in Figure 2; plot centers were on average 1090 meters apart.

Our two experimental factors are light and fern presence (Table 2). Treatments included three light levels: high ("Open" treatment); medium, with shade provided by one tree to the north side of the planting ("Tree" treatment); and low, with shade provided by multiple trees surrounding the plant ("Canopy" treatment). Half of all treatments were situated near a mature *D. wallichiana* fern (20–30cm from the base) and half were not near (>2m from the base of the closest fern). In each plot, we designated six planting sites in each treatment, for a total of 36 planting sites per plot (3 light treatments × 2 fern treatments × 6 understory species = 36 planting microsites; see Figure 3).

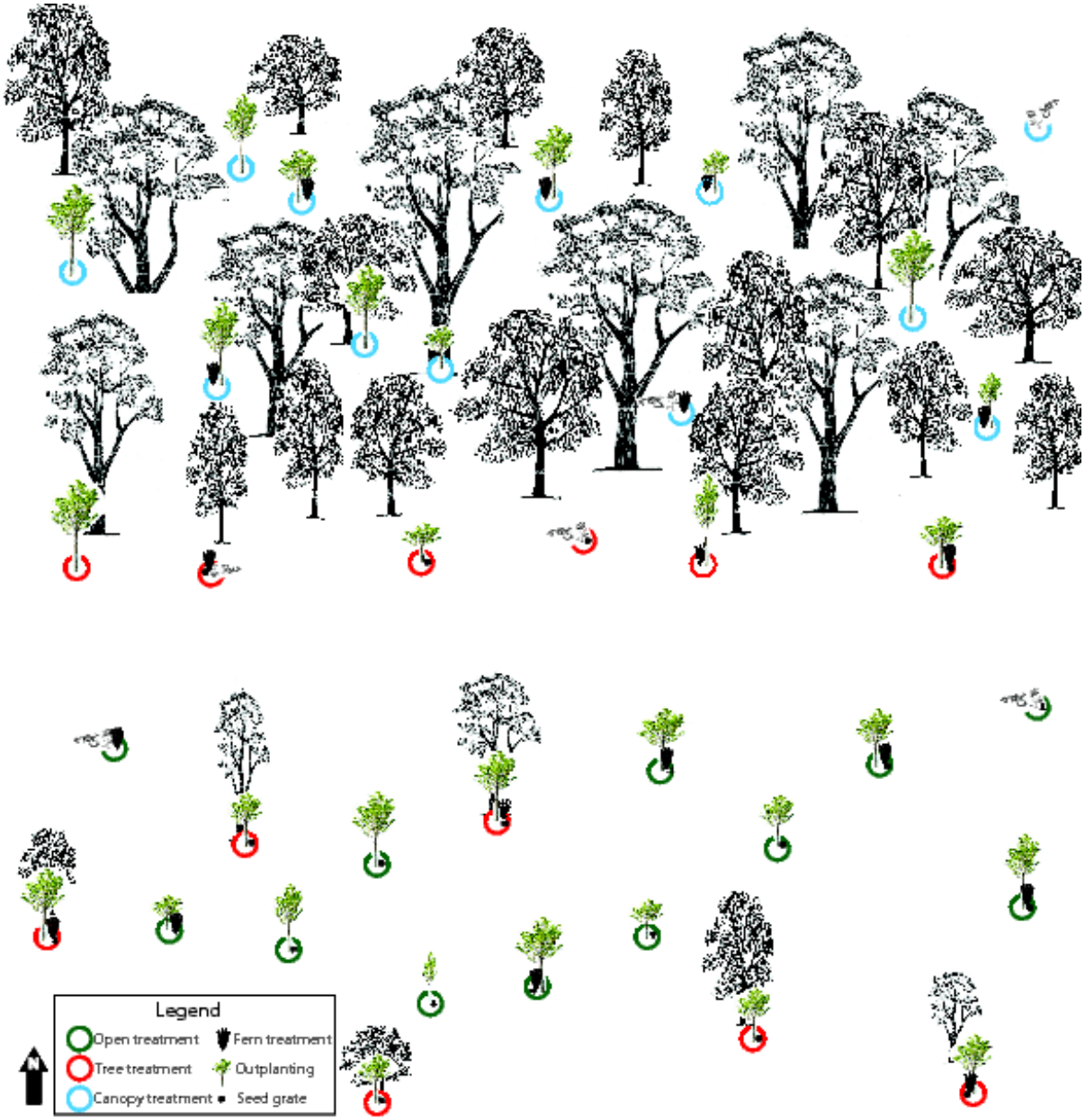
Table 2. Two-factorial experimental design. The two factors are light (with three conditions—open (high light), tree (medium light), and canopy (low light)) and fern (with two conditions—fern and no fern).

		Fern Condition	
		F – Fern	**N - No Fern**
Light Condition	**O - Open (High Light**; 0–20% canopy cover with an average of 15%**)**	OF Treatment (Open, Fern)	ON Treatment (Open, No fern)
	T - Tree (Medium Light; 20–80% canopy cover with an average of 50%**)**	TF Treatment (Tree, Fern)	TN Treatment (Tree, No fern)
	C - Canopy (Low Light; >80% canopy cover with an average of 88%**)**	CF Treatment (Canopy, Fern)	CN Treatment (Canopy, No fern)

2.2.4. Outplantings

The Future Forests Nursery in Kailua Kona germinated all seedlings from seed collected at Kona Hema in 2008 (as much as possible, seed came from the same elevation as the plantings; additional seed came from slightly lower elevation forest (ca. 1000−1150 m) that was lightly grazed and retains a higher diversity of forest understory plants). Trees were grown in slightly tapered rectangular pots. Seedlings were from 3 to 8 months old when planted. In June−July 2009, we outplanted 720 seedlings of the six study species. In each of the 20 plots, we planted six individuals of each of the six species—one of each species under each treatment, for a total of 36 outplantings per plot (Figure 3).

Figure 3. Schematic of plot design, with circles indicating the 36 planting microsites, each of which includes a seedling (depicted by a small green tree) and a seed planting area (depicted by a grate). Microsites indicated by blue circles are "canopy" treatments (in areas of high tree density); those with red circles are "tree" treatments (with trees only to the north; the trees are either single trees surrounded by pasture or trees along the forest edge); those with green circles are "open" treatments (surrounded by no trees). Half of the microsites in each light level are "fern" treatments, as indicated by the fern icon. For each treatment (combination of light level and fern/no-fern), there is one individual of each species planted.



2.2.5. Direct Seeding

The Future Forests nursery collected and prepared seeds of the six experimental species in Autumn 2009 and Winter 2010. Nursery staff cleaned the seeds of fruit flesh to prevent decomposition, but

seeds were not soaked or otherwise treated prior to planting. In May 2010, we planted seeds in all six treatments in the same 36 planting sites per plot in which we outplanted seedlings. We planted one species per planting microsite to simplify analysis [47]; species of seeds planted and seedlings planted were paired randomly. We planted seeds 10–20 cm from the base of the *D. wallichiana* fern and at least 20 cm from the outplanted seedling. We planted six seeds of one species at each microsite for *P. hawaiensis* , *M. sandwichense, C. Montana,* and *M. lessertiana*. We planted three seeds at each *A. stellata* microsite because of scarcity of seeds available. *P. albidus* seeds were far too small (<1 mm) to count individually; we thus spread 0.1 dram of *P. albidus* seeds in each *P. albidus* microsite.

2.2.6. Planting Technique

We planted each of the 720 experimental seedlings in the center of a 1m diameter circle that had been sprayed with 1% solution of Glyphosate herbicide 10–35 days prior to planting. Glyphosate inhibits the plant's photosynthetic pathway, killing any foliage it touches within 12 hours with essentially no effect on the plants' surroundings (*i.e.*, there is no interaction with the soil, and once the chemical is metabolized, it stops photosynthesis and is quickly inactivated). During application, the individual spraying the herbicide held a 1 m × 1 m piece of plywood against the fern, completely shielding fern foliage from contact with the herbicide.

We cleared grass (including stolons of *P. clandestinum*) using a hand sickle, and set it aside for use as mulch. We used a pick-axe to break grass roots and loosen soil to 8 cm depth within the 1m circle. We recorded the approximate sizes of rocks and roots, loosening rocks but not removing them from the 1m circle. We left rhizomes, both of target *D. wallichiana* ferns and of other ferns (almost all of them dead) intact (average number of rhizomes per circle was 0.5). We also left coarse woody debris (CWD) intact; CWD was present in 9% of microsites, covering on average 20% of those 1 m circles in which it was present.

We conducted direct seeding quickly, in 1–2 minutes, to simulate the likely effort of restoration volunteers. We planted seeds in the same 1 m diameter circles as the seedlings, but ten months later; the grass had thus received herbicide treatment about 11 months before seed planting. To enhance direct seeding success, we covered seeds with a small amount of soil (a depth roughly three times the seeds' diameter) that had been loosened with a 15 cm hoe. Because a common cause of failure in direct seeding efforts is seed predation [48,49], we then covered seeds with 30 cm^2 of wire mesh with 1 cm weave to protect them from *Pternistis erckelii* and *Lophura leucomelano* (both non-native pheasants) and *Rattus rattus* (black rats).

2.3. Monitoring and Ecological Data Collection

We measured canopy cover at each outplanting and seeding site with a Nikon hemispherical lens. We used data from the hemispherical photographs for analysis, calculating canopy cover from the 180 ° images using the Gap Light Analyzer software (produced by Simon Fraser University).

To quantify survivorship and growth, we monitored all plantings (seedlings and seeds) at least yearly. Frequent monitoring assured that seedling locations were not lost (when seedlings grew slowly or died, it was often very difficult to find them). Table 3 details monitoring times. During all monitoring sessions, we collected data on multiple aspects of seed and seedlings: whether seeds had

germinated and, if they had, germinant height; seedling height (from ground level to the highest apical meristem); seedling crown width (two perpendicular measurements of the widest portion of the crown; crown length (from lowest branch to highest apical meristem); stem basal diameter (because many seedlings had not reached 1.3 m above ground, a standard measurement for tree diameter in forestry and ecology called "Breast Height"); and (up until, but not including, year 3) number of live leaves larger than 1 cm in length or width.

Table 3. Monitoring Schedule.

Date of monitoring	Time elapsed since seedling outplanting	Time elapsed since seed planting
January 2010	6 months	n/a
July 2010	1 year	2 months
Dec2010	1.5 years	7 months
July 2011	2 years	14 months
July 2012	3 years	26 months

2.4. Economic Data Collection

We obtained costs of each component of the project from the preserve manager, personnel of Future Forests Nursery, and our observations of the time required to complete each task. We estimated the average cost per surviving or germinating individual based on survivorship and germination rates in the various light conditions. Detailed calculations, including amounts for each component of final cost, are in the Supplementary Information. We made three key assumptions in these cost estimates: (1) paid labor was available for US$10/hour; (2) staff time for volunteer organization and supervision was available at US$25/hour; and (3) staff time required for volunteer coordination was 1.5 times planting time.

2.5. Statistical Analysis

We analyzed data using Generalized Linear Mixed Models [50,51], which allowed use of the full spectrum of data while accounting for the grouping of samples into plots and species. That is, since plants within the same plot were within 50 m of one another, they were not considered independent in analyses. Similarly, individuals of the same species were not considered independent, unless species was the explanatory variable in a particular analysis.

We ran different analyses to account for the error structures of our response variables (see Table 4). We reduced resulting models in a backward stepwise manner, omitting explanatory variables that failed to explain significant variation in the response variable. For the seedling survivorship (a dichotomous response variable), we used a binomial error structure. For seedling relative height (a continuous response variable), we used a Gaussian error structure, and included only surviving seedlings in analysis. For germination success (count of germinated seeds), we used a Poisson error structure. See Table 4 for details on analyses conducted, and Table 5 for details and statistics on the model selection procedure.

Table 4. Summary of GLMM analyses.

Question	Response variable(s)	Fixed Effects	Random Effects	Error Structure
Did seedling survivorship vary by treatment?	Survivorship at 3 years (Dead or Alive)	Treatment	Species, Plot	Binomial
Did seedling survivorship vary by species?	Survivorship at 3 years (Dead or Alive)	Species	Plot, Treatment	Binomial
Did seedling relative height vary by light level or fern?	Relative Height (Height at 3 yrs / Height at planting)	% Canopy, Fern presence/absence	Species, Plot	Gaussian
Did seedling relative height vary by species?	Relative Height (Height at 3 yrs / Height at planting)	Species	Plot, Treatment	Gaussian
Did seed germination rate vary by light level or fern presence?	Number of germinated seeds	% Canopy, Fern presence/absence*	Plot, Species	Poisson
Did seed germination rate vary by species?	Number of germinated seeds	Species	Plot, Treatment	Poisson

(*For seed germination analyses, light and fern conditions were run as separate models because continuous and dichotomous variables cannot be jointly run with Poisson error structure).

Table 5. Model selection process and results.

			Fern		Light		Fern*Light	
Response Variable	**Fixed Variable(s)**	**AIC**	**t / z**	**P**	**t / z**	**P**	**t / z**	**P**
Height	Fern*light	2074	−0.951	0.3421	−2.778	0.0057	1.102	0.271
	Fern + light	2065	0.192	0.848	−2.843	0.0046	---	---
	Light	2061	---	---	−2.846	0.0046	---	---
Germination	Fern*light	435	−0.152	0.879	0.727	0.467	0.101	0.919
	Fern + light	433	−0.16	0.873	1.125	0.261	---	---
	Light	336	---	---	0.959	0.337	---	---
Survival	Fern*light	688	0.498	0.619	−4.804	<0.0001	0.266	0.79
	Fern + light	686	2.283	0.022	−6.17	<0.0001	---	---
	Light	689	---	---	−6.23	<0.0001	---	---

3. Results

3.1 Seedling Survival

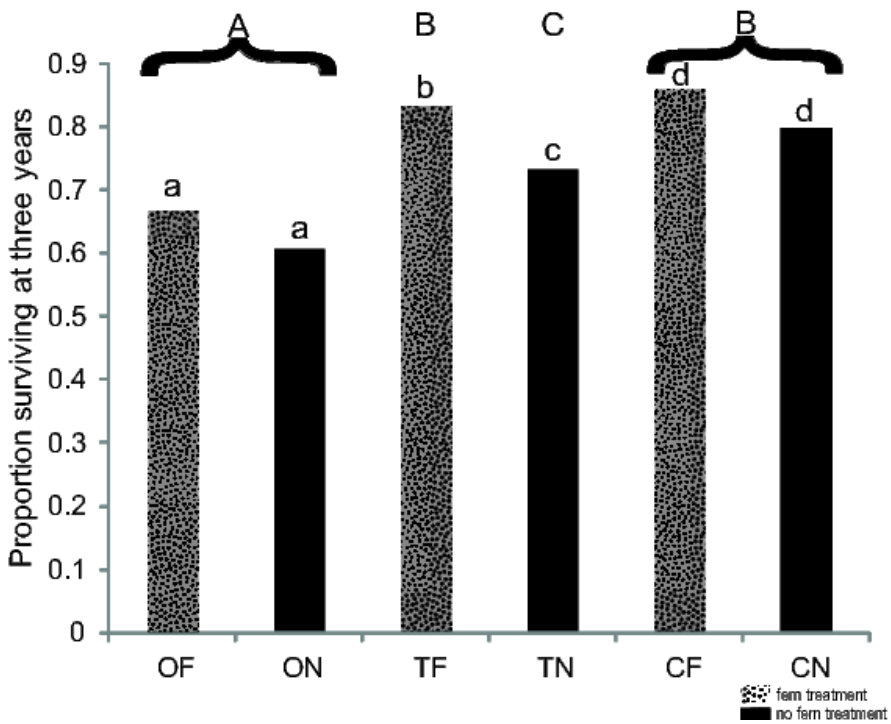
Overall, 75% of our outplanted seedlings survived. Survival was significantly related to both fern presence and light level, with higher survival next to ferns (79% *vs.* 71% for seedlings not next to ferns; z = 2.283; $p = 0.022$) and in medium and low light levels (81% *vs.* 64% for seedlings in high light; z = −6.17; $p < 0.0001$) (see Figure 4)**.** Seedling survivorship was higher in canopy and tree treatments than in open treatments (z = 5.277; $p < 0.0001$). We also found that seedling survivorship

was greater in the Tree-Fern (TF) than in the Tree-No Fern (TN) treatment (z = −2.199; p = 0.03). While the other light conditions demonstrate similar trends (Figure 4), we found no statistically significant differences between the Open-Fern (OF) and Open-No Fern (ON) treatments (z = −1.247 p = 0.212) or the Canopy-Fern (CF) and Canopy-No Fern (CN) treatments (z = −1.263 p = 0.21). Seedling mortality in the Tree-Fern (TF) treatment was not significantly different from seedling mortality in the two Canopy treatments together (z = 0.115; p = 0.908). We re-ran analyses using only planting sites with live ferns at year three, finding slightly different z- and p-values, but no overall change in results (Figure 4). Details on post-hoc analyses of survivorship differences by treatment are in the Supplementary Information.

Seedling survivorship was lower at higher (drier) elevations (z = −3.254; p = 0.00114), that is, ~1400 m as compared to ~1250 m. Relative change in height did not differ significantly by elevation (t = −1.879; p = 0.061).

Controlling for treatment and plot, seedling survivorship was higher for *M. sandwichense* (92% survivorship; z = 3.321 ; p = 0.0009) and for *A. stellata* (87% survivorship; z = 2.154; p = 0.0312), and lower for *P. albidus* (46% survivorship; z = −4.974 ; p < 0.0001), than for the remaining three species (which had an average of 76% survivorship between them) (Table 6).

Figure 4. Seedling survivorship at three years, by treatment.



Overall, seedling survivorship was higher next to ferns. When broken down by treatment, seedling survivorship was significantly greater for the Tree-Fern (TF) treatment than for the Tree-No Fern (TN) treatment, but not for the Open-Fern (OF) treatment *vs.* the Open-No Fern (ON) treatment, nor for the Canopy-Fern (CF) *vs.* the Canopy-No Fern (CF) treatment (these comparisons represented by lowercase letters). TF treatments exhibited no difference in seedling survivorship from Canopy treatments (CF and CN combined), but TN treatments exhibited lower survivorship than both canopy treatments (CF and CN combined). Seedling survivorship was significantly lower in open treatments than other light levels (these comparisons represented by uppercase letters).

Table 6. Results for Surviorship, Relative Height, and Seed Germination by species.

Species	Outplanting Survivorship	Outplanting Relative Height (Average ± Std Dev.)	Seed Germination
M. sandwichense	92%*	3.8 (±1.9)[a]	0.1%
A. stellata	87%*	1.7 (± 1.3)[c]	15.0%
C. montana	79%•	3.7 (± 2.3)[a]	2.1%
P. hawaiianse	75%•	3.0 (± 1.6)[b]	0.8%
M. lessertiana	73%•	2.0 (± 1.0)[c]	1.9%
P. albidus	46%•	3.0 (±1.3)[b]	0.0%

Seedling survivorship was higher for *M. sandwichense* and *A. stellata* (denoted by *) and lower for *P. albidus* (denoted by •) than for the remaining three species. Outplanting relative height was similar for *M. sandwichense* and *C. montana* (denoted by [a]); *A. stellata* and *M. lessertiana* (denoted by [c]); and *P. hawaiianse* and *P. albidus* (denoted by [b]).

3.2. Seedling Relative Height

We calculated seedling relative height as height at monitoring divided by height at planting. Relative height at three years was not significantly related to fern presence (t = −0.951; p = 0.342), but was related to light levels (t = −2.78; p = 0.0058), with the highest growth at intermediate and high levels of canopy cover (Tree and Canopy treatments)**.** Species-specific differences in relative height do not address our primary study questions, but are relevant for management. Species' changes in relative height fell into three significantly different groups (see Table 6). *M. sandwichense* and *C. Montana* had the greatest height increases, with averages of 3.77 (± SD 1.89, n = 110) and 3.72 (± SD 2.33, n = 95). *A. stellata* and *M. lessertiana* had the smallest height increases, with averages of 1.74 (± SD 1.34, n = 116) and 2.01 (± SD 0.999, n = 85), respectively. The remaining two species, *P. hawaiianse* and *P. albidus*, had intermediate average relative heights: 2.98 (± SD 1.56, n = 79) and 2.99 (± SD 1.32, n = 56). The Supplementary Information details post-hoc tests which determined the significant differences between these groupings.

3.3. Seed Germination

Because *P. albidus* seeds were too small to feasibly count, and because we did not observe germination of a single *P. albidus seed*, we omit *P. albidus* from germination calculations. Considering the other five species only, 2.8% (n = 3240) of planted seeds germinated. The number of germinated seeds did not vary significantly by light level (z = 1,158; p = 0.247) or fern presence (z = −0.211; p = 0.833). The proportion of seeds that germinated was greater for *A. stellata* than for all other species (z = 5.073; p < 0.00001; Table 6).

3.4. Fern Size and Dieback

Ferns were slightly smaller in open treatments than in canopy and tree treatments. At planting, mean frond length was 71.6 (± SD 17.5) cm in the open and 79.3 (± SD 16.75) cm in tree canopy treatments (t = 4.096, p = 0.0001); after three years and a notable drought in 2010-2011, average frond length was 51.5 (± SD 22.9) cm in the open and 57.8 (± SD 18.6) cm in tree and canopy treatments

(t = 2.409, p = 0.0168). Out of the 360 ferns adjacent to which we planted, 64% (230 ferns) still had live fronds after three years. Ferns had live fronds in 59% of Open micro-sites, 61% of Tree micro-sites, and 72% of Canopy micro-sites; differences in fern dieback between the treatments were not significant (CF-OF: z = −1.134, p = 0.257; CF-TF: z = 0.000, p = 1.000). Causes of variation in fern dieback were not clear, but drought is the most likely cause.

3.5. Costs of Various Planting Regimes

Taking into account most relevant expenses for our sixteen hypothetical planting scenarios and based on survivorship rates in our experiment, the projected cost per adult surviving plant was lowest in the Outplanting, Volunteers, Shade scenario ($7.59). The projected cost per survivor was highest in the Direct Seeding, Paid Personnel, Open plantings scenario ($20.11). See Table 7 for details.

Table 7. Breakdown of per-plant projected costs for each of sixteen hypothetical restoration scenarios.

	Scenario Details			**Outcomes**	
	Labor rate	**Seed *vs.* Seedling**	**Light levels**	**Survivorship / Germination Rate**	**Cost per surviving seedling**
Scenario					
Outplanting, Volunteers, Shade	*Low*	*Seedling*	*Canopy + Tree*	80.6%	$ 7.59
Outplanting, Volunteers, All light	*Low*	*Seedling*	*All light levels*	75.1%	$ 8.14
Outplanting, Volunteers, Open and Tree	*Low*	*Seedling*	*Open + Tree*	71.3%	$ 8.59
Direct Seeding, no *P. albidus*, Volunteers, Shade	*Low*	*Seed*	*Canopy + Tree*	2.9%	$ 9.25
Outplanting, Volunteers, Open only	*Low*	*Seedling*	*Open only*	64.2%	$ 9.53
Direct Seeding, no *P. albidus*, Volunteers, All light	*Low*	*Seed*	*All light levels*	2.8%	$ 9.56
Direct Seeding, no *P. albidus*, Volunteers, Open and Tree	*Low*	*Seed*	*Open + Tree*	2.7%	$ 9.72
Direct Seeding, no *P. albidus*, Volunteers, Open only	*Low*	*Seed*	*Open only*	2.6%	$ 10.25
Outplanting, Paid Personnel, Shade	*High*	*Seedling*	*Canopy + Tree*	80.6%	$ 12.63
Outplanting, Paid Personnel, All light	*High*	*Seedling*	*All light levels*	75.1%	$ 13.55
Outplanting, Paid Personnel, Open and Tree	*High*	*Seedling*	*Open + Tree*	71.3%	$ 14.29
Outplanting, Paid Personnel, Open only	*High*	*Seedling*	*Open only*	64.2%	$ 15.86
Direct Seeding, no *P. albidus*, Paid Personnel, Shade	*High*	*Seed*	*Canopy + Tree*	2.9%	$ 18.16
Direct Seeding, no *P. albidus*, Paid Personnel, All light	*High*	*Seed*	*All light levels*	2.8%	$ 18.77
Direct Seeding, no *P. albidus*, Paid Personnel, Open and Tree	*High*	*Seed*	*Open + Tree*	2.7%	$ 19.09
Direct Seeding, no *P. albidus*, Paid Personnel, Open only	*High*	*Seed*	*Open only*	2.6%	$ 20.11

4. Discussion

Extensive restoration efforts are underway across Hawai'i [18,52–54], some of them combining cultural and ecological restoration in novel and promising ways [55]. Globally, while some natural regeneration occurs in abandoned pasture land [56], in many systems pastures will not return to native forest without human intervention [57]. In Hawai'i, native forest is not growing on abandoned pastureland, possibly because of low resource-use efficiency of the native Hawaiian flora [58,59] and certainly because of competition from non-native grasses [60] and the fire cycle they help to create [61]. We employ an experimental approach to provide insight into potentially useful tools for achieving culturally and financially acceptable restoration targets [62]. An acceptable and feasible target in this case may be a system that conserves some biodiversity, notably by improving habitat for the critically endangered *C. Hawaiiensis*, while providing locally desired ecosystem services [63], such as enhanced groundwater recharge [64] and opportunities for collecting native plants for traditional use [65].

Our overall survival rate for seedlings (75%) is higher than that found similar efforts (that is, restoration outplantings in pasture grasses in the tropics); at high light levels in particular, our outplantings' survivorship (64%) was higher than survivorship in similar studies [66]. Possible factors contributing to our high survivorship are greater care in planting, facilitation by ferns, and favorable moisture conditions at least at lower elevations – within our study area rainfall decreases slightly with elevation [42], and we found higher mortality at higher elevations (*i.e.*, 1450 m *vs.* 1250 m). The species-specific differences in survivorship we found are consistent with past work; in an outplanting study in dry forest on Hawai'i Island, for instance, survival rates ranged from 23% to 91% across species [67]; similarly, in a study of restoration in degraded montane Costa Rican pasturelands, survival rates for native tree species planted in full sun ranged from about 0% to about 90% [66,68].

We found that planting seedlings in close proximity to a fern (20–30 cm from the base) significantly enhanced survivorship, as did medium and low light levels (that is, Tree and Canopy treatments). That the effect of the fern was still significant even in analysis including only ferns with live fronds at 3 years suggests a particularly strong relationship (because this analysis, which used only 64% of fern treatments, had a substantially reduced sample size). The enhancement by ferns of seedling survival is particularly interesting given recent calls for research on the potential of interspecific facilitative interactions to aid restoration efforts [32,33]. In recent decades, the importance of facilitation in plant communities has received increasing study, enriching the formerly prevailing focus on competitive effects [69].

The way that facilitative effects vary with environmental conditions, however, has received little attention [70] until recently. The "stress gradient" theory proposes that facilitation increases as environmental conditions become more severe [71]. Thus, facilitative effects may be particularly strong in more extreme conditions, such as in alpine or arid environments [72], or in very dry years [73]. While we hypothesized that this might be the case in our study—that is, that the ferns would have the strongest effects on seedlings in the open treatments—our results do not support this. The high mortality of our fern nurse plants, however, may have masked their potential effect. In our Open treatments, only 59% of ferns survived to three years (as compared to 72% in Canopy treatments); while this difference in mortality was not significant, the high fern mortality in our most extreme light treatment may have precluded detection of the hypothesized signal. In addition, ferns in open

treatments tended to be smaller than those in tree and canopy treatments; this smaller size may have further masked potential differentials in facilitation.

The enhancement by ferns of seedling survival—including for only those seedlings whose treatment fern survived the full 3 years—indicates that ferns in our experiment do not compete with seedlings. Among our other hypothesized mechanisms of fern interaction——as shade provider, a water collection screen, or indicator of more suitable planting sites——all are consistent with our results and merit further study. In particular, that the fern effect was significant even with data encompassing microsites where ferns died back suggests support for, and encourages future research on, our "suitable planting site indicator" hypothesis, which receives little attention in the scholarly literature. The "nurse plant" hypothesis seems similarly under-studied and under-applied in restoration interventions worldwide [32,33]. The few studies that exist, including our study, encourage further work on "nurse plants" and facilitation; for instance, studies on logged or grazed land comparing natural regeneration in the presence and absence of mature plants (hypothesized facilitators) found greater diversity and/or abundance of seedlings or saplings near mature plants [74–76]. Similarly, the few experiments testing the role of facilitation (specifically, proximity to mature plants) on restoration outplantings found that nurse plants aided seedling survivorship and/or growth [33,77]. The mechanisms at play remain little studied [32].

The large proportion (36%) of ferns that died back during our experiment complicates interpretation of the finding that the presence of a fern aided seedling survivorship. Although our modifications of the ferns' immediate surroundings may have negatively impact the ferns despite our extreme care in planting, a more likely reason for fern dieback was the drought. We did not monitor ferns uninvolved in the experiment, but it appeared that many *D. wallichiana* died back during the extreme drought; land managers in the area have also observed fern "death" in dry years [78]. Though differences in dieback were not significant between treatments, we observed slightly higher fern mortality in open treatments; it is possible that had this experiment taken place during a wetter period, there would have been less fern dieback in open (drier) areas in particular, and the fern's impact in open treatments might have been significant.

Our findings of higher survivorship and relatively higher seedling heights in medium and high canopy levels (Tree and Canopy treatments, respectively) are not surprising given the ecological habits of our outplanted species, all of which thrive in understory [43]. Recent research in a lowland moist forest in Hawai'i found that relative growth rates were higher at 25% light than at 10% and 5% light [79]; that study, though it did not place plants in light levels higher than 25%, is consistent with our finding of greatest growth in medium light levels. More generally, this finding is consistent with much work on regeneration and restoration in former pasturelands [67,80]. Species-specific differences in growth are also to be expected [68], though the particular differences we found have potentially far-reaching management implications . Most notably, the consistent success of *M. sandwichense* in open areas suggests that it may be adapted to a much wider, or different, range of conditions than that in which it currently exists. This is turn suggests both the use of *M. sandwichense* in future pasture restoration efforts and further research into its success.

In other tropical pasture landscapes the most important factor in restoration may be seed dispersal [16]. Many systems in Hawai'i are in a Catch 22 situation: seed dispersal, especially of heavy-seeded species, is impeded because of changes in frugivorous bird populations; the return of these dispersers,

however, necessitates habitat including large-fruited flora. Another study conducted in Kona Hema Preserve found that inadequate seed dispersal and competition with a non-native grass limited seedling establishment [81]. We planted both seedlings and seeds, with one-time control of grasses, to explore options for overcoming these obstacles.

Our overall 2.8% seed germination rate is on the same order of magnitude as germination rates found in many other direct seeding studies. In a *P. Clandestinum*-dominated dry forest system also on Hawai'i Island, for example, Brooks *et al.* [19] had 3.4% germination in areas with both herbiciding and "broadcast" seeding, and about 0.5% germination for areas with herbiciding alone, seeding alone, or no treatment. Rates of germination can vary widely, however. Studies in abandoned pasture in Costa Rica observed germination rates from 0 to 78% [66]. In a tropical forest system in Thailand, a direct seeding experiment using wire mesh to protect seeds (as did our experiment) achieved 10% to 73% germination of seeds planted [48]. A study in a seasonal forest in Mexico planted seeds of mature-forest species in three forest ages; between 5% and 41% of seeds germinated [82]. It is likely that low precipitation and an extreme drought [83] in 2009–2010 limited our germination rates.

Other studies testing germination between different habitat types (including pasture *vs.* forested areas, and under nurse shrubs in pasture *vs.* under grass in pasture), like ours, found minimal or no differences in germination between habitat types. One explanation identified by many of these studies was that pasture grasses provide dense cover that leads to soil temperature and moisture similar to that in forests [77,82,84]. Different germination rates for different species are not surprising, as germination and establishment rates are often part of life history strategies [85]. For instance, larger seeded-species generally exhibit higher establishment rates than smaller seeds [86], a pattern borne out for large-seeded *A. stellata* in our study.

For outplanted seedlings, nursery rearing of seedlings (including seed collection and preparation) comprised over 80% of restoration costs per plant. When success/survivorship rates are incorporated into costs, however, outplanting was ca. 20% more cost effective. By contrast, past comparisons of restoration costs have found direct seeding to be more cost-effective than outplanting, in Costa Rican and Californian sites [84,87]. In our case, the projected cost difference per survivor between direct seeding and outplanting is not large despite substantial differences in survival/germination. For instance, for shade-only and volunteer scenarios, in our system outplanting would cost ca. US$7.59 per survivor, while direct seeding would cost ca. US$9.25 per survivor.

The decision of whether to outplant or direct seed will hinge upon numerous non-financial considerations. While the more common approach in restoration projects is outplanting [84], seeds have non-financial advantages over outplantings that may in some cases justify slightly higher costs. Direct seeding may increase long-term viability of forests by allowing those seeds and seedlings most suited to a particular location to germinate and thrive [88]. In addition, in places where non-native pathogens, invertebrates, or small amphibians are a concern, seeds may be preferable to avoid introductions that can inadvertently accompany nursery soil. In areas where access is difficult, such as mountainous terrain, the much greater ease of transporting seeds may be critical [48,49]. Because it requires substantially less planting time than outplanting, direct seeding may also be applicable to much larger spatial areas [19].

5. Conclusion

This study explores options for restoring former pasturelands to native forest: planting near existing native species, planting in high or medium light levels (including planting next to solitary remnant trees or adjacent to forest edges), and direct seeding as compared to outplanting. Increased understanding of facilitation processes and how they vary with environmental gradients (whether those gradients are caused by human or non-human forces) may spur new ideas and tools for ecological restoration [32,33,70]. Similarly, an understanding of how particular species can thrive in various light conditions may increase possibilities for restoration [26,27]. Our results demonstrate that a variety of restoration techniques can be successful and cost-efficient, increasing the options available to restoration practitioners. These findings can aid restoration decision-making that takes into account both landscape characteristics (e.g., existing flora and light levels) and resources available (e.g., money, nursery space, and volunteers) to maximize desired benefits.

Supplementary Material

Supplementary information can be accessed at:

http://www.mdpi.com/2071-1050/5/3/1317/s1.

Acknowledgements

We are most grateful to the many volunteers who made this experiment possible, working as individuals and as part of the Hawai'i Youth Conservation Corps and the Boy Scouts of America (Crew 111). Individual volunteers D Ulrich, J Lynch, and B Rownd were indispensible. This study would not have succeeded without The Nature Conservancy of Hawai'i, in particular Preserve Manager Mel Johansen, Preserve staff Lester Gebin and Jake Coffelt, and TNC staff member Eldridge Naboa. E Broderick, R Chai, M Conte, A Doty, J Eastling, T Gibbs, J Hashimoto, E Lee, L Mease, and I Zafira provided invaluable field assistance. We benefited greatly from advice from K Dahlin, J Goldstein, D Karp, N Lincoln, C Mendenhall, L Pejchar, T Raab, P Vitousek, and N Zimmerman. We thank the U.S. Fish and Wildlife Service for funding purchase of seedlings; for research support, we thank P and H Bing, the Stanford School of Earth Sciences (McGee Research Fund, E-IPER Summer Research Funds, and the Undergraduate Research Fund), the Stanford Woods Institute Undergraduate Research Program, the Winslow Foundation, and the Heinz Foundation.

Conflict of Interest

The authors declare no conflict of interest.

References

1. Enserink, M. Plan to quench the Everglades' thirst. *Science* **1999**, *285*, 180.
2. U.S. Department of the Interior. The Department of the Interior's Economic Contributions. Available online: http://www.doi.gov/ppa/upload/DOI-Econ-Report-6-21-2011.pdf (accessed on 28 February 2013).

3. Nesshöver, C.; Aronson, J.; Blignaut, J. Chapter 9: Investing in Ecological Infrastructure. In *TEEB—The Economics of Ecosystems and Biodiversity for National and International Policy Makers*; Brink, P.T., Ed.; Routledge: New York, NY, USA, 2011.
4. Liu, J.; Li, S.; Ouyang, Z.; Tam, C.; Chen, X. Ecological and socioeconomic effects of China's policies for ecosystem services. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 9477–9482.
5. Yin, R.; Yin, G.; Li, L. Assessing China's Ecological Restoration Programs: What's Been Done and What Remains to Be Done? *Environ. Manage.* **2010**, *45*, 442–453.
6. Hilderbrand, R.H.; Watts, A.C.; Randle, A.M. The myths of restoration ecology. *Ecol. Soc.* **2005**, *10*, 19–30.
7. Roberts, L.; Stone, R.; Sugden, A. The rise of restoration ecology. *Science* **2009**, *325*, 555.
8. Goldman-Benner, R.L.; Benitez, S.; Boucher, T.; Calvache, A.; Daily, G.; Kareiva, P.; Kroeger, T.; Ramos, A. Water funds and payments for ecosystem services: practice learns from theory and theory can learn from practice. *Oryx* **2012**, *46*, 55.
9. Alexander, S.; Nelson, C.R.; Aronson, J.; Lamb, D.; Cliquet, A.; Erwin, K.L.; Finlayson, C.M.; De Groot, R.S.; Harris, J.A.; Higgs, E.S. Opportunities and challenges for ecological restoration within REDD+. *Restor. Ecol.* **2011**, *19*, 683–689.
10. Aide, T.M.; Zimmerman, J.K.; Pascarella, J.B.; Rivera, L.; Marcano-Vega, H. Forest Regeneration in a Chronosequence of Tropical Abandoned Pastures: Implications for Restoration Ecology. *Restor. Ecol.* **2000**, *8*, 328–338.
11. Craven, D.; Hall, J.; Verjans, J.M. Impacts of Herbicide Application and Mechanical Cleanings on Growth and Mortality of Two Timber Species in Saccharum spontaneum Grasslands of the Panama Canal Watershed. *Restor. Ecol.* **2009**, *17*, 751–761.
12. Fleming, G.M.; Diffendorfer, J.E.; Zedler, P.H. The relative importance of disturbance and exotic-plant abundance in California coastal sage scrub. *Ecol. Appl.* **2009**, *19*, 2210–2227.
13. Duncan, R.S.; Chapman, C.A. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*; Levey, D.J., Silva, W.R., Galetti, M., Eds.; CAB International: Oxford, UK, 2002; pp. 437–450.
14. Mendoza, I.; Gomez-Aparicio, L.; Zamora, R.; Matias, L. Recruitment limitation of forest communities in a degraded Mediterranean landscape. *J. Veg. Sci.* **2009**, *20*, 367–376.
15. Moran, C.; Catterall, C.P.; Kanowski, J. Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biol. Conserv.* **2009**, *142*, 541–552.
16. Holl, K.D. Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. *Biotropica* **1999**, *31*, 229–242.
17. Carpenter, F.L.; Mayorga, S.P.; Quintero, E.G.; Schroeder, M. Land-use and erosion of a Costa Rican Ultisol affect soil chemistry, mycorrhizal fungi and early regeneration. *Forest Ecol. Manag.* **2001**, *144*, 1–17.
18. Horiuchi, B.; Jeffrey, J. Native plant propagation and habitat restoration at Hakalau Forest National Wildlie Refuge, Hawaii. In National Proceedings: Forest and Conservation Nursery Associations (1999, 2000, and 2001). Conferenence in Kailua-Kona, HI, USA, 21-25 August 2000, **2002**; p. 233.

19. Brooks, S.; Cordell, S.; Perry, L. Broadcast seeding as a potential tool to reestablish native species in degraded dry forest ecosystems in Hawaii. *Ecol. Restor.* **2009**, *27*, 300–305.
20. Goldstein, J.H.; Pejchar, L.; Daily, G.C. Using return-on-investment to guide restoration: a case study from Hawaii. *Conserv. Lett.* **2008**, *1*, 236–243.
21. Prach, K.; Pyšek, P. Using spontaneous succession for restoration of human-disturbed habitats: Experience from Central Europe. *Ecol. Eng.***2001**, *17*, 55–62.
22. Wali, M. Ecological succession and the rehabilitation of disturbed terrestrial ecosystems. *Plant Soil* **1999**, *213*, 195–220.
23. Cusack, D.; Montagnini, F. The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. *Forest Ecol. Manag.* **2004**, *188*, 1–15.
24. Parrotta, J.A.; Turnbull, J.W.; Jones, N. Introduction——Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecol. Manag.* **1997**, *99*, 1–7.
25. Falk, D.A.; Palmer, M.A.; Zedler, J.B. *Foundations of Restoration Ecology*; Island Press: Washington, DC, USA, 2006.
26. Kobe, R.K.; Pacala, S.W.; Silander, J.A.; Canham, C.D. Juvenile Tree Survivorship as a Component of Shade Tolerance. *Ecol. App.* **1995**, *5*, 517–532.
27. Loik, M.E.; Holl, K.D. Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. *Restor. Ecol.* **1999**, *7*, 382–391.
28. Dos Santos, U.M.; Goncalves, J.F.D.; Feldpausch, T.R. Growth, leaf nutrient concentration and photosynthetic nutrient use efficiency in tropical tree species planted in degraded areas in central Amazonia. *Forest Ecol. Manag.* **2006**, *226*, 299–309.
29. Kelly, J.; Jose, S.; Nichols, J.D.; Bristow, M. Growth and physiological response of six Australian rainforest tree species to a light gradient. *Forest Ecol. Manag.* **2009**, *257*, 287–293.
30. Duncan, R.S.; Chapman, C.A. Tree-shrub interactions during early secondary forest succession in Uganda. *Restor. Ecol.* **2003**, *11*, 198–207.
31. Royo, A.A.; Carson, W.P. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. Forest Res.* **2006**, *36*, 1345–1362.
32. Gómez-Aparicio, L. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *J. Ecol* **2009**, *97*, 1202–1214.
33. Padilla, F.M.; Pugnaire, F.I. The role of nurse plants in the restoration of degraded environments. *Front Ecol Enviro* **2006**, *4*, 196–202.
34. Graves, M.W.; Addison, D.J. The Polynesian settlement of the Hawaiian Archipelago: Integrating models and methods in archaeological interpretation. *World Archaeol.* **1995**, *26*, 380–399.
35. Cuddihy, L.W.; Stone, C.P. *Alteration of Native HAWAIIAN Vegetation: Effects of Humans, Their Activities and Introductions*; Cooperative Natl. Park Resources Studies Unit, Univ. Hawaii: Honolulu, HI, USA, 1990.
36. Smith, C.W. Impact of alien plants on Hawaii's native biota. In *Hawaii's Terrestrial Ecosystems: Preservation and Management*; Scott, J.M., Stone, C.P., Eds.; University of Hawai'i: Honolulu, Hawai'i, **1985**; pp. 180–250.
37. Loope, L.L.; Giambelluca, T.W. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. *Climatic Change* **1998**, *39*, 503–517.

38. Holt, A. An alliance of biodiversity, agriculture, health, and business interests for improved alien species management in Hawaii. In *Invasive Species and Biodiversity Management*; Sandlund, O.T., Schei, P.J., Viken, A.S., Eds. Kluwer Academic Publishers: Dordrecht, The Netherlands, 2001; pp. 65–75.
39. George, L.O.; Bazzaz, F. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* **1999**, *80*, 833–845.
40. Ashton, M.S.; Gunatilleke, C.; Singhakumara, B.; Gunatilleke, I. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *Forest Ecol. Manag.* **2001**, *154*, 409–430.
41. Slocum, M.G.; Aide, T.M.; Zimmerman, J.K.; Navarro, L. Natural regeneration of subtropical montane forest after clearing fern thickets in the Dominican Republic. *J. Tropl. Ecol.* **2004**, *20*, 483–486.
42. Giambelluca, T.W.; Chen, Q.; Frazier, A.G.; Price, J.P.; Chen, Y.-L.; Chu, P.-S.; Eischeid, J.K.; Delparte, D.M. Rainfall Atlas of Hawai'i. *Bull. Amer. Meteor. Soc.* **2012**, doi: 10.1175/BAMS-D-11-00228.1.
43. Wagner, W.L.; Herbst, D.R.; Sohmer, S.H. *Manual of the Flowering Plants of Hawai'i: Revised Edition*; Bishop Museum Press: Honolulu, HI, USA, 1999.
44. USFWS. Revised Recovery Plan for the 'Alala *(Corvus hawaiiensis)*. U.S. Fish & Wildlife Service: Portland, OR, USA, 2009.
45. Sakai, H.F.; Carpenter, J.R. The Variety and Nutritional Value of Foods Consumed By Hawaiian Crow Nestlings, An Endangered Species. *Condor* **1990**, *92*, 220–228.
46. Culliney, S.M. Seed Dispersal by the Critically Endangered Alala (Corvus Hawaiiensis). Colorado State University: Fort Collins, CO, USA, 2011.
47. Turnbull, L.A.; Rees, M.; Crawley, M.J. Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.* **1999**, *87*, 899–912.
48. Woods, K.; Elliott, S. Direct seeding for forest restoration on abandoned agricultural land in Northern Thailand. *J. Trop. For. Sci.* **2004**, *16*, No. 2.
49. Hau, H.C. Tree seed predation on degraded hillsides in Hong Kong. *Forest Ecol. Manag.* **1997**, *99*, 215–221.
50. Zuur, A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. GLMM and GAMM. In *Mixed Effects Models and Extensions in Ecology with R*, 1st ed.; Springer Science+Business Media, LLC: New York, NY, USA, 2009.
51. Bolker, B.M.; Brooks, M.E.; Clark, C.J.; Geange, S.W.; Poulsen, J.R.; Stevens, M.H.H.; White, J.S.S. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **2009**, *24*, 127–135.
52. Ostertag, R.; Cordell, S.; Michaud, J.; Cole, T.C.; Schulten, J.R.; Publico, K.M.; Enoka, J.H. Ecosystem and Restoration Consequences of Invasive Woody Species Removal in Hawaiian Lowland Wet Forest. *Ecosystems* **2009**, *12*, 503–515.
53. Cordell, S.; McClellan, M.; Carter, Y.Y.; Hadwan, L.J. Towards restoration of Hawaiian tropical dry forests: the Kaupulehu outplanting programme. *Pacific Conservation Biology* **2008**, *14*, 279–284.

54. Wester, L. Weed Management and the Habitat Protection of Rare species—A Case Study of the Endemic Hawaiian Fern Marsilea villosa. *Biol.Conserv.* **1994**, *68*, 1–9.
55. Mueller-Dombois, D.; Wirawan, N. The Kahana Valley Ahupua'a, a PABITRA study Site on O'ahu, Hawaiian islands. *Pac. Sci.* **2005**, *59*, 293–314.
56. Griscom, H.P.; Griscom, B.W.; Ashton, M.S. Forest Regeneration from Pasture in the Dry Tropics of Panama: Effects of Cattle, Exotic Grass, and Forested Riparia. *Forest Ecol. Manag.* **2009**, *17*, 117–126.
57. Aide, T.M.; Cavelier, J. Barriers to Lowland Tropical Forest Restoration in the Sierra Nevada de Santa Marta, Colombia. *Restor. Ecol.* **1994**, *2*, 219–229.
58. Funk, J.L.; Vitousek, P.M. Resource-use efficiency and plant invasion in low-resource systems. *Nature* **2007**, *446*, 1079–1081.
59. Cordell, S.; Ostertag, R.; Rowe, B.; Sweinhart, L.; Vasquez-Radonic, L.; Michaud, J.; Colleen Cole, T.; Schulten, J.R. Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. *Biol. Conserv.* **2009**, *142*, 2997–3004.
60. Scowcroft, P.G.; Jeffrey, J. Potential significance of frost, topographic relief, and Acacia koa stands to restoration of mesic Hawaiian forests on abandoned rangeland. *Forest Ecol. Manag.* **1999**, *114*, 447–458.
61. Tunison, J.T.; D'Antonio, C.M.; Loh, R.K. Fire and Invasive Plants in Hawaiʻi Volcanoes National Park. In *Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species (Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management)*, Galley, K.E.M., Wilson, T.P., Eds.; Tall Timbers Research Station: Tallahassee, FL, USA, 2001.
62. Giardina, C.P.; Litton, C.M.; Thaxton, J.M.; Cordell, S.; Hadway, L.J.; Sandquist, D.R. Science driven restoration: A candle in a demon haunted world—Response to Cabin. *Restor. Ecol.* **2007**, *15*, 171–176.
63. Cramer, V.A.; Hobbs, R.J.; Standish, R.J. What's new about old fields? Land abandonment and ecosystem assembly. *Trends Ecol. Evol.* **2008**, *23*, 104–112.
64. Brauman, K.A.; Freyberg, D.L.; Daily, G.C. Forest structure influences on rainfall partitioning and cloud interception: A comparison of native forest sites in Kona, Hawai'i. *Agr. Forest Meteorol.* **2010**, *150*, 265–275.
65. Ticktin, T. The ecological implications of harvesting non-timber forest products. *J. of Appl Ecol* **2004**, *41*, 11–21.
66. Holl, K.D.; Loik, M.E.; Lin, E.H.V.; Samuels, I.A. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restor. Ecol.* **2001**, *8*, 339–349.
67. 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.
68. Carpenter, L.F.; Nichols, D.; Sandi, E. Early growth of native and exotic trees planted on degraded tropical pasture. *Forest Ecol. Manage.* **2004**, *196*, 367–378.
69. Callaway, R.M. *Positive Interactions and Interdependence in Plant Communities*; Springer: Dordrecht, The Netherlands, 2007.

70. Brooker, R.W.; Maestre, F.T.; Callaway, R.M.; Lortie, C.L.; Cavieres, L.A.; Kunstler, G.; Liancourt, P.; Tielbörger, K.; Travis, J.M.J.; Anthelme, F.; *et al*. Facilitation in plant communities: the past, the present, and the future. *J. Ecol.* **2008**, *96*, 18–34.
71. Maestre, F.T.; Callaway, R.M.; Valladares, F.; Lortie, C.J. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* **2009**, *97*, 199–205.
72. Cavieres, L.A.; Badano, E.I.; Sierra-Almeida, A.; Gómez-González, S.; Molina-Montenegro, M.A. Positive interactions between alpine plant species and the nurse cushion plant Laretia acaulis do not increase with elevation in the Andes of central Chile. *New Phytol.* **2005**, *169*, 59–69.
73. Gómez-Aparicio, L.; Zamora, R.; Gómez, J.M.; Hódar, J.A.; Castro, J.; Baraza, E. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecol. Appl.* **2004**, *14*, 1128–1138.
74. Zanini, L.; Ganade, G. Restoration of Araucaria forest: the role of perches, pioneer vegetation, and soil fertility. *Restor. Ecol.* **2005**, *13*, 507–514.
75. Vieira, I.C.G.; Uhl, C.; Nepstad, D. The role of the shrub Cordia multispicata Cham. as a "succession facilitator" in an abandoned pasture, Paragominas, Amazonia. *Vegetatio* **1994**, *115*, 91–99.
76. Duncan, R.S.; Chapman, C.A. Tree–shrub interactions during early secondary forest succession in Uganda. *Restor. Eco.* **2003**, *11*, 198–207.
77. Holl, K.D. Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *J. Ecol.* **2002**, *90*, 179–187.
78. Greenwell, S. The Changing Picture in Hawaiian Range Management. *J. Range Manage* **1959**, *12*, 99–103.
79. McDaniel, S.; Ostertag, R. Strategic light manipulation as a restoration strategy to reduce alien grasses and encourage native regeneration in Hawaiian mesic forests. *Appl. Veg. Sci.* **2010**, *13*, 280–290.
80. Esquivel, M.J.; Harvey, C.A.; Finegan, B.; Casanoves, F.; Skarpe, C. Effects of pasture management on the natural regeneration of neotropical trees. *J. Appl. Ecol.* **2008**, *45*, 371–380.
81. Denslow, J.S.; Uowolo, A.L.; Hughes, R.F. Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia* **2006**, *148*, 118–128.
82. Bonilla-Moheno, M.; Holl, K.D. Direct Seeding to Restore Tropical Mature-Forest Species in Areas of Slash-and-Burn Agriculture. *Restor. Ecol.* **2010**, *18*, 438–445.
83. NOAA, National Oceanic and Atmospheric Administration. Drought Grips Hawaii in 2010. *ClimateWatch Magazine*, 5 January 2011.
84. Cole, R.J.; Holl, K.D.; Keene, C.; Zahawi, R.A. Direct seeding of late-successional trees to restore tropical montane forest. *Forest Ecol Manag* **2011**, *261*, 1590–1597.
85. Silvertown, J.W. Seed size, life span, and germination date as coadapted features of plant life history. *Am. Nat.* **1981**, 860–864.
86. Dalling, J.W.; Hubbell, S.P. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *J. Ecol.* **2002**, *90*, 557–568.
87. Palmerlee, A.P.; Young, T.P. Direct seeding is more cost effective than container stock across ten woody species in California. *Native Plants J.* **2010**, *11*, 89–102.

88. Minnesota DNR. *Direct seeding of Native Hardwood Trees: An Innovative Approach to Hardwood Regeneration*; Minnesota Department of Natural Resources: Minnesota, MN, USA, 2012.

© 2013 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 license (http://creativecommons.org/licenses/by/3.0/).