PACIFIC SCIENCE Early View
A Quarterly Devoted to the
Biological and Physical Sciences of the Pacific Region

Dry forest restoration and unassisted native tree seedling recruitment at Auwahi, Maui

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Abstract

Efforts to restore highly degraded but biologically significant forests draw from a limited toolbox. With less than 10% of their former distribution remaining, Hawaiian dry forests, though critically endangered, remain important biological and cultural refugia. At restoration onset (1997), vegetation of restoration and control areas of degraded Auwahi dry forest, Maui island were similar, dominated by non-native graminoids (restoration 78.3%; control 75.4%), especially *Cenchrus* (*Pennisetum*) *clandestinus*. In 2012, unrestored control area vegetation was basically unchanged. In contrast, in the restoration area in 2012, native shrub cover increased from 3.1% to 81.9% while cover of non-native graminoids declined from 75.4% to 3.3%. In 2012, non-planted seedlings of 14 of 22 native tree and six of seven native shrub species were observed in restoration plots, the majority (99%) were five native (*Dodonaea viscosa, Coprosma foliosa, Osteomeles anthyllidifolia*, *Chamaesyce celastoides*, *Nestegis sandwicensis*) and one non-native species (*Bocconia frutescens*). By 2012, stem counts of native woody plants had increased from 12.4 to 135.0/100m^2 and native species diversity increased from 2.4 to 6.6/100m^2. By 2012, seven rare dry forest tree species, *Charpentiera obovata, Nothocestrum latifolium, Ochrosia haleakalae*, *Pleomele auwahiensis*, *Santalum ellipticum, S. haleakalae*, and *Streblus pendulinus* had established seedlings and/or saplings within the restoration site, especially notable in that natural reproduction is largely lacking elsewhere. Without development and implementation of appropriate management strategies, remaining Hawaiian dry forest will likely disappear within the next century. Multi-component restoration incorporating ungulate exclusion, weed control, and outplanting as described here offers one strategy to conserve and restore tracts of high value but degraded forests.

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Pacific Science, vol. 68, no. 1
July 16, 2013 (Early view)

Official Journal of the Pacific Science Association

Introduction

Disproportionately impacted by grazing, wildfire, and displacement by agriculture and human settlements, tropical dry forests are globally among the most threatened of ecosystems (Janzen 1988, Olson and Dinerstein 2002, Miles et al. 2006). In the Hawaiian archipelago, dry forests, though diverse, are among the most fragmented, reduced, and ecologically degraded ecosystems, with less than 10% of their original pre-Polynesian contact area remaining (Bruegmann 1996). Loss and degradation of the patchwork of Hawaiian dry forest types that formerly occurred on leeward slopes to 1,500m elevation began with more frequent fires associated with agriculture and *Rattus exulans* (Pacific rat) introduction associated with colonizing Polynesians ca 1000-1200AD (Athens 2009, Wilmshurst et al. 2011). Following European contact in 1778, the proliferation of non-native species, particularly feral and domestic ungulates, fire-adapted grasses, and additional rodent species accelerated forest decline (Cuddihy and Stone 1990, D'Antonio and Vitousek 1992, Blackmore and Vitousek 2000, Cordell and Sandquist 2008). Though largely undocumented, introduced invertebrates and pathogens have undoubtedly reduced fitness of dry forest species, exemplified recently by the devastating impacts on the keystone dry forest tree *Erythrina sandwicensis* Degener by the invasive African gall-forming wasp *Quadrastichus erythrinae* (Rubinoff et al. 2010).

Despite their degraded state, Hawaiian dry forests remain important natural refugia harboring high numbers of threatened species (Rock 1913) including over 25% of Federally-listed Endangered Hawaiian plant species (Cabin et al. 2002). Auwahi dry forest on Maui island, the study site reported here, was previously known to be among the most diverse of Hawaiian ecosystems (Rock 1913). Currently, Auwahi has 13 species with World Conservation Union (IUCN) Red List status, exceeding New Caledonia dry forests, considered among the world's most endangered tropical dry forests (Gillespie and Jaffre 2003; Table 1). Culturally, dry forests are highly valued by native Hawaiians for ethnobotanical source materials, especially prized durable hardwoods for tools and weapons, and species with utilitarian, medicinal or religious significance (Medeiros et al. 1998). Despite being recognized in global conservation priorities (Olson and Dinerstein 2002), remaining Hawaiian dry forests will likely be lost in the next 50-100 years unless effective management strategies can be developed to stabilize and restore them.

Beginning in 1845, Auwahi's forest understory was destroyed by cattle grazing and burning (Lennox 1967, S. Erdman, personal communication). The native understory was replaced by extensive stands of the invasive shrub *Ageratina adenophora* (Spreng.) King & Robinson that dominated until 1945 when eliminated by a biological control program coupled with severe drought (Medeiros et al. 1986). In response, ranchers planted slips of *Cenchrus* (*Pennisetum*) *clandestinus* (Hochst. Ex Chiov.) Morrone [Common name and hereafter referred to as kikuyu grass] throughout Auwahi ca. 1950 to enhance cattle pasturage and reduce erosion (P. Erdman, personal communication). By 1965, kikuyu grass had spread extensively, developed rank mats, and was regarded as a primary threat to forest health at Auwahi and responsible for a dramatic decline of native trees (Lennox 1967).

Kikuyu grass, native to highland forest margins of central and east Africa at 1950-2700m, is noted for its vigorous vegetative reproduction and allelopathic chemical production (Marais 2001). Though useful as forage in marginal situations, kikuyu grass is also invasive in Hawai'i, California, La Réunion, Australia, New Zealand, and South Africa, and listed as a noxious weed with prohibited transport by the US Department of Agriculture (Weber 2003). At Auwahi, kikuyu grass rarely produces seeds (S. Erdman, personal communication). As seed-producing kikuyu grass cultivars in Hawai'i were developed or introduced after 1950 (Fukumoto and Lee 2003), the kikuyu grass cultivar at Auwahi is likely the 'wild, unimproved type' reported to be largely sterile (Marais 2001).

By the late 1960s, approximately 95% of ca. 4000 ha of Auwahi dry forest on leeward Haleakalā had been destroyed (Lennox 1967). The rarity of the forest type and diverse tree flora (49 species) combined with continued forest decline and the troubling long-term (50-100 years) failure of native tree reproduction prompted a regional biological inventory to describe Auwahi as a 'museum forest', i.e. a high diversity forest lacking recruitment (Medeiros et al. 1986).

In the 1960s, forest protection efforts began at Auwahi by excluding domestic and feral ungulates with fencing that unfortunately accelerated kikuyu grass growth and increased tree mortality (P. Erdman, personal communication). Despite effective kikuyu grass control in the 1990s in Auwahi exclosures with newly-developed glyphosate-based herbicides, few native seedlings recruited, tree mortality continued, and minimal conservation benefit was realized.

In 1997, a multi-phased restoration effort involving ungulate exclusion, herbicidal control of kikuyu grass mats, and mass planting native nurse shrub *Dodonaea viscosa* Jacq. seedlings was initiated on a 4 ha tract of relict dry forest at Auwahi. Nurse planting involves outplanting selected nurse-plant species around target species, usually with the goal of stimulating target species seedling recruitment (Gomez-Aparicio 2009). Potential benefits associated with nurse plantings include sun and wind moderation, cooler and moister soils, increased perch trees for seed-dispersing birds, and perhaps improved nutrient cycling and mycorrhizae (Padilla and Pugnaire 2006), as well as recovered hydrological functioning (Perkins et al. 2012). The primary objective of this paper was evaluation of a multi-phased restoration technique in a highly degraded Hawaiian dry forest.

Methods

Study Site

Auwahi forest is located at 1160-1250 m elevation in Auwahi district on leeward flanks of Haleakalā volcano on 3,000-5,000 year old lava (20° 38' 24" N, 156° 20' 24" W) on privately-owned ‘Ulupalakua Ranch, Maui, Hawaiian Islands. The restoration area is 4 ha of relictual forest where an ungulate-proof exclosure was constructed with U.S. Fish and Wildlife Service (USFWS) funds. The terrain consists of a series of rocky ridges and interconnecting gullies (slope 20-30 degrees) with generally rocky substrate and sparse soil accumulations. Mean annual precipitation is ca. 730 mm with a pronounced dry season from April to September (Giambelluca et al. 2011) and mean monthly temperatures between 13.9°C and 18.3°C (Scholl et al. 2007).

Restoration methodology:

In 1997, restoration was initiated with construction of a 1.3m high perimeter fence excluding domestic cattle and feral ungulates from the 4 ha site. Kikuyu grass mats were suppressed with one primary herbicide treatment (ca. 1.5% glyphosate) and one follow-up treatment several months later to treat resprouts. Treated grass mats were not removed but left to decay. Seedlings of the native *Dodonaea* (ca. 0.25m ht), were grown in tree planting tubes and planted at high densities (ca. 1-meter spacing) by community volunteers. *Dodonaea* was selected as the primary nurse-plant for its ease of propagation, hardiness, rapid growth, quick time to reproduction, and its historical presence as a primary component of the original understory vegetation (Lennox 1967). *Dodonaea* shrubs were planted in open areas where mats of kikuyu grass formerly occurred throughout the restoration site. Plantings of seedlings of other depleted native species (Table 1), also in tree planting tubes, were generally clustered to maximize particular habitat types or facilitate future outcrossing pollination.

Vegetation sampling:

To initially compare control and restoration areas, four randomly located 100 m transects were established in each area and vegetation sampled with point- and line-intercept in both 1997 and 2012. Understory vegetation < 0.5 m ht was sampled with point-intercept while canopy shrub and tree species > 0.5 m ht were recorded with line-intercept. In the control area, 68 100m^2 plots were randomly located and woody species were counted and classified by basal diameter in 2012. In addition, to more closely track vegetation trajectories in the restoration area, 84 100m^2 plots were randomly located within the restoration site and the number of stems for each woody species per plot recorded in size classes based on basal diameter. In a randomly selected subset (31 of 84 100m^2 plots), estimates of cover were made visually to the nearest 5% (or to nearest 1% when cover < 5%) for all vascular plant species. Count plots and cover estimates of species were assessed in 1997 prior to restoration and again in 2012. Methods follow Mueller-Dombois and Ellenberg (2003).

Statistical analyses:

This study is not an investigation of the efficacy of restoration treatments per se, but rather a comparison of spatiotemporal floristic differences between two specific areas within one site (inside vs. outside the restoration area) over a 15-year period. The restoration site was chosen with the landowner and funder to provide protection and attempt restoration of a particularly biologically important forest tract of an endangered plant community. From an experimental perspective, it would have been preferable to have multiple fenced and unfenced sites to evaluate multiple restoration treatments, but the rarity and conservation value of the studied forest type, and the lack of comparable unprotected areas, precluded such an experimental design. In essence, therefore, the study is pseudoreplicated, with only one restoration site that received a series of synchronized treatments (ungulate exclusion, herbicidal applications, and native nurse-shrub planting) and one adjacent untreated area. Paired t-tests compared differences in cover of major vegetation categories and species as well as mean seedling recruitment within restoration site plots between 1997 and 2012. T-tests compared mean differences in seedling recruitment between control plots and restoration site plots in 2012 only.

Bonferroni corrections were used to adjust for multiple t-tests. Transformations were applied to cover data (arcsin) and seedling number data (square root + 0.05) to improve normality and meet assumptions of parametric statistical tests (Zar 1999). Data analyses were performed using Minitab 15 and Sigmaplot 10.

Results

Restoration vs. control area in 1997 (point- and line-intercept):

Initially, vegetation of restoration and control areas was very similar. In 1997, understory vegetation (point-intercept) of both areas was similarly dominated by non-native graminoids (restoration 78.3% ± 2.8; control 75.4% ± 4.2, P=0.27), especially kikuyu grass (restoration 75.4% ± 2.3; control 70.7% ± 4.3, P=0.18). Native tree cover (line-intercept) was also similar between restoration and control areas (restoration 5.7% ± 3.0; control 8.6% ± 4.6, P=0.69). Cover of native shrubs (line-intercept) was higher in control areas but not significantly so (restoration 3.1% ± 1.2; control 19.7% ± 9.8, P=0.20).

Control area 1997-2012 (point- and line-intercept):

When resampled in 2012, understory vegetation of the control area was basically unchanged from 1997. Non-native graminoid cover remained dominant (1997: 75.4% ± 4.2 vs. 2012: 87.4% ± 4.3; P=0.18) with slight increases in kikuyu grass (70.6% ± 4.3 vs. 77.6% ± 2.4; P=0.30). Native shrub cover (line-intercept) in the control area remained relatively constant (1997: 19.7% ± 9.8 vs. 2012: 21.8% ± 13.9; P=0.71), while native tree cover declined slightly (1997: 8.6% ± 4.6, 2012: 7.7% ± 2.0; P=0.84).

Restoration area 1997-2012 (point- and line-intercept):

In contrast to control areas, by 2012, non-native graminoids, especially kikuyu grass, had declined dramatically in the restoration area from 75.4% ± 2.3 to 3.3% ± 2.3 (P<0.0001). Correspondingly, cover of native shrubs (line-intercept) increased from 3.1% ± 1.2 to 81.9% ±

9.9 (P<0.05), especially *Dodonaea* (+59.5% ± 6.6) but also *Coprosma foliosa* Gray (+10.5% ± 4.2), and *Osteomeles anthyllidifolia* (Sm.) Lindl. (+8.3% ± 3.3). In the restoration area, native tree cover increased from 5.7% ± 3.0 to 18.5% ± 8.4 (P=0.32). Cover increases of *Dodonaea*, *Coprosma*, and *Osteomeles* represent both wild and planted individuals (see count plot data) whereas increases in plots of the two depleted native tree species *Pleomele auwahiensis* St. John (+1.2% ± 0.2) and *Xylosma hawaiiense* Seem. (+0.8% ± 0.6) represent planted individuals, surviving after 15 years.

Restoration area 1997-2012 (cover estimates):

The most significant changes by guild (1997-2012) were decreases in total non-native cover (-84.3%), especially non-native graminoids (-73.1%) and non-native herbs (-11.0%) and increases in total native cover (+57.6%), native shrubs (+59.7%), rock (+27.9%), and leaf litter (+51.5%) (Table 2, Figure 1 and 2). The most significant changes by species were decreases of kikuyu grass (-70.6%) and *Asclepias physocarpa* (Mey.) Schlechter (-11.1%) and increases of *Dodonaea* (+51.9%), *Osteomeles* (+6.2%), and *Coprosma* (+1.7%) (Table 3). Large scale increases of native shrubs used as nurse-plants, especially *Dodonaea*, are due to the growth and spread of planted individuals and subsequent natural recruitment. In cover estimates of *Dodonaea*, 66.2% cover increase was due to planted individuals, while 33.8% was from surviving original individuals and sapling recruitment. Cover of native tree species changed little (-3.1%) according to cover estimates, perhaps reflecting the limitation of the technique of visually assigning cover estimates for tree species in structurally complex vegetation (Table 3).

Restoration area 1997-2012 (count plots):

By 2012, seedlings of 14 of 22 native tree and six of seven native shrub species had been observed in plots within the restoration area. The great majority (99%) of seedlings in plots belonged to six species: three native shrubs (*Dodonaea, Coprosma, Osteomeles*), two native trees (*Chamaesyce celastroides* (Bois.) Croizat & Degener var. *lorifolia* (Gray) Degener & Degener, *Nestegis sandwicensis* (Gray) Degener, Degener, & Johnson, and one invasive tree (*Bocconia frutescens* L.) (Table 4). By 2012, stem counts of native woody species had increased by an order of magnitude from 12.4 ± 1.4/100m^2 to 135.0 ± 9.7 ($P < 0.001$). In plots, native species diversity increased from 2.4 ± 0.2/100m^2 to 6.6 ± 0.2 ($P < 0.001$).

Discussion

From 1997-2012, ungulate exclusion, weed control, and nurse-planting have apparently been important factors in facilitating long-term suppression of formerly dominant invasive kikuyu grass (Table 3), re-establishment of native shrub understory (Table 2, Figure 2), seedling recruitment by some native tree, shrub, herb, grass, and vine species (Table 4), and apparently some degree of biotic resistance to reinvasion by light-demanding non-native flora, particularly fire-adapted grasses (D'Antonio and Vitousek 1992).

The absence of seed set and seed banks of kikuyu grass and resultant sparse recruitment of kikuyu grass seedlings following herbicide applications appears to have been an important factor in restoration efficacy at Auwahi. Treated kikuyu grass decomposed within ca. 1-2 years, providing mulch and weed protection while nurse-plants established (Medeiros et al. 2003, Medeiros and von Allmen 2006). Survival of outplanted nurse-plant seedlings, especially *Dodonaea*, was very high (>95%, unpublished data). For several years after outplanting, growth of nurse-plants was rapid perhaps due to heightened nutrient availability accompanying kikuyu grass decomposition. Within two years, outplanted *Dodonaea* shrubs averaged 1m^3 in cover and began to interlock canopies. Although no quantitative assessment was made, the thick mulch of decomposing kikuyu grass mats and shading provided by densely planting rapid-growing shrub nurse-plants appeared to deter reinvasion by a regional suite of light-loving invasive plant species. Elsewhere, shrub nurse-plants have had strongest benefits on target tree species including enhanced germination and seedling survival (Padilla and Pugnaire 2006, Gomez-Aparicio 2009).

Other dry forest restoration projects in Hawaii have documented that just ungulate exclusion and invasive plant control have been insufficient to spur unassisted seedling recruitment of many dry forest species (Cabin et al. 2000, Cabin et al. 2002, Brooks et al. 2009). At Auwahi, the restoration strategy combining non-native grass removal, ungulate exclusion and reestablishment of native shrub understory through nurse-planting (Table 2) appears to have recreated safe sites for enhanced native seedling establishment. As of 2012, unassisted seedling recruitment had been observed in the restoration site for 64% of native trees and 86% of native shrub species (Table 4). Following the rainy season, cohorts of hundreds of seedlings of *Dodonaea, Coprosma,* and *Chamaecyse* have been observed. In addition to the creation of safe sites, increases in seedling recruitment in some cases may be due to heightened levels of available seed as planted individuals begin to produce fruit.

By 2012, seven rare dry forest tree species, *Charpentiera obovata* Gaud., *Ochrosia haleakalae* St. John, *Pleomele*, *Nothocestrum latifolium* Gray, *Santalum haleakalae* Hillebr. var. *lanaiense* Rock (Harbaugh), *S. ellipticum* Gaud., and *Streblus pendulinus* (Endl.) Muell., had established seedlings and/or saplings within the restoration site. Though the number of observed seedlings was in some cases limited, the recruitment is significant in that natural reproduction is largely lacking elsewhere in wild populations. Four of these species have IUCN Red List status; one (*S. haleakalae lanaiense*) is considered Endangered (USFWS). For example, in 2012, two wild *Nothocestrum latifolium* seedlings were discovered below perch trees distant from mature *Nothocestrum* individuals apparently the result of seed dispersal by birds, likely the non-native *Zosterops japonicus* (Japanese White-eye). Though modest, this recruitment represents the only currently known natural regeneration of the species. *Nothocestrum latifolium* is the sole native larval host plant for Blackburn's hawkmoth, *Manduca blackburni* listed as Endangered by the USFWS (Rubinoff and San Jose 2010).

The conditions in the restoration area that promote recruitment of native species appear also to facilitate establishment of certain non-native woody species. While most non-native species declined dramatically, the invasive neotropical tree *Bocconia frutescens* increased in restoration area count plots. Despite control efforts, *Bocconia* recruitment in the restoration area was significantly higher than the same area in 1997 or adjacent unrestored areas in 2012 (Table 4). As such, weed control in the restoration area (ca. 48 person-hrs/year) is currently devoted predominantly to *Bocconia*. Without these efforts, *Bocconia* would likely increase and dominate portions of the restoration area. These results demonstrate the vulnerability even of relatively restored ecosystems to non-native woody species such as *Bocconia* with the ability to recruit seedlings in shaded or semi-shaded sites.

As success in rare plant reintroductions is mixed (Hobbs 2007), long-term survival and self-sustaining recruitment of reintroduced species in Auwahi is encouraging. Since 1997, nine highly depleted native species were reintroduced. Three survive but have yet to reach maturity -- *Alectryon macrococcus* Radlk. var. *auwahiensis* Linney, *Xylosma*, and *Zanthoxylum hawaiiense* Hillebr.; two persist with limited recruitment -- *Claoxylon sandwicense* Mull. Arg., *Pisonia brunoniana* Endl.; and one failed -- *Sisyrinchium acre* Mann. All original outplantings of two short-lived Endangered (USFWS) species -- *Bidens micrantha* Gaud. subsp. *kalealaha* Nagata & Ganders, *Vigna o-wahuensis* Vogel, and a highly depleted endemic grass (*Panicum tenuifolium* Hook. & Arnott.) failed to persist. However, the three species became established in the restoration site through repeated cohorts of seedling recruitment, some at considerable distances from original planting sites.

One unfortunate but informative case of selective herbivory of an extremely rare species by a non-native ungulate involved the vine *Vigna o-wahuensis*, a USFWS Endangered species with a total wild population of fewer than 100 individuals (Anon. 1994). In 2010, two juvenile feral pigs entered the restoration site, their smaller size allowing entry through perimeter fence mesh (since repaired). Before their removal, the pigs apparently searched for and destroyed the entire outplanted population of approximately 100 established *Vigna* without significantly impacting other plant species. The pigs excavated the plants, consuming all parts including roots. By 2012, 24 newly-emerged *Vigna* seedlings were recorded in count plots (all near original plantings).

Without native rodents, the Hawaiian biota largely lacks adaptations deterring high levels of predation on native plants, invertebrates, and birds, especially nesting populations (Drake and Hunt 2009). Rodents are a primary factor limiting seed production and perhaps seedling recruitment of Hawaiian plant species. Hawaiian dry forest trees with rodent-palatable seeds typically suffer near complete loss of seed crop and absence of seed bank (Chimera and Drake 2011), a fate shared with highly depleted species elsewhere in the Pacific (Meyer and Butaud 2009). Though predator-resistant fencing is costly and difficult, long-term rodent control would likely have positive and profound cascading effects on native invertebrate, bird, and plant populations released from predation (Innes et al. 2012).

The impact of non-native rodents on seeds of certain native trees has been exacerbated by extinctions of native frugivorous birds, restricting ‘seed shadows’ to beneath canopy areas (Foster 2009, Chimera and Drake 2010). Large-seeded (>7mm) Hawaiian dry forest trees (*Alectryon, Nestegis*, *Pleomele*, and *Pouteria*), no longer dispersed by birds such as the extirpated Hawaiian Crow (*Corvus* spp.) capable of processing large seeds, often lose entire seed crops to rodent predation and characteristically lack seed banks (Culliney et al. 2012).

What will be the future trends at the Auwahi restoration site? The outcome clearly depends on climate change, invasive species, future land uses, management priorities, and perhaps other unforeseen factors. Without control of the invasive tree *Bocconia*, it appears likely that this species will continue to be dispersed into and invade the restoration site. More positively, the unassisted recruitment of native tree seedlings will increase the complexity and height of the emerging forest. Community composition will increasingly reflect native species-native species competition instead of invasive species-native species competition. In some sense, a native version of a novel ecosystem has developed, as proposed by Hobbs et al. (2009, 2013). Mutualistic native-non-native species interactions, such as pollination and seed dispersal, may further assist in restoring ecosystem functioning, as has been documented elsewhere in Hawaii (Cole et al. 1995, Foster and Robinson 2007). One example from the Auwahi restoration site is the apparent dispersal of small-seeded (<7mm) native species such as *Coprosma, Leptecophylla tameiameiae* (Cham. & Schltdl.) Weller*, Osteomeles, Santalum ellipticum,* and *Wikstroemia monticola* Skottsb. by non-native birds, especially the small near ubiquitous passerine *Zosterops japonicus* and gallinaceous Ring-necked pheasant (*Phasianus colchicus*).

How transferable are lessons from Auwahi for restoration of other degraded forests? Several somewhat unique site factors may have contributed to efficacy of the restoration protocol at Auwahi. First, ranchlands and natural areas surrounding Auwahi harbor a relatively low diversity of non-native species (Medeiros et al. 1986). This situation, combined with the absence of seed banks and relatively simple chemical control of kikuyu grass, creates an uncommonly manageable dominant invasive species. Secondly, *Dodonaea*, the nurse-plant utilized here and a component of the original forest understory, was readily available, easy to propagate, grew rapidly, and had high outplanting survival.

Without appropriate management strategies, complete conversion of remaining Hawaiian dry forest will likely occur within the next century. The multi-component restoration effort described here offers one strategy to conserve and restore tracts of dry forests in Hawaii and perhaps elsewhere. With climate change and rampant movement of non-native species, native ecosystems are under siege worldwide, and restoration, already difficult, has become increasingly complicated (Harris et al. 2006). Future management efforts to mitigate climate change in areas such as watersheds may draw from challenges and lessons gleaned from restoration of degraded forests.

Acknowledgements

We thank and acknowledge Sumner, Pardee and Betsy Erdman, ‘Ulupalakua Ranch owners, for their uncommon conservation ethic and support of science. We thank the Pacific Island Ecosystems Research Center and the Ecosystems and Invasives Programs of U.S. Geological Survey for essential support; the U.S. Fish and Wildlife Service for project funding; Robert Cabin, Curt Daehler, Lloyd Loope, Richard Camp, Kevin Brinck, and two anonymous reviewers for manuscript comments; Andrea Buckman, Ka'ai Bustamente, Keahi Bustamente, Diana Crow, Tracy Erwin, Stephanie Joe, Fernando Juan, Ainoa Kaiaokamelie, Paul Krushelnycky, Lindsey Manual, Luke McLean, Forest Starr, Kim Starr, and Brianna Welker for field work assistance, and the tireless dedication and devotion of the hundreds of volunteers who gave up their Saturdays helping to plant and restore this unique dry forest community. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table 1. Native species of Auwahi restoration area.

Taxa	Hawaiian name	Family	guild	Status
Alectryon macrococcus[3]	*mahoe*	Sapindaceae	tree	P
Alphitonia ponderosa	*kauila*	Rhamnaceae	tree	E, P
Alyxia oliviformis	*maile*	Apocynaceae	vine	E, P
Bidens micranthra subsp. *kalealaha*[3]	*kōko'olau*	Asteraceae	shrub	P
Carex wahuensis		Cyperaceae	sedge	E
Chamaesyce celastroides var. *lorifolia*	*'akoko*	Euphorbiaceae	tree	E, P
Charpentiera obovata	*pāpala*	Amaranthaceae	tree	E, P
Claoxylon sandwicense	*po'olā*	Euphorbiaceae	shrub	P
Cocculus trilobus	*huehue*	Menispermaceae	vine	E
Coprosma foliosa	*pilo*	Rubiaceae	shrub	E, P
Diospyros sandwicensis	*lama*	Droseraceae	tree	E
Dodonaea viscosa	*'a'ali'i*	Sapindaceae	shrub	E, P
Leptecophylla tameiameiae	*pūkiawe*	Epacridaceae	shrub	E
Mariscus hillebrandii		Cyperaceae	sedge	E
Melicope adscendens[3]	*alani*	Rutaceae	shrub	E, P
Metrosideros polymorpha	*'ōhi'a*	Myrtaceae	tree	E
Myoporum sandwicense	*naio*	Myoporaceae	tree	E, P
Myrsine lanaiense	*kolea*	Myrsinaceae	tree	E, P
Myrsine lessertiana	*kolea lau nui*	Myrsinaceae	tree	E, P
Nestegis sandwicensis	*olopua*	Oleaceae	tree	E
Nothocestrum latifolium[1,4]	*'aiea*	Solanaceae	tree	E, P
Ochrosia haleakalae[1,4]	*hōlei*	Apocynaceae	tree	E, P
Osteomeles anthyllidifolia	*'ūlei*	Rosaceae	shrub	E, P
Panicum tenuifolium	*konakona*	Poaceae	grass	P
Peperomia blanda	*'ala'ala wai nui*	Piperaceae	herb	E
Pipturus albidus	*māmaki*	Urticaceae	shrub	E
Pisonia brunoniana	*pāpala kēpau*	Nyctaginaceae	tree	P
Planchonella sandwicensis	*'āla'a*	Sapotaceae	tree	E
Pleomele auwahiensis[2]	*halapepe*	Agavaceae	tree	E, P
Polyscias oahuensis	*'ohe mauka*	Araliaceae	tree	E
Santalum ellipticum	*'iliahi alo'e*	Santalaceae	tree	E, P
Santalum haleakalae var. *lanaiensis*[2,3]	*'iliahi*	Santalaceae	tree	E, P
Sicyos pachycarpus	*anunu*	Cucurbitaceae	vine	E
Sisyrinchium acre	*mauu houlā'ili*	Iridaceae	herb	P
Sophora chrysophylla	*māmane*	Fabaceae	tree	E, P
Streblus pendulinus	*a'ia'i*	Moraceae	tree	E, P
Vigna o-wahuensis[3]		Fabaceae	vine	P
Wikstroemia monticola	*'ākia*	Rubiaceae	tree	E
Xylosma hawaiiense	*maua*	Flacourtiaceae	tree	P
Zanthoxylum hawaiiense[1,3]	*a'e*	Rutaceae	tree	P

Status of species P=planted, E=extant within the restoration area.
Superscript indicates endangerment status[1] = Endangered IUCN Red List, [2] = Vulnerable IUCN Red List, [3] = Endangered USFWS, [4] = Candidate USWFS

Table 2. Mean % cover (SE) of guilds within restoration site based on cover estimates of 31 randomly located 100m^2 plots before and after 15 years of restoration.

cover category	% cover 1997	% cover 2012
Non-native grasses***	74.82 (3.90)	1.79 (0.42)
Native shrubs***	8.62 (2.58)	68.04 (3.23)
Non-native herbs***	12.01 (3.09)	1.06 (0.45)
Native trees	12.17 (3.10)	10.43 (2.62)
Native grasses	0	1.07 (0.51)
Native vines	0.30 (0.06)	0.49 (0.19)
Native herbs	0	2.75 (2.25)
Native sedges	0.18 (0.06)	0.39 (0.18)
Non-native sedges**	0.33 (0.10)	0.01 (0.003)
Native ferns	0.26 (0.12)	0.27 (0.21)
Non-native tree	0.77 (0.25)	1.11 (0.55)

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 3. Mean % cover (SE) of selected species within restoration site based on cover estimates of 31 randomly located $100m^2$ plots before and after 15 years of restoration. Non-native species are in bold.

Cover category	% cover 1997	% cover 2012
Cenchrus clandestinus***	70.90 (4.10)	0.26 (0.11)
*Dodonaea viscosa****	3.60 (1.44)	55.55 (3.86
Asclepias physocarpa**	11.18 (2.90)	0.12 (0.10)
*Osteomeles anthyllidifolia**	2.64 (0.85)	8.86 (2.28)
Coprosma foliosa ***	1.35 (0.62)	3.09 (0.66)
Pleomele auwahiensis[2]***	0.0003 (0.0003)	1.02 (0.24)
Ochrosia haleakalae[1,4]*	0	0.73 (0.35)
Myrsine lessertiana	1.67 (1.07)	1.00 (0.67)
*Chamaesyce celastroides***	0.02 (0.01)	0.66 (0.24)
Metrosideros polymorpha	0.81 (0.57)	0.76 (0.43)
Santalum ellipticum	0.71 (0.43)	0.36 (0.25)
Cheirodendron trigynum	0.32 (0.32)	0
Charpentiera obovata	0.29 (0.21)	0
Nothocestrum latifolium[1,4]	0	0.26 (0.19)
Polyscias oahuense	0.32 (0.32)	0.10 (0.10)
Xylosma hawaiiense	0	0.19 (0.16)
Santalum haleakalae lanaiensis[2,3]	0	0.03 (0.03)
Zanthoxylum hawaiiense[1,3]	0	0.02 (0.01)

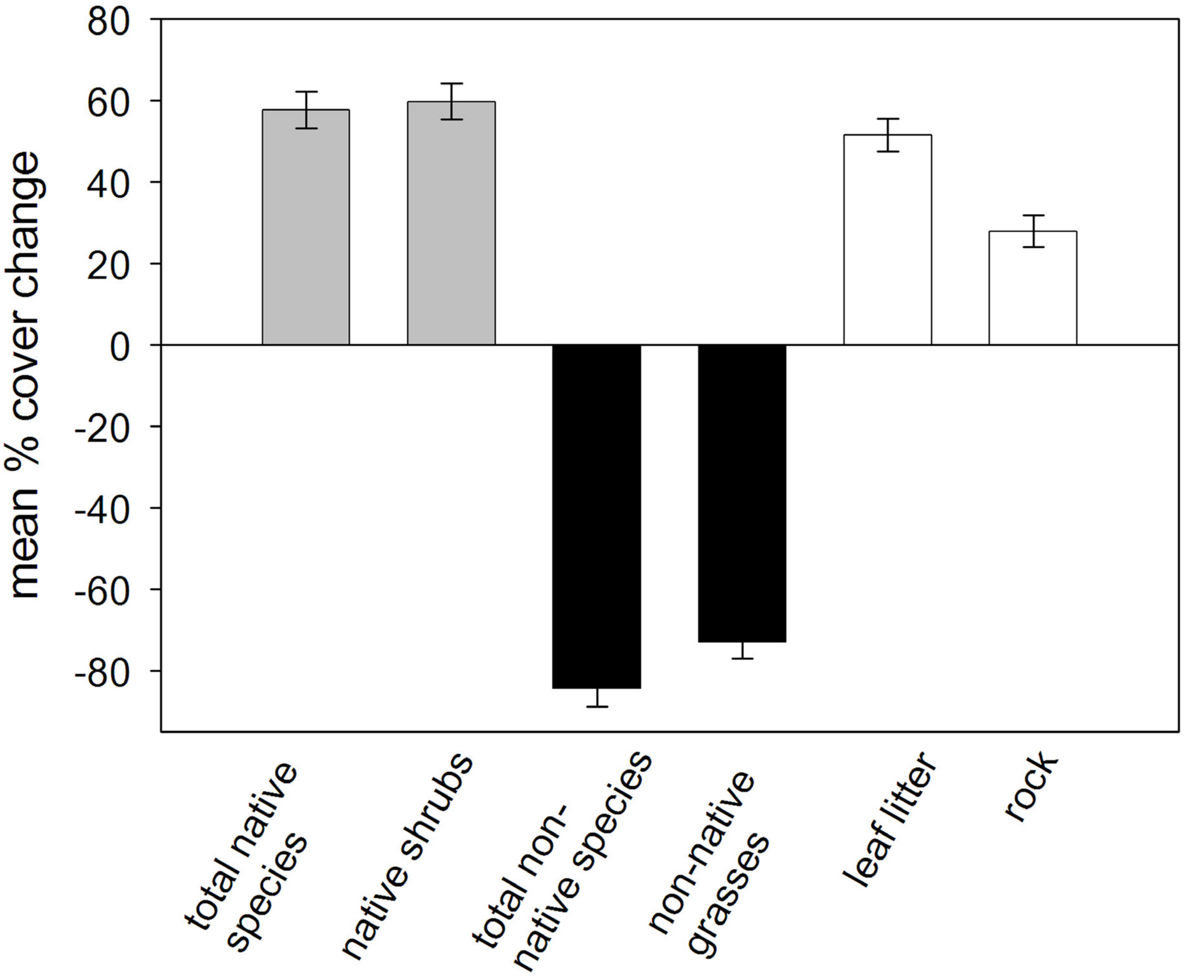
Superscript indicates endangerment status[1] = Endangered IUCN Red List, [2] = Vulnerable IUCN Red List, [3] = Endangered USFWS, [4] = Candidate USWFS

* $P \leq 0.05$, ** $P \leq 0.01$, ***$P \leq 0.001$

Table 4. Mean (SE) numbers of naturally occurring tree seedlings within 100m^2 count plots inside restoration site (1997 and 2012; n = 84) and outside as controls (2012 only; n = 68). Non-native species are in bold.

Taxa	Control (n = 68) 2012[a]	Restoration site (n = 84) 1997[b]	2012[c]
Dodonaea viscosa	1.15 (0.30)	2.26 (0.31)	55.83 (6.28) [a,b]
Coprosma foliosa	0.91 (0.72)	0.74 (0.27)	30.18 (4.50) [a,b]
Chamaecyse celastoides	0	0.10 (0.06)	3.43 (1.10) [a,b]
Osteomeles anthyllidifolia	0.03 (0.02)	0.12 (0.04)	3.24 (0.68) [a,b]
Bocconia frutescens	0.04 (0.03)	0.23 (0.09)	1.82 (0.41)[a,b]
Nestegis sandwicensis	0	0.08 (0.05)	1.14 (0.29) [a,b]
Pleomele auwahiensis[2]	0	0	0.27 (0.13) [a,b]
Myrsine lanaiense	0	0.02 (0.02)	0.19 (0.14)
M. lessertiana	0.01 (0.01)	0.036 (0.03)	0.17 (0.08)
Wikstroemia monticola	0	0	0.14 (0.05)
Ochrosia haleakalae[1,4]	0	0.01 (0.01)	0.10 (0.06)
Santalum haleakalae lanaiensis[2,3]	0	0	0.06 (0.06)
Nothocestrum latifolium[1,4]	0	0	0.036 (0.02)

Figure 1. Mean % cover changes between 1997 and 2012 within restoration site based on cover estimates of 31 randomly located $100m^2$ plots before and after 15 years of restoration. Bars represent standard error. All changes in % cover were significant to $P \leq 0.001$.



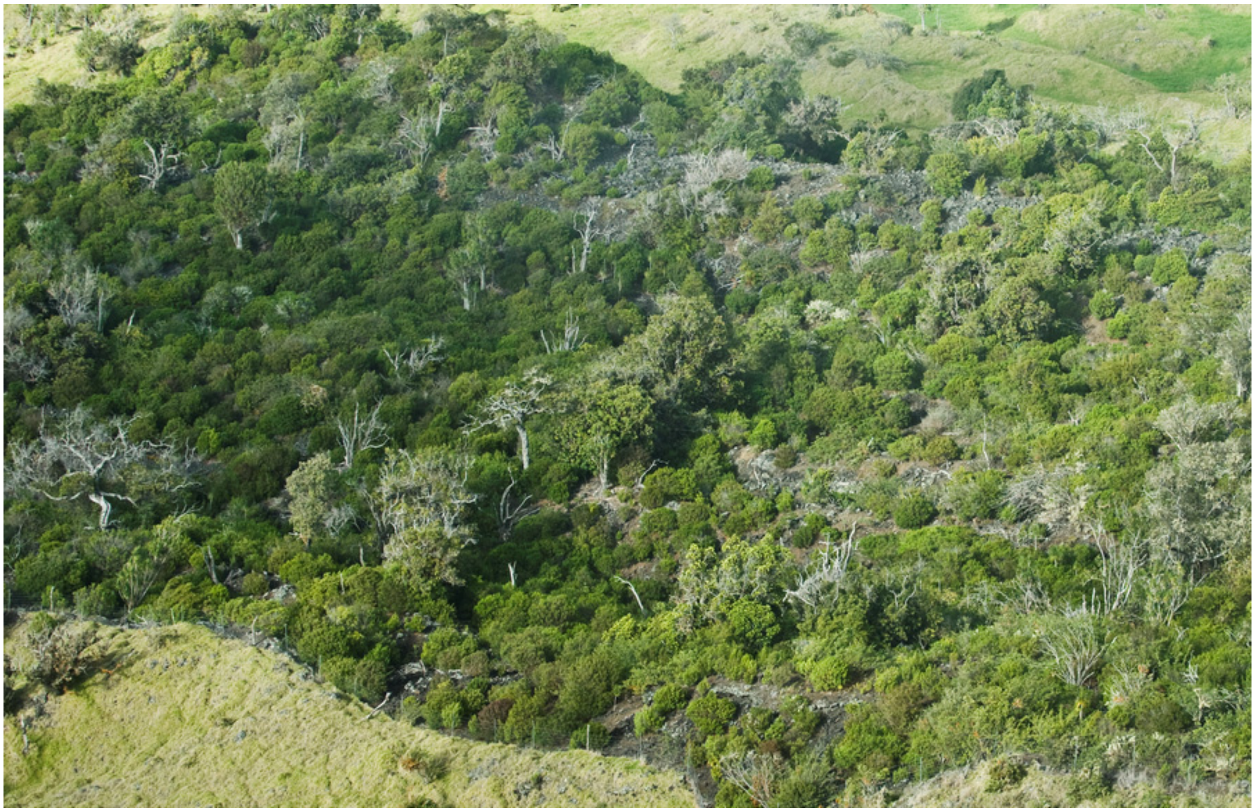


Figure 2. Auwahi restoration site, 2011.

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