

Active restoration enhances recovery of a Hawaiian mesic forest after fire

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ABSTRACT

Identifying management actions required to maintain desired ecological conditions in response to high intensity disturbance events remains a critical question, especially as disturbance regimes and species composition shift due to human activities and climate change. Feedbacks between novel fire disturbance and invasive species on islands, in particular, have resulted in the degradation and conversion of native ecosystems into more alien-species-dominated communities. Further, monitoring and evaluation of management responses to these events remains sparse. We draw on 14 years of monitoring to assess the effects of fire and management response (weed removal and experimentally controlled outplanting of native plants), on the structure, composition and diversity of a native, mesic tropical forest in Hawai'i. Natural regeneration of the native, disturbance-adapted tree, *Acacia koa* was rapid and abundant and formed the dominant canopy component after 14 years. However, naturally recruited native small trees and understory plants all declined in abundance over the course of the study. In contrast, nonnative, invasive species were highly successful at establishing at the site and currently dominate the understory. Outplanted native species (*Acacia koa*, *Dodonea viscosa*, and *Alyxia stellata*) had relatively high survival and significantly increased native species abundance and richness at the site. We conclude that despite high natural recruitment of a native overstory tree (*Acacia koa*), restoration management intervention enhanced the native component of post-fire vegetation. However, continued intervention will likely be required over the long-term to facilitate the recovery of vegetation to the pre-fire, native-dominant conditions. As high intensity disturbances increase across island ecosystems, understanding and monitoring the successional trajectory of both nonnative and native forest species can improve the efficiency of management response and allow managers to adapt to changes in conditions as well as prioritize actions across larger disturbance events.

1. Introduction

Despite our best efforts to integrate disturbance regimes into management planning, high intensity events like fires, windstorms, and floods often require direct intervention to mitigate their impacts on ecosystem function and diversity. Disturbance presents opportunities for ecological invasion (Norin et al., 1995; Hobbs and Huenneke, 1996; Jauni et al., 2015) and, in the absence of management, can lead to permanent shifts in ecosystem structure and composition (Buckley et al., 2007; Yelenik and D'Antonio, 2013). Management actions, on the other hand, can also have their own legacy effects on vegetation, which, in turn, can influence future patterns of disturbance (Wardell et al., 2003; Trauernicht et al., 2013). How best to intervene to maintain desired ecological conditions remains a critical question, not only in light of limited budgets locally, but also globally as disturbance regimes and species composition shift under our feet due to human activities

and climate change. Effectively adapting to these changes requires monitoring the ecological consequences of management response to disturbance events, especially over medium to long timeframes.

Ecological restoration is a key strategy to re-establish and improve ecosystem structure, diversity, and services, largely in response to human impacts (Jackson and Hobbs, 2009). Restoration has become especially critical for island ecosystems that are highly vulnerable to impacts from invasive species and novel disturbance regimes (Vitousek, 1988; D'Antonio and Vitousek, 1992; Reaser et al., 2007). In Hawai'i, for example, nonnative species account for nearly half of the islands' vascular plants, the vast majority of which have been introduced since European contact either unintentionally, or for use in the forestry, horticulture and ranching industries (Vitousek et al., 1996). Many of these plant species have naturalized and contributed to the reduction in extent and integrity of native ecosystems through interactions with land use change, nonnative ungulates, and disturbance (D'Antonio and

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Vitousek, 1992; Weller et al., 2011). In these circumstances, intensive, relatively small-scale restoration efforts are necessary to remove and limit the encroachment of nonnative biota simply to maintain the native ecosystem function and diversity. Restoration of island ecosystems is also a strategy to mitigate indirect effects of ecological degradation. On Guam, for example, the goal of many watershed restoration efforts is to reduce stress on nearshore coral reefs by limiting the expansion of and reclaiming ‘badlands’, or areas of heavy soil erosion attributable to vegetation loss from intentional burning, off-road activities, and storm events (Kottermair et al., 2011; Shelton and Richmond, 2016). As other factors, such as development and climate change, continue to exacerbate stresses on island ecosystems, natural resource managers face increasing pressure to prioritize restoration areas and demonstrate ecological outcomes and benefits of management actions (Friday et al., 2015; Wada et al., 2017).

Novel fire regimes driven by human-caused ignitions and exotic, fire-prone vegetation are a major factor contributing to the degradation of island ecosystems (Vitousek, 1988). The vegetation on oceanic islands, in particular, largely evolved under conditions of infrequent fires due to the relative infrequency of lightning strikes and volcanic events, the only natural sources of wildland fire ignition. Human arrival to oceanic islands increased the frequency of both intentional and accidental fires, as indicated by the contemporary use of fire and patterns of ignitions on islands globally (Perry and Enright, 2002; King, 2004; Trauernicht et al., 2015). The subsequent expansion of fire-adapted savanna vegetation at the expense of forest cover due to human-caused fire on islands has been documented in the archaeological record (Athens and Ward, 2004; Dickinson and Athens, 2007; Perry et al., 2012) and has been greatly exacerbated by the introduction of fire-adapted exotic grasses and shrubs after European contact (Vitousek et al., 1996). Fire disturbance in island ecosystems typically leads to a decline in native species diversity and a shift towards lower-statured, fire-prone vegetation often dominated by invasive, disturbance-adapted plants (Hughes et al., 1991; Bouchet et al., 1995; LaRosa et al., 2008; Garzon-Machado et al., 2012). This post-fire homogenization of vegetation appears to represent a stable state shift to savanna vegetation (Perry and Enright, 2002; D’Antonio et al., 2011; Yelenik and D’Antonio, 2013), the result of which is an increase in the probability of future fires and the modification of critical functions and services provided by native ecosystems (Wada et al., 2017). Despite our knowledge of the value of native ecosystems and their limited capacity to recover after fire on islands, very little research has been conducted to assess the effectiveness of post-fire rehabilitation efforts in these systems.

The ecological degradation caused by fire in native Hawaiian ecosystems is well documented (LaRosa et al., 2008). Despite the ability of some native plant species to recover after fire disturbance, the encroachment of nonnative weeds typically reduces native plant diversity and alters habitat structure as described above. Some of the best applied work on enhancing post-fire recovery in Hawai‘i is documented in a series of technical reports in Hawai‘i Volcanoes National Park (Loh et al., 2007, 2009; McDaniel et al., 2008). Loh et al. (2009) identified a suite of native species with the ability to recover after fire and used these species in a series of large-scale replanting efforts at three, low- to mid-elevation burn sites ranging from wet forest to seasonally dry, open woodlands. Native species were re-established at the sites through outplanting and direct seeding within plots forming a network of ‘nodes’ spaced evenly across relatively large burn areas (eg. 120–400 ha). Given the large size of these fires and the prohibitive cost of removing the nonnative grasses and ferns that carried the fires, the objective of park managers was to establish native species that had a high likelihood of recruiting and/or resprouting after future fires, thereby increasing the resilience of the native component of these landscapes. Resampling in these areas a decade later demonstrated successful establishment of native species (McDaniel et al., 2012); however, the true test will come in the advent of the next fire (R. Loh,

pers. comm.).

At other sites in Hawai‘i, the recovery of native forest cover is often the management goal, especially where fire has impacted high-value native habitat. Hawaiian forests face a variety of ecological conditions that limit the establishment and survival of native species more so than that of nonnative species, even in the absence of large-scale disturbance. Nonnative animals directly increase native plant mortality, ranging from the well-studied damage caused to adult plants and seedlings by feral ungulates (e.g., pigs, goats, and sheep; Spatz and Mueller-Dombois, 1973; Weller et al., 2011; Murphy et al., 2014) to herbivory by nonnative, terrestrial molluscs (Joe and Daehler, 2008; Shiels et al., 2014). Seed ecology research also demonstrates how the odds are stacked against native species establishment. Introduced rats promote dispersal of nonnative, small seeded species (Shiels, 2011), dramatically decrease germination in native, large-seeded species such as *Pritchardia* palms (Shiels and Drake, 2015), and have been implicated in the collapse of Hawaiian forests following Polynesian settlement (Athens, 2008). Research in montane mesic forests in Hawai‘i indicates both dispersal limitation as well as competition with introduced understory grasses deterred native plant regeneration (Denslow et al., 2006). In a Hawaiian dry forest, nonnative birds were the primary seed dispersal agent and native plants constituted < 8% of dispersed seeds (Chimera and Drake, 2010). Even in a wet Hawaiian forest where native species dominated the seed rain, nonnative species were more abundant in the soil and more likely to form persistent seed banks (Drake, 1998). The near absence of native species regeneration in nonnative-dominated forests, which comprise approximately 40% of forest cover in Hawai‘i (Gon et al., 2006), as well as in exotic tree plantations, provides further evidence of the competitive disadvantage of native plants (Mascaro et al., 2008; Ostertag et al., 2008).

Fire disturbance creates opportunities for the establishment of some native plants (e.g. *Acacia koa*; Scowcroft and Wood, 1976) but also a suite of exotic plants regarded by managers in Hawai‘i and elsewhere as ‘ecosystem modifiers’ (Crooks, 2002). These typically include introduced, fast-growing pioneer trees such as *Falcataria moluccana*, *Psidium cattleianum*, *Miconia calvescens*, and *Trema orientalis*, some fire-adapted trees like *Melaleuca quinquerivna*, understory shrubs such as *Rubus argutus* and *Clidemia hirta*, as well as various exotic grasses. Post-fire management in Hawaiian forests therefore requires targeted weed removal following the disturbance and, given all the factors described above, active outplanting to promote the regeneration of native species. However, the lack of information on post-fire environments in Hawai‘i regarding (i) the composition, timing, trajectory, and source of weed species establishment and (ii) the recruitment and survival of naturally regenerating vs. outplanted native species limits the efficiency and impact of these efforts. Understanding the successional patterns in Hawaiian forests after fire and the outcomes of active rehabilitation efforts can therefore help to prioritize post-fire planning for, and response to, future fires.

This study used data collected over 14 years from permanent plots established in a Hawaiian mesic forest after the 2003 Kumaipo Fire to examine the short-term dynamics of species succession and the longer-term outcomes of management intervention to promote the recovery of native forest cover. The fire was only four hectares, however, it occurred in an area of extremely high conservation value, providing habitat for more than 40 species of threatened and endangered plants and animals (Fig. 1). Aside from being one of Hawai‘i’s most biodiverse forest types, the lowland mesic forest where this fire occurred is currently restricted to only 1800 ha on O‘ahu, or 1.1% of island land area (Gon et al., 2006), and contains high numbers of single-island endemic species (Wagner et al., 1999). The Kumaipo Fire also occurred within weeks of the formation of a watershed management partnership of multiple agencies including the Hawai‘i Department of Land and Natural Resources Division of Forestry and Wildlife (DOFAW), the Honolulu Board of Water Supply (HBWS), the University of Hawai‘i (UH), and non-profit organizations including Ka‘ala Farm, Inc., Mohala I Ka

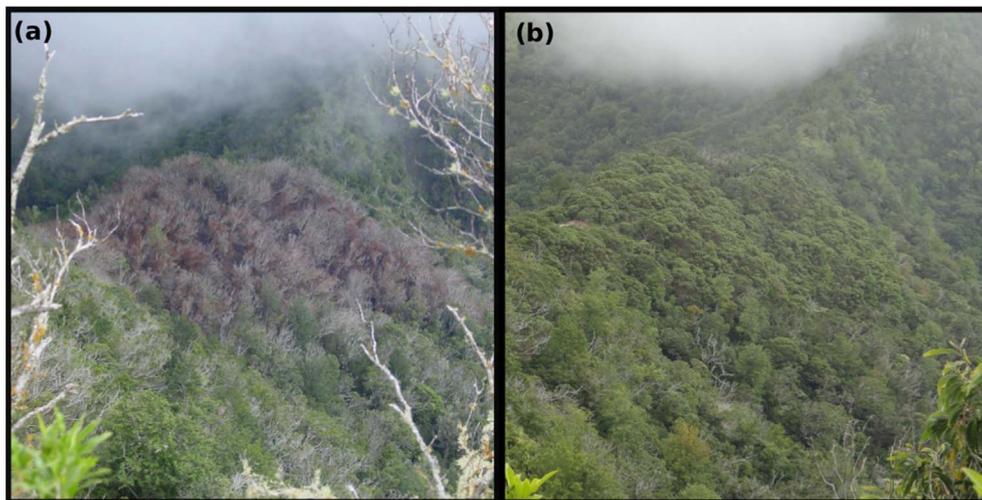


Fig. 1. View of Kumaipo Burn taken (a) immediately following the fire in 2003 (left) and (b) in 2015, illustrating *Acacia koa* canopy establishment.

Wai, and 'Ilio'ulaokalani Coalition. This partnership mustered resources for post-fire response including erosion control, multiple weed control trips, seed collection and outplanting, and the establishment of long-term monitoring plots. Despite the relatively small size of the fire, the monitoring plots provide a unique opportunity to assess the outcomes of intensive, site level management over the first two years post-fire.

By examining multiple attributes of post-fire vegetation over time, we sought to address the following questions: (1) How do patterns in the post-fire establishment and composition of native and nonnative plant species and communities vary over time relative to adjacent, unburned forest?; (2) What are the sources of native and nonnative components of post-fire regeneration?; and (3) To what degree does outplanting of native species enhance natural, native regeneration? By answering these questions, we hope to provide insight for managers responding to future fire incidents in native Hawaiian forests. Fire remains a key threat to these native plant communities and will likely worsen in the future for mesic native ecosystems under projected decreases in rainfall (Timm et al., 2015; Wada et al., 2017). Further, given that many of the nonnative species invading Hawaiian forests are broadly distributed, and considered major threats among island and continental ecosystems alike (e.g. *Clidemia hirta*, *Lantana camara*, *Psidium cattleianum*; (Vitousek, 1988; Lowe et al., 2000), understanding how these species respond to disturbance events will have relevance to forest management elsewhere.

2. Methods

2.1. Study site

The study site is in the Wai'anae mountain range on the island of O'ahu on Kumaipo ridge, a saddle between the Wai'anae Kai Forest Reserve (WKFR) and Makaha valley (Fig. 2). The site sits at 670 m elevation just below mount Ka'ala (21°26'N, 158°12'W) with a mean annual rainfall of c. 1800 mm. The forests of these two valleys represent some of the few remaining areas of native lowland, mesic forest on O'ahu. The fire started on September 8th, 2003 (likely from an unintended campfire), burned approximately 4 ha of native koa-ōhi'a (*Acacia koa*-*Metrosideros polymorpha*) forest, and was fully controlled October 2nd, 2003. Due to difficulty with access and limited resources for monitoring, the fire continued to burn slowly and consume much of the litter and duff at the site for weeks after initial attack. Fire severity for vegetation was high, with 100% mortality of standing vegetation. The burned forest provided critical habitat for at least 6 endangered species of plants, and overall the WKFR is home to 37 species of threatened and endangered plant species as well as at least one endangered snail (*Achatinella mustelina*) and one endangered native bird,

the O'ahu elepaio (*Chasiempis sandwichensis ibidis*; Vanderwerf et al., 2013).

2.2. Post-fire response (management history)

Staff from DOFAW, HBWS and UH assessed the burn site one week after the fire was controlled in October 2003. Erosion was the initial concern and DOFAW airlifted coconut coir and burlap/straw wattle erosion bars to the site in February 2004 and installed them with volunteer groups between March and June 2004. Over this same time period, UH researchers established vegetation monitoring plots (described below), while active weeding of invasive plants and seed collections of native species began for site rehabilitation. DOFAW and UH nurseries grew seedlings of three native species, *Acacia koa* (koa) a relatively fast growing canopy tree, *Dodonea viscosa* (a'ali'i) a shrub/midstory tree and *Alyxia stellata* (maile), a liana, in sufficient numbers for outplanting. Four volunteer work trips occurred between February and May 2005 to weed all plots (focusing on *Buddleja asiatica*) and plant all outplants (84 total) at the site, tagging each with a unique identification code. Seven additional multi-agency and volunteer work trips occurred between November 2007 and November 2008 and focused primarily on weed control. The weeding effort targeted known problem species (including *Buddleja asiatica*, *Rubus argutus*, *Clidemia hirta*, *Schinus terebinthifolius*, *Grevillea robusta*, *Psidium cattleianum*, *Melinis minutiflora*, and *Megathyrsus maximus*) across the entire area of the burn including all the monitoring plots. Several portions of the northern side of the burn area were not weeded due to very steep terrain.

2.3. Long-term monitoring plots

To monitor vegetation succession within the burn site, 56 2 × 2 m permanent plots were set up in 2004 at random points along the length of five randomly placed transects running 40–60 m, parallel to the site's slope. An additional 16, 2 × 2 m plots were established in the unburned forest at the same elevation, adjacent to the burn, for comparison. Half of the plots in the burn site were randomly selected to receive an 'outplanting' treatment consisting of planting one seedling each of *Acacia koa*, *Dodonea viscosa*, and *Alyxia stellata* within the plot boundary. In December 2004, all emergent seedlings were counted and identified to species, the basal diameter of any woody plant > 1 cm was measured, and percent understory cover (i.e., the cover of vegetation from the ground up to 1.5 m) was estimated at each plot within the burn site. To assess soil seed bank composition, a 5 cm soil corer was used to collect two soil samples at each permanent plot described above with an additional 17 paired samples in the forest (for a total of 112 burn site samples and 66 forest samples) in September 2004 and again

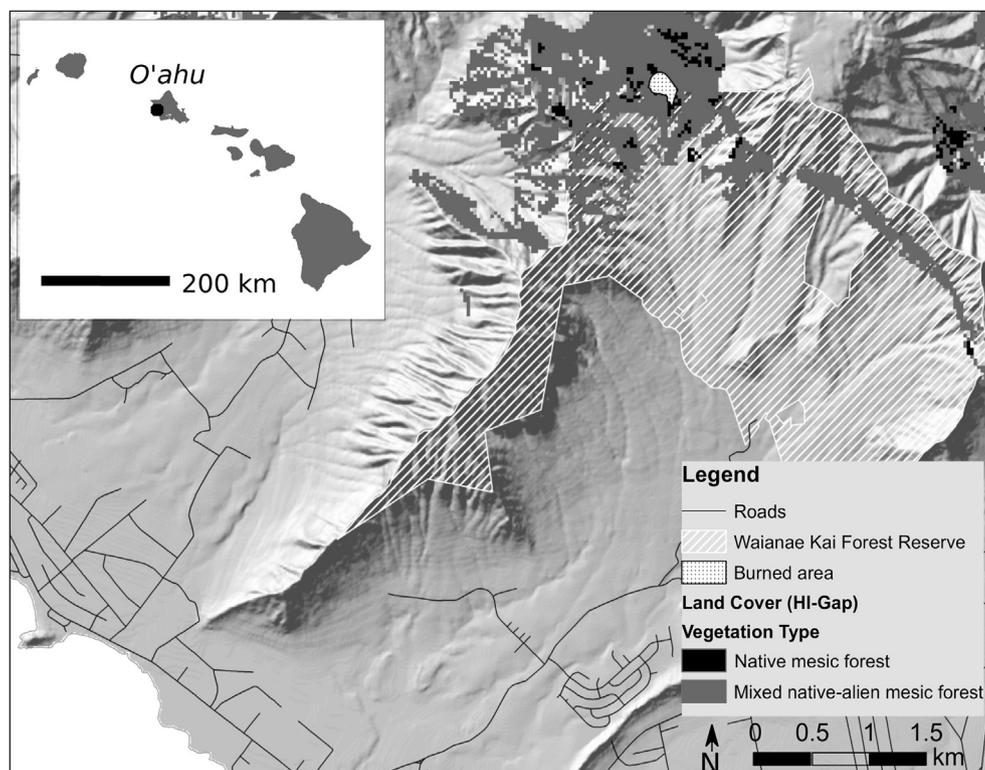


Fig. 2. Map of the Kumaipo Fire in the Waianae Kai Forest Reserve, illustrating the limited extent of native forest.

in February 2005. Soil samples were spread into trays in a greenhouse, watered regularly, and monitored weekly for 6 weeks and then monthly for 2 additional months over which time the number and species of all plant seedlings to emerge from each soil sample was recorded. The same data above (apart from soil samples) were collected from the burn site plots again in May 2005 after outplanting treatments were established. Vegetation data in the burn site was collected again in May 2006, and, in addition, the growth and survival of outplants was assessed. All plots in the burn site were surveyed again in March 2017, during which time all plant species were recorded within each plot, as was the percent cover of native and nonnative understory vegetation, the basal diameter of all woody plants > 1 cm, and outplant survival. In addition, canopy cover above each plot was measured using a spherical densiometer.

2.4. Analysis

To assess changes in plant species composition (within the burn site over time and between burn and forest sites), we examined the change in species frequency across plots. Given that weeding effort was applied over the entire surveyed area of the burn site, frequency data were pooled across both control and treated (outplanted) plots. The contribution of outplanted individuals to the frequency of *Acacia koa*, *Dodonea viscosa*, and *Alyxia stellata* was tracked and is explicitly outlined in the results. Nonmetric multidimensional scaling (NMDS) using a subset of plots ($N = 26$) for which species abundance data were available from each survey period, was also used to compare the shifts in community composition relative to unburned forest using the vegan package in R. We tested for the effects of outplanting treatment (outplanting versus control plots) on vegetation in our study plots 14 years post fire. Specifically we assessed the effects of outplanting on native species richness, total basal area, native canopy cover, and native understory cover using general linear mixed models (glmm), where transect was a random effect. For the latter three variables, we used outplanting treatment as a variance covariate (Zuur et al., 2009). Basal area values were log-transformed. To assess the effect of outplanting on

the probability of *Acacia koa* occurring in the plot, we used a glmm with a binomial error structure. All analyses were carried using the nlme and glmmADMB packages in R version 3.3.2.

3. Results

3.1. Plant community succession

The frequency of native species in the unburned forest plots illustrates the diversity of native species in the ecosystem impacted by the fire, but also a high frequency of nonnative species (i.e., *Clidemia hirta* and *Psidium cattleianum*; Fig. 3). During the first survey period in December 2004, within 14 months after the fire and prior to outplanting, 25 plant species had colonized the burn site, including 10 native and 15 nonnative species (See Table S1 in Supplemental Information). The most frequent native species across plots in the burn site included the overstory tree *Acacia koa*, the fern *Pteridium aquilinum* (Bracken fern or kilau), the vine *Canavalia galeata* ('awikiwiki), and seedlings and saplings of the small trees/shrubs *Pipturus albidus* (māmaki) and *Scaevola gaudichaudiana* (naupaka; Fig. 4a). The other native species included the ferns *Sphenomeris chinensis* (pala'ā) and *Doodia kunthiana* (pamoho), the vine *Cocculus orbiculatus* (huehue) and the sedges *Carex wahuensis* and *Gahnia beecheyi*. The most frequent nonnative species across plots in the burned area in 2004 were the shrubs *Buddleja asiatica*, *Rubus argutus*, *Phytolacca octandra*, and the tree *Psidium cattleianum* (strawberry guava), as well as short-lived, weedy Asteraceae species including *Crassocephalum crepidioides*, *Erigeron bonariensis*, and *Pluchea carolinensis* (Fig. 4b). Other notable invasive species included the canopy trees *Schinus terebinthifolia* (Christmas berry) and *Trema orientalis* (gunpowder tree), the shrub *Lantana camara*, and two nonnative grass species, *Megathyrsus maximus* (guinea grass) and *Melinis minutiflora* (molasses grass).

By the second survey in May 2005, *Acacia koa* was still the most frequent native species, occurring in 81% of plots, with 18% of those occurrences (8 plots) attributable to outplanted individuals. The native ferns *Microlepia strigosa* (palapalai), *Nephrolepis exaltata*, and *Christella*

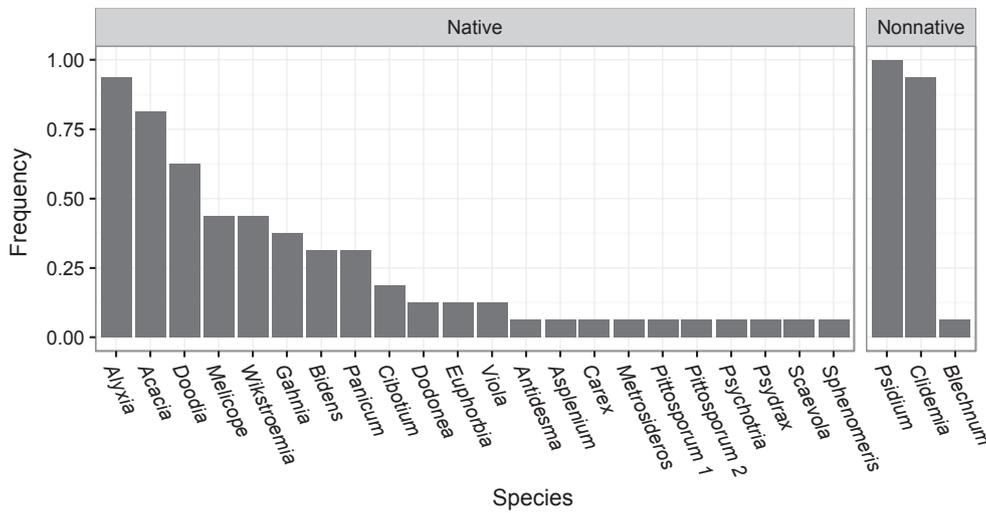


Fig. 3. The frequency of native and nonnative plant species surveyed the unburned forest plots adjacent to the fire.

sp., the endemic fern *Sadleria pallida* (‘ama‘u), and the native small shrub *Solanum americanum* (pōpoplo) were the only new native species to establish (Fig. 4a and Supplemental Material). In contrast, 12

additional nonnative species established, including the overstory tree *Grevillea robusta* (silk oak), the grass *Andropogon virginicus* (broom-sedge), and a suite of fern species including *Blechnum appendiculatum*,

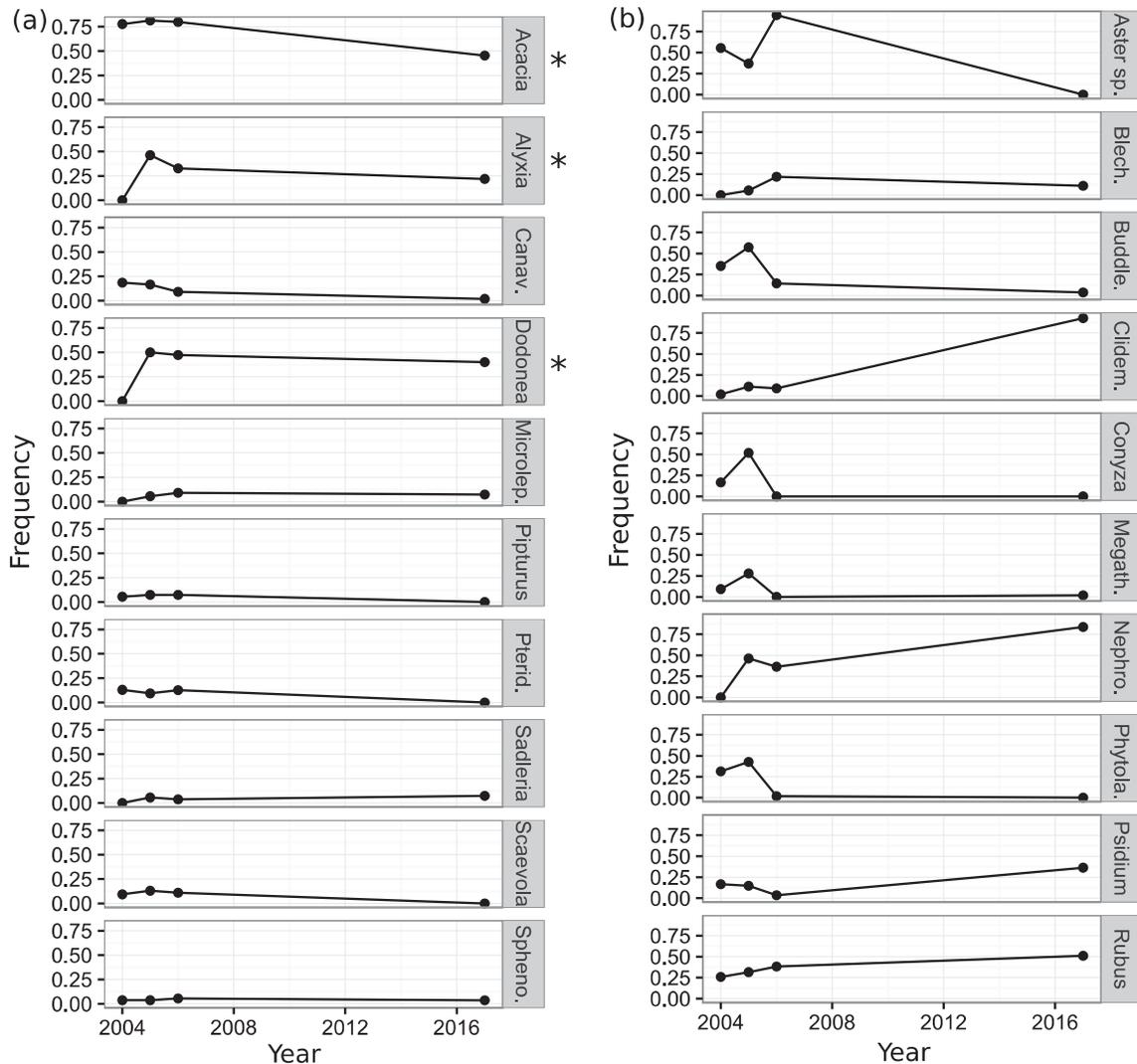


Fig. 4. Changes in frequency across burned plots of the 10 most frequent (a) native and (b) nonnative plants from 2004 to 2017. Asterisks (*) indicate species that were outplanted at the site in 2005. 100% of the plots that had *Alyxia* and *Dodonea* present had been outplanted with these species. For *Acacia*, this figure was 18%, 14% and 16% in 2005, 2006, and 2017 respectively.

Nephrolepis multiflora, *Adiantum* sp., *Pityrogramma* sp., and *Macrothelypteris torresiana*. By the May 2006 survey, no new native species had established and only three nonnative species were identified that had not been recorded in prior surveys. Weedy asters and *Acacia koa* were the most frequent species in 2006, with *Acacia koa* in 80% of the plots, of which 14% (6 plots) were attributable solely to outplanted trees. At the final survey in 2017, *Acacia koa* formed the dominant component of the canopy and mean canopy cover across the site was 73% ($\pm 25\%$ standard deviation). In 2017, *Acacia koa* frequency declined to 46%, of which 16% (4 plots) contained only outplanted individuals. In addition, there was little natural recruitment of *Alyxia stellata* and none of *Dodonea viscosa*, the two native species that were outplanted in addition to *Acacia koa*. In contrast, the dominance of nonnative, understory species *Clidemia hirta* and *Nephrolepis multiflora* greatly increased to 93% and 84%, respectively by the 2017 survey. In terms of site colonization, one fern-like native species, *Psilotum nudum* (moa), and three nonnative, overstory tree species, *Toona ciliata*, *Psidium guajava* (common guava), and *Melia azedarach* (Chinaberry) had also become established since the last survey.

The plant community showed distinctive shifts in composition over time as indicated by the nonmetric multi-dimensional scaling (NMDS) plots (Fig. 5). Relative to the adjacent, unburned forest, the plant community in the initial 2004 survey shifted substantially along the first NMDS axis, indicating nearly a complete compositional change in both the native and nonnative species present in the unburned forest. Compositional shifts from 2004 and 2005, and from 2005 to 2006, were also apparent in the NMDS analysis, reflecting further changes in composition as species colonized the site over time. The survey data for the burn site in 2004, 2005, and 2006 indicated far greater compositional overlap with each other than with the adjacent unburned forest. The plant community at the burn site in 2017 illustrated another clear

shift along the primary NMDS axis, however, it remained clearly distinguishable from the adjacent forest plant community 14 years after burning. Among plots in the burn site, those with and without outplanting were relatively indistinguishable in the NMDS from 2004 to 2006, but did show some compositional divergence by the 2017 survey (Fig. S2). However plots with and without outplanting did not overlap with forest plots, indicating different species composition at the final survey. Of the three native species shared between the burn site in 2017 and the unburned forest, *Acacia koa* (koa), *Dodonea viscosa* (a'ali'i), and *Alyxia stellata* (maile), the latter two were only present in the burn site due to restoration efforts.

3.2. Soil seed bank

Seedling emergence from the soil seed bank samples taken 11 months after the fire (September 2004) revealed seven nonnative and zero native species in the soil seed bank, all of which emerged from just 18 of the 56 plots (32.1%) sampled in the burn site (Fig. 6). The plant species recorded were the shrubs *Buddleja asiatica*, *Clidemia hirta*, and *Phytolacca octandra* and the weedy, herbaceous asters *Erigeron bonariensis*, *Emilia* sp., *Youngia japonica*, and *Crassocephalum crepidioides*. In contrast, soil samples taken from the burn site 16 months after the fire (February 2005) indicated viable seed banks in 54 of the 56 plots (99.6%; Fig. 6). The same plant species above (except *Y. japonica*) were present in addition to 1 native (*Solanum americanum*) and one non-native (*Rubus rosifolia*) shrub, 2 more weedy asters (*Sonchus oleraceus*, *Pluchea carolinensis*), and the small native tree *Pipturus albidus* (māmaki). *Buddleja asiatica* and *Clidemia hirta* were the most abundant species in the soil seed bank in both sampling periods. The frequency of germinating *Buddleja asiatica* seeds across plots increased from 19.6% to 96.4% between the first and second sampling period, whereas the frequency of *Clidemia hirta* increased from 17.9% to 28.6%. The only native species to emerge from the burn site soil samples, *Pipturus albidus* and *Solanum americanum*, were each only present in one plot.

The seed bank sampled from the adjacent forest showed a similar pattern, with an increase in the frequency of plots with viable seed bank increasing from 36.3% in 2004 to 91.0% in 2005 (Fig. 6a). Only three plant species emerged from forest soil samples taken in 2004: the native tree *Acacia koa* (present in five plots) and the nonnative shrubs *Buddleja asiatica* and *Clidemia hirta*. As in the burn site, *Buddleja* and *Clidemia* dominated the soil seed bank in terms of frequency across forest plots and increased, respectively, from 24.2% to 93.9% and 24.2% to 87.9% between the two sampling periods. In addition to these three species, the second sampling period detected five additional nonnative species (the tree *Trema orientalis*, the shrub *Rubus rosifolius*, and the weedy asters *Ageratum conyzoides*, *Pluchea carolinensis*, and *Erigeron bonariensis*) and two native small trees *Scaevola gaudichaudiana* and *Pipturus albidus*. *Pipturus* was the most frequent native species, occurring in the seed bank in 45.4% of forest plots.

3.3. Outplant survival and effects on plant community

After one year (2005–2006), outplant survival in the burn site was relatively high for *Dodonea viscosa* (80%) and *Alyxia stellata* (75%) and much lower for *Acacia koa* (40%; Fig. S1). Survival of the remaining outplants after the first year through 2017 remained high for *Dodonea viscosa* (79%) but declined for both *Alyxia stellata* (50%) and *Acacia koa* (30%; Fig. S1). Despite the low survival of outplanted *Acacia koa*, natural recruitment of *Acacia koa* seedlings was high at the site. We recorded 30 *Acacia koa* trees in the overstory (e.g. dbh > 15 cm) across our plots in 2017, including 9 in plots without outplanting and 21 in plots that were outplanted (Fig. S2). Given the relatively small size of our sample area (56 plots \times 4 m²), these numbers indicate high densities of koa trees at the site, even in the absence of outplanting (e.g. c. 900 and 400 individuals per ha with and without outplanting, respectively). Despite abundant natural recruitment, there were more *Acacia*

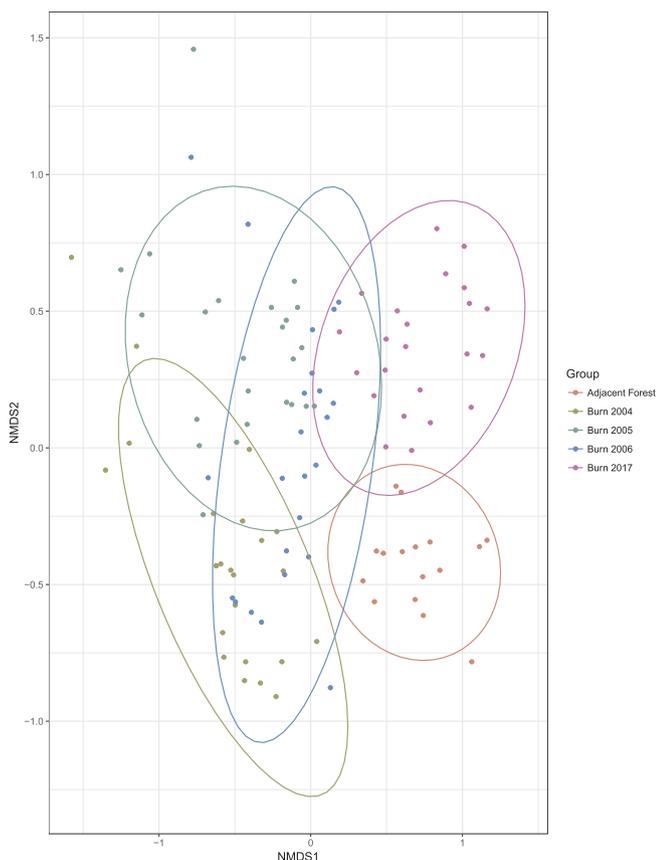


Fig. 5. Nonmetric multidimensional scaling (NMDS) of the plant community composition using a subset ($N = 26$) of burn plots measured over time compared to adjacent forest plots measured in 2005. Each point represents a plot; colors represent years surveyed.

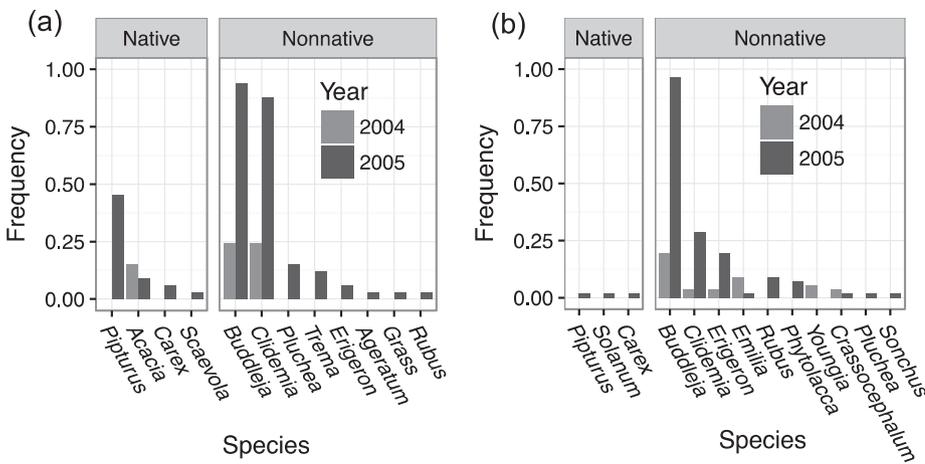


Fig. 6. Frequency of native and nonnative species in the (a) unburned forest and (b) burn site soil seed bank sampled 11 months (2004) and 16 months (2005) after the fire.

koa trees in plots that were outplanted than in the control plots (Fig. S2). In addition, there was a tendency for higher probability of naturally occurring *Acacia koa* in outplanted plots than in control plots ($\beta = 1.0$, $SE = 0.05$, $z = 1.88$, $p = .06$).

Plots with outplanting had significantly greater basal area of woody plants ($\beta = 5.39$, $SE = 1.12$, $t = 4.82$, $p < .001$), as well as a greater number of native species than control plots ($\beta = 1.27$, $SE = .23$, $t = 5.59$, $p < .001$; Fig. 7a). Total basal area across the burn site ($5.39 \text{ m}^2 \text{ ha}^{-1}$) was slightly less than the adjacent forest ($7.21 \text{ m}^2 \text{ ha}^{-1}$), however, the basal area of native species in the burn ($5.18 \text{ m}^2 \text{ ha}^{-1}$), was substantially greater than the adjacent forest

($1.66 \text{ m}^2 \text{ ha}^{-1}$). The native species *Acacia koa* and *Dodonea viscosa* (all outplanted) comprised 62% and 34%, respectively, of the total basal area in the burn site in 2017. By contrast in the forest, *Psidium cattleianum* comprised 77% of the basal area (with 99% of individuals < 10 cm dbh), and native basal area was more evenly distributed across eight woody species, including *Acacia koa*, *Metrosideros polymorpha*, *Antidesma platyphyllum*, and *Melicope oahuensis*. The dominance of *Acacia koa* in the burn site was not directly attributable to outplanting, as naturally regenerating koa was more abundant than outplanted koa in these plots (Fig. S2). In contrast, the increase in native species richness in outplanted vs. control plots was due to the addition of

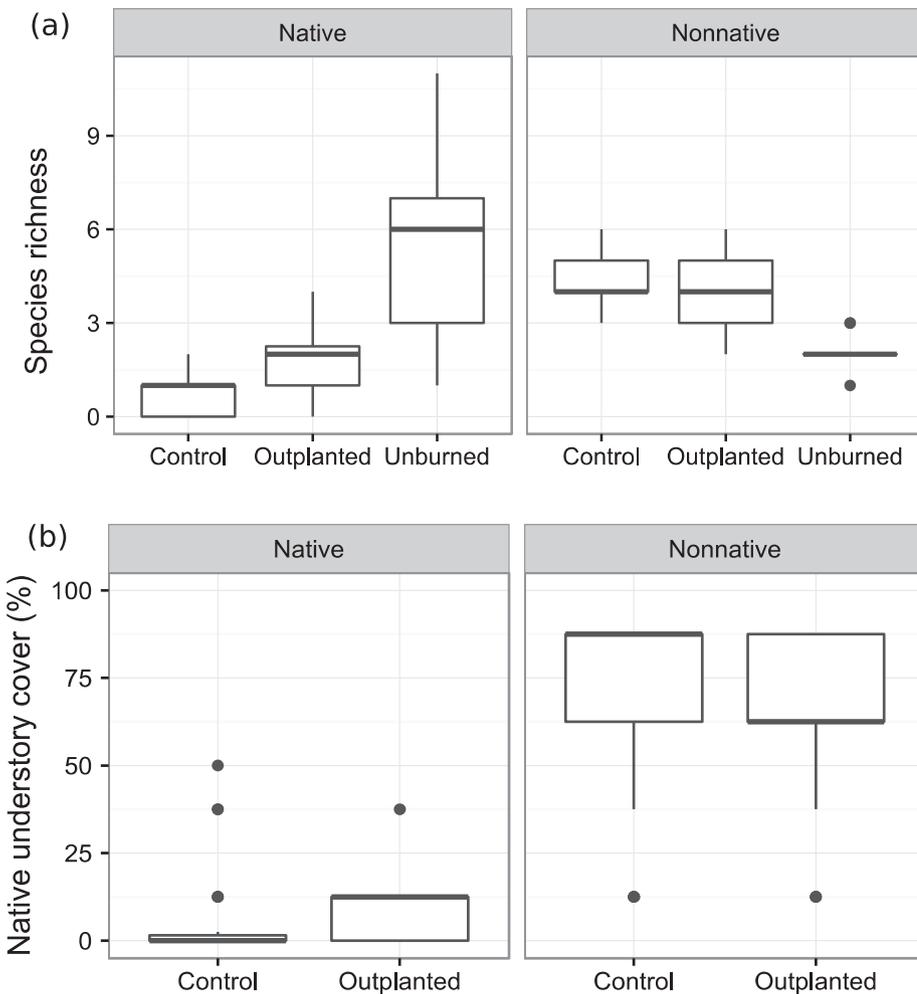


Fig. 7. Effect of outplanting on (a) species richness (relative to richness of the unburned forest) and (b) the percent native and nonnative understory cover.

Dodonaea viscosa and *Alyxia stellata*, for which no natural recruitment was initially observed for either species. However, seedlings of *Alyxia stellata* were found in the 2017 survey, indicating natural recruitment is occurring from the outplanted individuals. Nonnative plants dominated the understory cover in both outplanted and control plots (Fig. 7b), and there were no significant differences in native or non-native understory cover in outplanted versus control plots ($\beta = 1.46$, SE = 3.07, $t = 0.48$, $p = .63$ and $\beta = 0.96$, SE = 5.33, $t = 0.2$, $p = .86$ respectively). The most dominant nonnative understory plants in terms of frequency across plots were *Clidemia hirta* and *Nephrolepis multiflora* (Fig. 4b). *Acacia koa* and the other outplanted species (*Dodonaea viscosa* and *Alyxia stellata*) were the most frequent native species by far (Fig. 4a). And while other native understory plants occurred at low frequencies, all species apart from *Sadleria* sp. declined in frequency between 2006 and 2017, including the ferns *Sphenomeris chinensis* and *Microlepia strigosa*, the sedge *Carex wahuensis*, and the liana *Canavalia galatea* (Fig. 4a).

4. Discussion

The coupling of disturbance and species invasions is common across many ecosystems and, given the degree to which human activities alter both disturbance regimes and plant species composition, is a critical process to understand in the context of natural resource management and restoration (Vitousek, 1988; Hobbs and Huenneke, 1996). Further, the impacts of nonnative, invasive species are particularly acute in island ecosystems (Reaser et al., 2007). Hawai'i is no exception, and our study provides an opportunity to examine how different ecological responses of native and nonnative plants to disturbance contribute to patterns of forest regeneration and, importantly, where management intervention can be most effective in promoting native species recovery. The limited capacity of Hawaiian forests to recover from fire disturbance is due, in large part, to the rapid establishment of nonnative plants in post-fire conditions (Hughes et al., 1991; LaRosa et al., 2008; D'Antonio et al., 2011). Indeed, a suite of Hawaiian plants have the ability to establish after fire from resprouting and the soil seed bank (Loh et al., 2009). However, invasive species, many of which are highly adapted for disturbance, currently comprise nearly half of the vascular flora in Hawai'i and are widely naturalized within native-dominated ecosystems (Vitousek et al., 1996).

The forest plot data reported above provide a baseline of native species composition from which to assess the trajectory of plant succession in the burned area, but also indicate that, even in the absence of disturbance, forest composition is highly altered by nonnative, invasive species (Fig. 3). A variety of ecological processes from dispersal to herbivory currently promote the establishment of nonnative over native species in Hawai'i (Chimera and Drake, 2010; Murphy et al., 2014; Shiels and Drake, 2015). Controlling nonnative plant species consequently comprises a significant effort of forest management and restoration projects in Hawai'i (Friday et al., 2015). With increasing fire activity throughout the Hawaiian Islands over recent decades (Trauernicht et al., 2015), it is critical that watershed managers understand how and when the use of limited resources can enhance recovery of native ecosystems after fire disturbance. Our work provides a new perspective on the composition and timing of plant colonization following disturbance and clearly illustrates the pervasiveness of nonnative plants in the post-fire environment in Hawai'i. In addition, these results expand our knowledge of post-fire management outcomes in Hawaiian forests, which was previously limited to other native forest types, all in Hawai'i Volcanoes National Park (Loh et al., 2007; McDaniel et al., 2008; Ainsworth and Kauffman, 2009, 2013).

Although the present conditions at the Kumaipo burn site have been influenced by post-fire outplanting and weed control, the endemic overstory tree *Acacia koa* also established well without human assistance in nearly 80% of plots in the burn area within the first year of sampling (Fig. 4a). *Acacia koa* is a dominant or co-dominant canopy component (with *Metrosideros polymorpha*) across many forest types in

Hawai'i (Mueller-Dombois, 1987; Baker et al., 2009) and these results support other documented and anecdotal observations of the species' ability to rapidly establish after fire (Judd, 1935; Scowcroft and Wood, 1976). Such high levels of *Acacia koa* recruitment may also have depleted the soil seed bank, explaining the absence of the species in the burned area soil seed bank, which was first sampled 11 months after the fire, in contrast to presence of *Acacia koa* seeds in the adjacent forest soils (Fig. 6). Other native species also established naturally within the first year prior to outplanting efforts, notably the woody species *Scaevola gaudichaudiana* and *Pipturus albidus* as well as a suite of ferns. However, these species occurred in fewer than 20% of plots surveyed, and the frequency of nearly all native plant species declined over the study period, with several species, including *Scaevola*, *Pipturus*, and *Pteridium*, absent from the site by the final survey (Fig. 4a). These patterns can be attributed to the ecology of some species. For example, the successional pattern for *Acacia koa*, which declined to 40% frequency across burn area plots by 2017 is likely due to density dependent mortality or self-thinning as the post-fire cohort of saplings matured into canopy trees (Scowcroft and Wood, 1976; Skolmen and Fujii, 1980). Mean canopy cover in the burn site also increased to 73% by the final 2017 survey, which likely created unfavorable conditions for *Pipturus*, a native species requiring higher light levels (Pattison et al., 1998) and which was absent from any of the adjacent forest plots. However, declines in the other native species which are more shade tolerant than *Pipturus* and occur in the adjacent forest correlate with substantial increases in nonnative plant frequency across the site over time (Fig. 4).

While the frequency of nonnative species, especially understory species, generally increased over time, the successional dynamics of individual species were more complex. Several species were moderately frequent across plots during the first survey, dominated species frequencies during the second and third survey (i.e., 2–3 years after the fire), and then were completely or nearly absent by 2017 (Fig. 4b). As with *Pipturus*, these patterns can be attributed to species responses to increasing canopy closure at the site over time. For example, many of the short-lived, herbaceous asters such as *Erigeron bonariensis* and *Emilia* sp. are more frequent in open, disturbed habitats in Hawai'i (Norin et al., 1995). Similarly, the woody shrubs *Buddleja asiatica* and *Phytolacca octandra* occurred in 57% and 43% of plots, respectively, at their peak 2 years after the fire and were absent or nearly absent by the final survey (Fig. 4b). Both species are common invaders at disturbed sites in Hawai'i (Burton, 1980) and the decline of *Buddleja* over time has been documented and attributed to canopy closure in experimental work (Buck, 1982). *Megathyrsus maximus* (guinea grass), a highly shade intolerant, C4 grass, showed a similar peak and decline at the site (Fig. 4b). The decline in *Megathyrsus maximus*, a problematic grass in terms of fire risk, is at least partially attributable to weed control at the site. However, its persistence at the site without subsequent expansion may also be in response to canopy closure, which is particularly encouraging for the application of forest restoration for fuels reduction (e.g. Ellsworth et al., 2015).

The second successional pattern among nonnative plants was a change from low to high frequency across plots, again likely tied to differences in the ecology of invading species. The shrub *Clidemia hirta* and the fern *Nephrolepis multiflora*, which were absent or nearly absent at the first survey, currently dominate the understory at the site, occurring in 93% and 84% of the plots, respectively, and contributing to the extensive cover of nonnative species in the understory (Fig. 7b). *Clidemia*, native to Central America, is listed as a noxious weed in Hawai'i (Smith, 1992) and is widespread in Hawaiian forests due to release from the herbivores and pathogens of its native range (DeWalt et al., 2004). Other work has linked *Clidemia* establishment to disturbances such as fire, citing similar time frames (e.g. several years) over which the species will eventually dominate vegetative cover at a site (Wester and Wood, 1977). Similarly, *Nephrolepis multiflora* occurs at high densities after fire and other disturbances in wet forests in Hawai'i

(Follett et al., 2003; McDaniel et al., 2008). In Hawai'i Volcanoes National Park, the frequency of *Nephrolepis* was 60–80% within burned plots, 2–4 times greater than in adjacent unburned areas (McDaniel et al., 2008). The two most abundant nonnative species after *Clidemia* and *Nephrolepis* were the tree *Psidium cattleianum* (strawberry guava) and the shrub *Rubus argutus* (blackberry). These species were explicitly targeted by later weed control efforts (e.g. 5–6 years after the fire), which suggests they would have become more abundant in the absence of post-fire management.

The NMDS plots effectively illustrated how these successional patterns resulted in distinct shifts in plant community composition over time (Fig. 5). Despite the ability of *Acacia koa* to establish a native overstory, the post-fire forest is clearly different from the adjacent, unburned forest (Fig. 5), even for burn site plots with outplanting (Fig. S2). A 14-year-old secondary forest would be expected to be compositionally distinct from old growth forest in most regions of the world. However, successional dynamics in native Hawaiian forests differ from continental tropical forests, due primarily to relatively low plant species diversity. For instance, *Metrosideros polymorpha* is a pioneer tree in both dry and wet forests over long time-scales (i.e., millennial scale lava flow chronosequences) as well as the dominant tree in most late successional Hawaiian rain forests (Mueller-Dombois, 1987; Stemmermann and Ihle, 1993). *Acacia koa* is a common successional species after disturbance and can dominate canopy composition, especially in mesic and/or seasonally dry forest types; however, older *Acacia koa* forests typically consist of mixed species canopies (Baker et al., 2009). After restoration and establishment of an even-aged *Acacia koa* stand at Keauhou on Hawai'i Island (with similar rainfall but at higher elevation than the Kumaipo burn site), stem densities of *Acacia koa* showed similar patterns of decline over time, but were greater after 14–17 years (1500 trees/ha; Baker et al., 2009) than at our study site. By 23 years after restoration, native trees other than koa comprised 14% of the basal area at Keauhou, likely having been recruited from adjacent, native-dominated forest (Scowcroft et al., 2008).

Although *Acacia koa* stand development at the Kumaipo burn site is consistent with similarly aged stands at other sites (Grace, 1995; Pearson and Vitousek, 2001; Constantinides, 2004), the understory composition is almost completely dominated by nonnative understory plants (Fig. 7b). The high frequency *Clidemia hirta* and *Nephrolepis multiflora* have likely contributed to the observed decline and limited establishment of native understory species, as discussed above. Perhaps more importantly, however, all of the canopy tree seedlings and saplings other than *Acacia koa* identified in burned plots were nonnative species, providing insight into the potential trajectory of the plant community. The suite of canopy tree species recruiting within the burn included *Grevillea robusta* (silk oak), *Psidium cattleianum* (strawberry guava), *Schinus terebinthifolia* (Christmas berry), *Trema orientalis* (gunpowder tree), *Toona ciliata*, and *Melia azedarach* (chinaberry), all recognized as successful invaders of Hawaiian ecosystems and targeted by weed management efforts. Given the diversification of canopy composition in older *Acacia koa* stands elsewhere (Scowcroft et al., 2008; Baker et al., 2009), patterns of tree recruitment at the burn site suggest it is unlikely that the composition of the burn site will return to that of the adjacent, native forest without future management intervention. In other words, our data indicate that as *Acacia koa* recruitment declines with canopy closure (Baker et al., 2009), nonnative trees are more likely than native trees to establish and co-dominate the future canopy along with *Acacia koa*; however, confirming this trend will require future monitoring.

The successional pathways among both native and nonnative plants illustrated by our results provide key information to prioritize management efforts. For instance, reactive, post-fire control of early colonizing weeds such as *Buddleja asiatica* that declined over the long-term may be an unnecessary use of resources. Instead it may be more efficient to monitor the initial influx of plants and target those species that establish 2–3 years after burning and which are more likely to persist at

the site, such as *Clidemia hirta*, *Nephrolepis multiflora*, and *Rubus argutus*. This time scale would also likely suit the targeting of nonnative canopy trees, such as *Psidium cattleianum* and the other tree species mentioned above, by allowing time for seedlings and saplings to be detected and controlled. Again, monitoring is key, as there are nonnative, fire-adapted tree species in Hawai'i such as *Melaleuca quinquenervia* (paperbark) in which rapid and widespread seedling establishment has been observed immediately following fire (C. Trauernicht, pers. obs.) and may therefore require quick management response. At the Kumaipo site and other burned areas of native forest, rapid post-fire recruitment of *Acacia koa* provides a foundation for forest restoration efforts, but evidence from other sites indicates that a pure *Acacia koa* canopy is unlikely to persist over the long-term (Baker et al., 2009). Therefore intermittently monitoring the establishment of both native and nonnative woody species can allow site managers to anticipate, at least to some degree, how forest composition is likely to change over longer time scales. As outlined above, for example, the Kumaipo site shows very low potential for the natural establishment of a diverse suite of native canopy or subcanopy trees after a fire. Enhancing the native component of post-fire forests in this context specifically, would then entail active outplanting to increase native species richness.

Outplanting is far more resource intensive and costly than weed management as part of forest restoration strategies in Hawai'i (Wada et al., 2017). It is therefore necessary to carefully consider the ecological benefits of outplanting the three native species (*Acacia koa*, *Dodonea viscosa*, and *Alyxia stellata*) at the Kumaipo site, especially in light of the abundant *Acacia koa* recruitment prior to any management intervention. First, the survival of outplanted *Acacia koa* was much lower (12% over 14 years) than that of *Dodonea viscosa* (64%) and *Alyxia stellata* (37.5%; Fig. 5). The relatively low survival (40%) for *Acacia koa* especially during the first year may be due to density dependent mortality due to high natural recruitment of conspecifics. Although supplemental water was initially used, there were also several weeks of drought in the months immediately following the outplanting that may have also affected survival (US Drought Monitor data). Low survival of *Acacia koa* outplants over the longer term mirrors the self-thinning patterns observed across naturally regenerating *Acacia koa* at the burn site and in even-aged stands elsewhere (e.g. Skolmen and Fujii, 1980). One interesting outcome, however, was the greater counts of naturally regenerating *Acacia koa* individuals in outplanted plots compared to control plots (Fig. S1). This may be due to the fact that the roots of outplanted *Acacia koa* were inoculated with nitrogen-fixing bacteria in the greenhouse, which may have conferred an advantage to *Acacia koa* regenerating from seed within treated plots. Alternatively, there may be some nurse plant effect of the outplanting treatment, which consisted of planting the three species together. Unfortunately, our study cannot directly point to the mechanism underlying this pattern. Second, in addition to increasing plot basal area, outplanting *Dodonea viscosa* and *Alyxia stellata* along with *Acacia koa* significantly increased native species richness at the site (Fig. 7a). This is an important management outcome given the limited and declining abundance of naturally regenerating native species. Recruitment of *Alyxia stellata* was also observed within outplanted plots in the 2017 survey. Whereas outplanting seems to have enhanced *Acacia koa* regeneration, natural recruitment may have been adequate for a native canopy to establish at the site. However, our data clearly show that the native plant component at the site would be less diverse and far less abundant at present without the addition of *Dodonea viscosa* and *Alyxia stellata* through outplanting (Figs. 4a and 7a).

Our results illustrate the ways in which restoration efforts at the Kumaipo burn site enhance native forest recovery following fire. *Acacia koa* is a common component in many native Hawaiian forest types and clearly confers some resilience to fire disturbance. Our results, however, also highlight the importance of framing this resilience in an appropriate temporal context and how and when management can increase this resilience. As stated above, *Acacia koa*'s ability to establish a

native canopy over the short to medium term provides a foundation for native forest recovery following fire. But longer term patterns of *Acacia koa* stand composition will be influenced by recruitment of other species. In this respect, although *Acacia koa* persists as a dominant component of old growth mesic forests in Hawai'i, its ecology in relation to disturbance is very similar to early successional, light-demanding species in other tropical forests. So-called 'pioneer' species in genera such as *Trema*, *Macaranga*, *Heliocarpus*, and *Cecropia* commonly establish in recently disturbed areas of other tropical forests but, unlike *Acacia koa*, do not typically persist as a component of old-growth forest canopies (e.g., Denslow, 1980; Goodale et al., 2012). Many tropical pioneer species, including *Trema orientalis*, *Heliocarpus popayensis*, and *Cecropia obtusifolia* are introduced and invasive in Hawai'i. In the case of Hawaiian mesic forests, our results indicate that fire disturbance provides an opportunity both for *Acacia koa* as well as a mix of nonnative, invasive plants to establish. Thus despite the relatively rapid development of an *Acacia koa* canopy (i.e., in 14 years), continued recruitment of invasive canopy trees species suggests that plant composition at the burn site will continue to diverge from adjacent, native-dominated forest. Post-fire management efforts within the first several years of disturbance enhanced species diversity and apparently facilitated *Acacia koa* establishment. The long-term survival of *Dodonea viscosa* and *Alyxia stellata* plants also increases the potential for the regeneration of these species *in situ*, as they failed to colonize the site from the surrounding forest.

Native canopy development and outplant survival at the Kumaipo burn site is encouraging. However, it is clear from our results that continued, active restoration (e.g., weeding, outplanting) is required initially to effectively achieve native forest recovery over the long term. Over 14 years of post-fire stand development, native understory species have declined at the site due, at least in part, to the dominance of the understory by the invasive, noxious shrub *Clidemia hirta* and the non-native fern *Nephrolepis multiflora* (Figs. 4b and 7b). In the case of *Nephrolepis multiflora*, which is known to carry high intensity fires in Hawaiian forests (Ainsworth and Kauffman, 2009) the site may currently be at a greater risk of burning in terms of fuel composition. Whereas weed control alone may increase the likelihood of native plant establishment, the lack of native tree dispersal and recruitment at the site indicates that outplanting will be required to maintain a native-dominated canopy as *Acacia koa* declines over the long-term (Baker et al., 2009).

5. Conclusion

Post-fire restoration is often framed as a short-term management response to limit invasive species establishment and promote the recovery of native ecosystems. Our research, however, demonstrates the importance of anticipating and monitoring the effects of fire and subsequent management actions on longer time scales. Restoring ecological structure and composition is an effective, long-term strategy to reduce flammability and fire risk in many continental ecosystems, and shows great promise for reducing the vulnerability of native ecosystems on islands to fire as well. For instance, the work in Hawaii Volcanoes National Park described above restored native plant communities with species adapted to fire disturbance to increase resilience to future fires (Loh et al., 2009; McDaniel et al., 2012). Elsewhere in Hawaii, researchers have demonstrated the ability of restoration to disrupt non-native, grassy fuels and reduce fire risk at both the site and landscape scales (Ellsworth et al., 2015; Wada et al., 2017). Similarly, researchers are exploring methods to enhance rates of forest establishment in savannas on Palau to limit the extent of fire-prone vegetation (Dendy et al., 2015). On Guam, community-based watershed restoration is a tool to reduce the indirect effects of fire-related erosion impacts on nearshore reefs (Shelton and Richmond, 2016). Each of these studies has applications for mitigating fire risk, but managers face significant challenges in terms of scaling up restoration outcomes.

The Kumaipo fire provides a case study of how intensive restoration can be just at the stand scale. Yet our results provide insight about how restoration actions in response to fire can be prioritized in space and time. For instance, weed control is an appropriate strategy during the initial stages of post-fire recovery in Hawai'i; however, these efforts should target longer-lived species and integrate monitoring so that management can identify and adapt to changes in weed composition over time. Our results also indicate that outplanting can effectively improve the native component of post-fire vegetation (Fig. 7a). Although abundant *Acacia koa* establishment after fire may provide managers with a head start on forest recovery, they must consider stand development over longer time scales and anticipate proactive outplanting, especially if other native canopy and/or subcanopy species are not regenerating at the site. For island and continental ecosystems where the combination of altered disturbance regimes and weed incursion modify or disrupt forest regeneration (e.g., Crooks, 2002; Reaser et al., 2007; Perry et al., 2012; Yelenik and D'Antonio, 2013), understanding the successional ecology of both native and nonnative, invasive species is critical to developing efficient and effective management responses. Continual monitoring at disturbed sites is also key for decision making, both to track shifts in species composition as well as for prioritizing actions over larger scale fires. When managers must contend with fires that burn dozens or hundreds of hectares, knowledge of the ecology and dynamics of these plant species and communities can help identify problematic areas, prioritize short- and long-term objectives, and maximize the efficiency of efforts to enhance native forest recovery.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.01.005>.

References

- Ainsworth, A., Kauffman, J.B., 2009. Response of native Hawaiian woody species to lava-ignited wildfires in tropical forests and shrublands. *Plant Ecol.* 201, 197–209.
- Ainsworth, A., Kauffman, J., 2013. Effects of repeated fires on native plant community development at Hawaii Volcanoes National Park. *Int. J. Wildland Fire* 22, 1044–1054.
- Athens, J.S., 2008. *Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest. *Biol. Invasions* 11, 1489–1501.
- Athens, J., Ward, J., 2004. Holocene vegetation, savanna origins and human settlement of Guam. *Rec. Austr. Mus. Suppl.* 29, 15–30.
- Baker, P.J., Scowcroft, P.G., Ewel, J.J., 2009. *Koa (Acacia koa) ecology and silviculture*. General Technical Report – Pacific Southwest Research Station, USDA Forest Service, 129 pp. 129.
- Bouchet, P., Jaffré, T., Veillon, J.-M., 1995. Plant extinction in New Caledonia: protection of sclerophyll forests urgently needed. *Biodivers. Conserv.* 4, 415–428.
- Buck, M.G., 1982. Hawaiian Treefern Harvesting Affects Forest Regeneration and Plant Succession. USFS Research Note PSW-355.
- Buckley, Y.M., Bolker, B.M., Rees, M., 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecol. Lett.* 10, 809–817.
- Burton, P., 1980. Plant invasion into an "ohi'a"-treefern rain forest following experimental canopy opening. In: Smith, C.W. (Ed.), Third Conference in Natural Sciences. Cooperative Park Studies Unit. Department of Botany, University of Hawaii, Honolulu, pp. 21–39.
- Chimera, C., Drake, D., 2010. Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. *Biotropica*.

- Constantinides, M., 2004. Growth Dynamics of 16 Tree Species on 42 Long-Term Growth Plots in Hawaii. Report for Hawaii Department of Land and Natural Resources Division of Forestry and Wildlife, Honolulu.
- Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97, 153–166.
- D'Antonio, C.M., Hughes, R.F., Tunison, J.T., 2011. Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands. *Ecol. Appl.* 21, 1617–1628.
- D'Antonio, C., Vitousek, P., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87.
- Dendy, J., Cordell, S., Giardina, C.P., Hwang, B., Polloi, E., Rengulbai, K., 2015. The role of remnant forest patches for habitat restoration in degraded areas of Palau. *Restor. Ecol.* 23, 872–881.
- Denslow, J.S., 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12, 47–55.
- Denslow, J.S., Uowolo, A.L., Hughes, R.F., 2006. Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia* 148, 118–128.
- DeWalt, S.J., Denslow, J.S., Ickes, K., 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85, 471–483.
- Dickinson, W.R., Athens, J.S., 2007. Holocene Paleoshoreline and Paleoenvironmental history of Palau: implications for human settlement. *J. Island Coast. Archaeol.* 2, 175–196.
- Drake, D.R., 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *J. Veg. Sci.* 9, 103–112.
- Ellsworth, L.M., Litton, C.M., Leary, J.J.K., 2015. Restoration impacts on fuels and fire potential in a dryland tropical ecosystem dominated by the invasive grass *Megathyrsus maximus*. *Restor. Ecol.* 23, 955–963.
- Follett, P.a., Anderson-Wong, P., Johnson, M.T., Jones, V.P., 2003. Revegetation in dead *Dicranopteris* (Gleicheniaceae) fern patches associated with Hawaiian rain forests. *Pac. Sci.* 57, 347–357.
- Friday, J.B., Cordell, S., Giardina, C.P., Inman-Narahari, F., Koch, N., Leary, J.J.K., Litton, C.M., Trauernicht, C., 2015. Future directions for forest restoration in Hawai'i. *New For.* 46, 733–746.
- Garzon-Machado, V., del Arco Aguilar, M.J., Gonzolez, F.V., Perez-de-Paz, P.L., 2012. Fire as a threatening factor for endemic plants of the Canary Islands. *Biodivers. Conserv.* 21, 2621–2632.
- Gon, S., Allison, A., Cannarella, R., Jacobi, J., Kaneshiro, K., Kido, M., Lane-Kamahele, M., Miller, S., 2006. The Hawaii Gap Analysis Project Final Report. Honolulu.
- Goodale, U.M., Ashton, M.S., Berlyn, G.P., Gregoire, T.G., Singhakumara, B.M.P., Tennakoon, K.U., 2012. Disturbance and tropical pioneer species: patterns of association across life history stages. *For. Ecol. Manage.* 277, 54–66.
- Grace, K.T., 1995. Analysis and Prediction of Growth, Grazing Impacts, and Economic Production of *Acacia Koa*. University of Michigan PhD Thesis.
- Hobbs, R.J., Huenneke, L.F., 1996. Disturbance, diversity, and invasions: implications for conservation. *Ecosystem Management: Selected Readings*.
- Hughes, F., Vitousek, P., Tunison, T., 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology* 72, 743–747.
- Jackson, S.T., Hobbs, R.J., 2009. Ecological restoration in the light of ecological history. *Science* 325, 567–569.
- Jauni, M., Gripenberg, S., Ramula, S., 2015. Non-native plant species benefit from disturbance: a meta-analysis. *Oikos* 124, 122–129.
- Joe, S.M., Daehler, C.C., 2008. Invasive slugs as under-appreciated obstacles to rare plant restoration: evidence from the Hawaiian Islands. *Biol. Invasions* 10, 245–255.
- Judd, C.S., 1935. *Koa* reproduction after fire. *J. For.* 33, 176.
- King, T., 2004. Fire on the Land: Livelihoods and Sustainability in Navosa, Fiji. Massey University, Palmerston North, New Zealand.
- Kottermair, M., Golabi, M.H., Khosrowpanah, S., Wen, Y., 2011. Spatio-Temporal Dynamics of Badlands in Southern Guam: A Case Study of Selected Sites. Water and Environmental Research Institute of the Western Pacific, University of Guam.
- LaRosa, A., Tunison, J., Ainsworth, A., Kauffman, J., Hughes, R., 2008. Fire and non-native invasive plants in the Hawaiian Islands bioregion. In: Zouhar, K., Smith, J., Sutherland, S., Brooks, M. (Eds.), *Wildland Fire in Ecosystems: Fire and Nonnative Invasive Plants*. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-42, pp. 225–241.
- Loh, R., Ainsworth, A., Tunison, T., D'Antonio, C., 2009. Testing Native Species Response to Fire – A First Step towards Building Fire Resilient Plant Communities at Hawaii Volcanoes National Park. Honolulu, HI.
- Loh, R., McDaniel, S., Schultz, M., Ainsworth, A., Benitez, D., Palumbo, D., Smith, K., Tunison, T., Vaidya, M., 2007. Rehabilitation of Seasonally Dry "ōhi'a Woodlands and Mesic Koa Forest Following the Broomsedge Fire, Hawaii Volcanoes National Park. Technical Report N. 147. Honolulu.
- Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the world's worst invasive alien species. A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12.
- Mascaro, J., Becklund, K.K., Hughes, R.F., Schnitzer, S.A., 2008. Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i. *For. Ecol. Manage.* 256, 593–606.
- McDaniel, S., Loh, R., Dale, S., Smith, K., Vaidya, M., 2008. Rehabilitation of "ōhi'a-Swordfern (*Metrosideros Polymorpha-Nephrolepis Multiflora*) Woodlands Following the Kupukupu Fire. Hawaii Volcanoes National Park, Honolulu.
- McDaniel, S., Loh, R., Wasser, M., 2012. Building resilient native Hawaiian ecosystems in a novel fire regime. *RxEffects* 4–12.
- Mueller-Dombois, D., 1987. Forest dynamics in Hawaii. *Trends Ecol. Evol.* 2, 216–220.
- Murphy, M., Inman-Narahari, F., Ostertag, R., Litton, C.M., 2014. Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. *Biol. Invasions* 16, 63–71.
- Norin, T., Danchi, K., Kitayama, K., Mueller-Dombois, D., 1995. Biological invasion on an oceanic island mountain: do alien plant species have wider ecological ranges than native species? *J. Veg. Sci.* 6, 667–674.
- Ostertag, R., Giardina, C.P., Cordell, S., 2008. Understorey colonization of eucalyptus plantations in Hawaii in relation to light and nutrient levels. *Restor. Ecol.* 16, 475–485.
- Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117, 449–459.
- Pearson, S.L., Vitousek, P.M., 2001. Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. *Ecol. Appl.* 11, 1381–1394.
- Perry, G.L.W., Enright, N.J., 2002. Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial "state-and-transition" model. *J. Biogeogr.* 29, 1143–1158.
- Perry, G.L.W., Wilmshurst, J.M., McGlone, M.S., McWethy, D.B., Whitlock, C., 2012. Explaining fire-driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. *Glob. Change Biol.* 18, 1609–1621.
- Reaser, J.K., Meyerson, L.A., Cronk, Q., De Poorter, M., Eldredge, L.G., Green, E., Kairo, M., Latasi, P., Mack, R.N., Mauremootoo, J., O'Dowd, D., Orapa, W., Sastroutomo, S., Saunders, A., Shine, C., Thrairsson, S., Vaiutu, L., 2007. Ecological and socio-economic impacts of invasive alien species in island ecosystems. *Environ. Conserv.* 34, 98–111.
- Scowcroft, P.G., Haraguchi, J.E., Fujii, D.M., 2008. Understorey structure in a 23-year-old *Acacia koa* forest and 2-year growth responses to silvicultural treatments. *For. Ecol. Manage.* 255, 1604–1617.
- Scowcroft, P.G., Wood, H.B., 1976. Reproduction of *Acacia koa* after Fire. *Pac. Sci.* 30, 177–186.
- Shelton, A.J., Richmond, R.H., 2016. Watershed restoration as a tool for improving coral reef resilience against climate change and other human impacts. *Estuar. Coast. Shelf Sci.* 183, 430–437.
- Shiels, A.B., 2011. Frugivory by introduced black rats (*Rattus rattus*) promotes dispersal of invasive plant seeds. *Biol. Invasions* 13, 781–792.
- Shiels, A.B., Drake, D.R., 2015. Barriers to seed and seedling survival of once-common Hawaiian palms: the role of invasive rats and ungulates. *AoB Plants* 7.
- Shiels, A.B., Ennis, M.K., Shiels, L., 2014. Trait-based plant mortality and preference for native versus non-native seedlings by invasive slug and snail herbivores in Hawaii. *Biol. Invasions* 16, 1929–1940.
- Skolmen, R.G., Fujii, D.M., 1980. Growth and development of a pure stand of *koa* (*Acacia koa*) at Keauhou-Kilauea. In: Smith, C. (Ed.), *Proceedings, Third Conference in Natural Sciences. Cooperative National Park Resources Study Unit, University of Hawaii, Honolulu*, pp. 301–310.
- Smith, C., 1992. Distribution, status, phenology, rate of spread, and management of *Clidemia* in Hawaii. In: Stone, C., Tunison, J., Smith, C. (Eds.), *Alien Plant Invasions in Native Ecosystems of Hawaii: Management and Research*. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, pp. 241–253.
- Spatz, G., Mueller-Dombois, D., 1973. The influence of feral goats on *koa* tree reproduction in Hawaii Volcanoes National Park. *Ecology* 54, 870–876.
- Stemmermann, L., Ihle, T., 1993. Replacement of *Metrosideros polymorpha*, Ohia, in Hawaiian dry forest succession. *Biotropica* 25, 36–45.
- Timm, O., Giambelluca, T.W., Diaz, H.F., 2015. Statistical downscaling of rainfall changes in Hawai'i based on the CMIP5 global model projections. *J. Geophys. Res.: Atmos.* 120, 92–112.
- Trauernicht, C., Murphy, B.P., Tangalin, N., Bowman, D.M.J.S., 2013. Cultural legacies, fire ecology, and environmental change in the Stone Country of Arnhem Land and Kakadu National Park, Australia. *Ecol. Evol.* 3, 286–297.
- Trauernicht, C., Pickett, E., Giardina, C., Litton, C., Cordell, S., Beavers, A., 2015. The contemporary scale and context of wildfire in Hawaii. *Pac. Sci.* 69, 427–444.
- Vanderwerf, E.A., Lohr, M.T., Titmus, A.J., Taylor, P.E., Burt, M.D., 2013. Current distribution and abundance of the O'ahu 'Elepaio (*Chasiempis ibidis*). *Wilson J. Ornithol.* 125, 600–608.
- Vitousek, P., 1988. Diversity and biological invasions of oceanic islands. *Biodiversity* 20, 181–189.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R., 1996. Biological Invasions as global environmental change. *Am. Sci.* 84, 468–478.
- Wada, C.A., Bremer, L.L., Burnett, K., Trauernicht, C., Giambelluca, T., Mandle, L., Parsons, E., Weil, C., Kurashima, N., Ticktin, T., 2017. Estimating cost-effectiveness of hawaiian dry forest restoration using spatial changes in water yield and landscape flammability under climate change. *Pac. Sci.* 71, 401–424.
- Wagner, W.L., Herbst, D.R., Sohmer, S.H., 1999. *Manual of the Flowering Plants of Hawai'i*, vols. 1 and 2, second ed. University of Hawaii and Bishop Museum Press, Honolulu.
- Wardell, D., Reenberg, A., Tøttrup, C., 2003. Historical footprints in contemporary land use systems: forest cover changes in savannah woodlands in the Sudano-Sahelian zone. *Glob. Environ. Change* 13, 235–254.
- Weller, S.G., Cabin, R.J., Lorence, D.H., Perlman, S., Wood, K., Flynn, T., Sakai, A.K., 2011. Alien plant invasions, introduced ungulates, and alternative states in a mesic forest in Hawaii. *Restor. Ecol.* 19, 671–680.
- Wester, L., Wood, H., 1977. Koster's curse (*Clidemia hirta*), a weed pest in Hawaiian forests. *Environ. Conserv.* 4, 35–41.
- Yelenik, S.G., D'Antonio, C.M., 2013. Self-reinforcing impacts of plant invasions change over time. *Nature* 503, 517–520.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.