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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 alienspecies-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 fireadapted 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 fireadapted trees like Melalueca quinquenervia, understory shrubs such as Rubus argutus and Clidemia hirta, as well as various exotic grasses. Postfire 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 longerterm 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

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