Forest Ecology and Management 409 (2018) 518–526

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The effects of introduced ungulates on native and alien plant species in an island ecosystem: Implications for change in a diverse mesic forest in the Hawaiian Islands

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ARTICLE INFO

Keywords:
Alien species
Diverse mesic forest
Exclosures
Hawaiian Islands
Ungulates

ABSTRACT

In island ecosystems, where endemic species have long been viewed as competitively inferior and more susceptible to herbivory relative to continental species, the impacts of invasive species may be especially pronounced. The sensitivity of island species to invasive species may lead to threshold effects causing irreversible changes in these ecosystems. Predictions that native, mostly endemic plant species are more adversely affected by ungulates than introduced alien plant species, and that competitive interactions between understory native and alien plant species are more severe when ungulates are removed were examined in a 15 year longitudinal study in a diverse mesic forest on Kaua'i (Hawaiian Islands). Over this time period the density of both native and alien overstory canopy trees declined more in unfenced control plots than in plots fenced to exclude ungulates; alien and native trees in the canopy responded similarly to ungulate exclusion via fencing. A differential effect of ungulates on native vs. alien plant species was pronounced in the understory, where the density of small individuals of native canopy species declined sharply in unfenced relative to fenced plots. In contrast, the density of small individuals of alien canopy species was less affected over time by ungulate exclusion. Native herbaceous and understory shrub species also decreased in density over time in unfenced plots relative to fenced plots, while alien understory species increased greatly in some fenced plots relative to unfenced plots. Despite the increase in alien understory plants, no evidence for competition between these alien species and small individuals of native canopy species in the understory could be detected, as numbers of plants in these two understory categories covaried similarly in the presence or absence of ungulates. The contrast between large numbers of native species in the canopy and the severe disruption of the understory in this forest suggests that ungulate removal implemented now or in the near future might prevent loss of the canopy and lead to regeneration of these species. The near absence of recruitment of any endangered species not already present in protected plots indicates that active restoration will be essential to prevent loss of many of the characteristic species of these forests.

1. Introduction

As natural areas become increasingly altered by fragmentation and invasive species, developing strategies for managing these areas has become essential. Traditional goals of re-establishing more natural levels of disturbance, and expecting that successional processes will result in recovery of communities, may not be feasible when degraded ecosystems resist restoration efforts (Suding et al., 2004; Suding and Hobbs, 2009). Restoring ecosystems to a natural state may be unrealistic in light of proliferation of novel ecosystems bearing little resemblance to past ecosystems (Hobbs et al., 2011; Hobbs et al., 2013; Ostertag et al., 2015; Cordell et al., 2016). We report here the results of a long-term study of the effects of removal of non-native ungulates from experimental plots in a highly diverse mesic forest in the Hawaiian Islands, and compare the results of this restoration effort with those of an earlier study of the same plots from 2005 (Weller et al., 2011).

In island ecosystems, where the impacts of invasive species are likely to be especially pronounced, threshold effects leading to

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https://doi.org/10.1016/j.foreco.2017.11.023
Received 2 October 2017; Received in revised form 8 November 2017; Accepted 10 November 2017
0378-1127/

irreversible changes in ecosystems may be common. Relative to continental species, island endemics have long been viewed as competitively inferior, more susceptible to herbivory, and less likely to withstand pathogens (Carlquist, 1974; Courchamp et al., 2003). Species endemic to California's Channel Islands were more palatable to sheep in feeding trials compared to their closest continental relatives (Bowen and Van Vuren, 1997), and endemic plants on the Ogasawara Islands were more susceptible to damage from introduced black rats (*Rattus rattus*) than introduced alien plant species (Abe and Umeno, 2011). In a study of 20 native and 21 invasive plant species in New Zealand, condensed tannins and total phenolics, which reduced consumption by a generalist herbivore, were higher for invasive than native species (Kurokawa et al., 2010). Berglund et al. (2009) found significant positive relationships between the number of invasive animal species and vulnerability of native animal species on islands. Reduced resistance to introduced herbivores is not restricted to island endemics; native *Viburnum* (Adoxaceae) in North America are far more susceptible to an invasive old-world beetle species than old-world *Viburnum* which appear to have evolved resistance to this insect (Desurmont et al., 2011).

Control of introduced ungulates on remote islands is increasingly common, and in many cases the removal of introduced herbivores appears to favor native plant species (Campbell and Donlan, 2005). After eleven years, removal of introduced ungulates using exclosures in a high-elevation area of the Canary Islands resulted in increased native plant species richness and recruitment from seed (Irl et al., 2012). Removal of goats from Pinta Island in the Galápagos Islands resulted in regeneration of native plant species (Hamann, 1993). Similarly, elimination of goats from Guadalupe Island off the west coast of Mexico led to greatly increased recruitment of native tree species (Aguirre-Muñoz et al., 2011). The benefits of ungulate removal presumably result from a combination of reduced consumption and trampling, and indirect effects associated with reduced erosion and changes in nutrient cycling. Removal of alien herbivores could also have adverse effects on native plant species if their removal leads to increased cover of alien plant species that might compete with native plants (Zavaleta et al., 2001; Zavaleta, 2002).

Like introduced ungulates, alien plant species are often suggested to have negative impacts on native plants in island ecosystems. Significant ecosystem impacts due to invasive plant species may include modified fire cycles (D'Antonio et al., 2011), changes in hydrology (Mark and Dickinson, 2008), and changes in nutrient status (Yelenik and D'Antonio, 2013). These impacts may have major effects on the balance between native and alien plant species, although direct competitive interactions between native and alien species have been difficult to quantify (Davis, 2009; Gurevitch and Padilla, 2004; Sax et al., 2002; Sax et al., 2007). Comparisons between related native and alien plant species in Hawai'i provided indirect evidence for potential competition (Funk and Throop, 2010). In this study, alien species invested less in defense than related native species, and by allocating more resources to growth and reproduction, might outcompete native species (Funk and Throop, 2010).

Spatial scale may affect conclusions about the impacts of alien species, with reductions in species richness at local scales but not at larger scales, suggesting that at these larger scales extinction of rare species might be less likely (Powell et al., 2013). Alternatively, Gilbert and Levine (2013) have argued that alien plant species reduce native seed production and decrease matrix permeability in metapopulations, leading to negative effects on native plant species that may not be fully realized for many years. Although Vilà et al. (2015) failed to demonstrate an impact of alien plant species on island species richness using meta-analysis, they noted that species richness might not reflect the full range of interactions between invaders and native plant species.

Interactions between native and alien plants in island ecosystems are likely to be modified by introduced herbivores, especially by ungulates that historically have been absent on these islands. If herbivores preferentially feed on native species because they have reduced defenses, alien plant species may become more invasive than in the absence of herbivores. Because removal of ungulates and other mammalian herbivores is often a first step in restoration efforts on islands (Norton, 2009), understanding the effects of removal of these non-native mammals on interactions between alien and native plants species is critically important. In several New Zealand restoration efforts, removal of grazing animals increased the cover of alien plant species, which either directly or indirectly had negative impacts on the plant species targeted for restoration (Norton, 2009). In subalpine tropical drylands in Hawai'i, an alien plant species increased dramatically in cover with removal of exotic herbivores (Kellner et al., 2011). Similar increases in alien plant species were noted in Hawaiian montane wet forest with removal of ungulates (Cole et al., 2012; Cole and Litton, 2014). These observations are consistent with Funk and Throop's (2010) suggestion that release from herbivory favors alien species that invest less in defense, and which may outcompete natives in the absence of herbivory.

We investigated the effects of ungulate removal and interactions between alien and native, mostly endemic plant species in a diverse mesic forest on Kaua'i in the Hawaiian Islands, the community type with the greatest species diversity in the Hawaiian Islands and one of the highest levels of endangerment (Wagner et al., 1990; Sakai et al., 2002). Our study extended over 15 years, using plots established in 1998 and last surveyed in 2005 (Weller et al., 2011). Long-term studies of this nature, although difficult to maintain, have the potential to reveal important insights into ecosystem processes and provide data useful for addressing management questions (Lindenmayer et al., 2012). Our first goal was to determine the effects of ungulate removal on native vs. alien plant species, and determine if patterns established in 2005 persisted and became more evident in subsequent years. If native plant species are more susceptible to the effects of alien ungulates, then growth and recruitment of these species may benefit disproportionately by ungulate removal. In the absence of such susceptibility, native and alien plant species may be similarly affected by introduced ungulates, or alien plant species in ungulate-free plots might benefit more from ungulate removal than native plants (e.g., Norton, 2009; Funk and Throop, 2010). We also determined whether the effects of ungulates were more evident for small individuals of native tree species occurring in the understory, or if effects were equally pronounced in the canopy and understory. In our earlier surveys we did not differentiate these effects. More pronounced effects in the understory would suggest that ungulate effects will be more consequential over time. Our second goal was to investigate whether ungulates might promote invasion of alien plant species that eventually would outcompete native species. Our ultimate goal was to determine whether protection from ungulate grazing would lead to passive restoration, and prevent loss of this highly diverse community type.

2. Materials and methods

2.1. Experimental design and sampling intervals: 1998–2013

We surveyed experimental plots (fenced ungulate exclosures) and control plots (without fencing) in diverse mesic forest in Mahanaloa Valley on western Kaua'i 15 years after plots were established. An earlier study (Weller et al., 2011) described the effects of ungulate removal after seven years and gives details of the study site and experimental methods. Briefly, five pairs of adjacent fenced and unfenced control plots were established along the length of the north-facing slope of Mahanaloa Valley (22°08′N, 159°42′W; elev. 609 m). Plots were 30 m × 30 m, and fencing around the experimental plots prevented entry by ungulates, which potentially included feral deer (*Odocoileus hemionus columbianus*), pigs (*Sus scrofa*), and goats (*Capra hircus*). In each plot 16 permanent sampling areas separated by 5 m were sampled in 1998 at the time the plots were fenced, and in 2003, 2005, and on Feb 4–7, 2013. For each sampled area, all plants located within a 1.5 m radius were sampled; the 16 sampled areas covered 12.5% of the total