

Resource Availability, Propagule Supply, and Effect of Nonnative Ungulate Herbivores on *Senecio madagascariensis* Invasion¹

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Abstract: Nonnative invasive herbivores can create complex biotic interactions by differentially feeding on native and nonnative invasive plant species. The herbivores may act as enemies of nonnative plants and prevent them from becoming invasive, or they may facilitate invasion by having a greater negative impact on native plants compared with nonnative plants. It is also possible that within the same ecosystem nonnative herbivores could either facilitate or inhibit invasion under different abiotic or biotic conditions. In this study we experimentally investigated how abiotic (soil nutrients) and biotic (propagule density) conditions influence the effect of invasive generalist herbivores on *Senecio madagascariensis*, an invasive plant species in Hawaiian dry forest plant communities. We used fenced exclosures to manipulate presence or absence of invasive ungulates (feral goats and sheep), and we used seed addition to manipulate propagule supply of *S. madagascariensis*. The experiment was replicated in a recently burned and an unburned site to examine how a resource pulse following fire may alter plant-herbivore interactions. There were very few seeds of *S. madagascariensis* in the seed rain of both sites, and recruitment was four times higher when seeds were experimentally added, suggesting that *S. madagascariensis* is dispersal limited in this area. Recruitment of *S. madagascariensis* was five times higher in the burned site compared to the unburned site, suggesting that increased resources promote recruitment. Recruitment was three times higher when herbivores were present compared to when they were excluded, but plants were much smaller when herbivores were present. We conclude that herbivores can alter *S. madagascariensis* recruitment, even during dry conditions, and that propagule availability influences where *S. madagascariensis* can become established.

Keywords: propagule limitation, fire, feral ungulates, Hawai'i, *Senecio madagascariensis*

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Nonnative invasive herbivores can create complex biotic interactions by differentially feeding on native and nonnative plant species. In the case of nonnative plants, the herbivores may act as enemies, controlling plant populations and preventing them from becoming invasive. Alternatively, herbivory may have a greater negative impact on native plants, compared to nonnative plants, facilitating the invasion of nonnative plant species (Simberloff and Von Holle 1999, Richardson and Pyšek 2006, Simberloff 2006). It is also possible that within the same ecosystem nonnative herbivores could either facilitate or inhibit invasion under different biotic or abiotic conditions. Here, we investigate how abiotic conditions influence the effect of nonnative,

generalist herbivores (feral goats and sheep) on the invasive plant species *Senecio madagascariensis* Poir.

Senecio madagascariensis is native to southern Africa and has invaded areas of Australia, Argentina, Kenya, Japan, and Hawai'i (Sindel 1989, 2009). It is a species of economic concern due to its production of pyrrolizidine alkaloids (PAs) that are toxic to grazing animals. *Senecio madagascariensis* was accidentally introduced to Hawai'i Island in the early 1980s, possibly through ground cover seed imported from Australia (Motooka et al. 2004). It has since become a target for eradication due to its ability to spread quickly to large areas of pastureland, its potential to reduce forage yields, and its production of PAs that are poisonous to livestock (Sindel 1989, Motooka et al. 1999, Le Roux et al. 2006). Species in the genus *Senecio* are well defended by their PAs against many generalist herbivores, and plants are capable of allocating more resources toward PA production in their invasive range, compared to their native range, due to founder effects and evolution after invasion (Joshi and Vrieling 2005, Cano et al. 2009). However, some herbivores, such as domestic sheep and goats, can limit the growth and spread of *Senecio* populations (Sindel 2009). For example, in a Hawaiian dry forest dominated by *Myoporum sandwicense* and *Sophora chrysophylla* (*Myoporum-Sophora* dry forest) the removal of nonnative, feral goats had a positive effect on *S. madagascariensis* population growth and no effect on native plant species, suggesting that herbivore removal may contribute to *S. madagascariensis* invasion and that nonnative herbivores inhibit invasion (Kellner et al. 2011).

The effect of herbivores on plant invasions has received extensive study in the Hawaiian Islands, where native plant species evolved in the absence of ungulate herbivores and many have a limited ability to defend themselves against native herbivores and pathogens or introduced herbivores like feral pigs, goats, and sheep (Goergen and Daehler 2001, DeWalt et al. 2004). Generalist herbivores may have a greater negative effect on native, compared to nonnative, species if the nonnative species have superior defensive traits, a pattern well

documented in Hawai'i due to reduced defensive traits in the native flora (Denslow 2003). Due to the presence of PAs in *S. madagascariensis*, it is likely that it is more resistant to herbivory than native species in Hawai'i.

The abiotic conditions at the time of herbivore removal also could affect the response of invasive plant populations. In general, conditions of high resource availability can promote the spread of invasive species (Davis et al. 2000). In addition, the removal of enemies may provide the greatest benefit to species that have high levels of resource use (Blumenthal 2006). Herbivore removal in a dryland ecosystem on Hawai'i island led to increased *S. madagascariensis* population growth and spread when the removal occurred during a higher rainfall year or time of high resource availability (Kellner et al. 2011). Here, we explore whether enhanced resource availability following fire may also contribute to increased invasion of *S. madagascariensis*, and whether there are interactions between resource availability and the removal of herbivores. We hypothesized that the removal of ungulate herbivores would increase the population growth of *S. madagascariensis* and that the plant invasion response to herbivore removal would be greater in areas with higher resource availability. We tested these hypotheses by replicating ungulate fencing and *S. madagascariensis* seed addition treatments in a recently burned and unburned dry forest area on Hawai'i Island.

Species with high propagule densities are likely to respond more rapidly to herbivore removal compared to species with limited propagule supply (Denslow 2003, Richardson and Pyšek 2006, Gurevitch et al. 2011). Native species in Hawaiian dryland ecosystems are primarily woody species with slow, conservative growth that have a relatively lower propagule supply compared to an abundant, invasive, short-lived species such as *S. madagascariensis*. Propagule supply was found to be important for determining the invasion rate of *Senecio vernalis*, a related species (Erfmeier et al. 2013). We examined *S. madagascariensis* population dynamics in a site where its abundance was low (less than 2% cover). It is thought that its abundance is kept low at

this site by ungulate herbivory (Kellner et al. 2011); however, the possibility of propagule limitation in this location has not been tested. We used an experimental seed addition to test whether *S. madagascariensis* was propagule limited, and how propagule availability interacted with herbivore removal. We did not expect *S. madagascariensis* to be propagule limited, but we expected invasion rates in response to herbivore removal to be faster when propagule densities were increased through seed addition.

The area of our study is one of the last remaining tracts of *Myoporum-Sophora* dry forest in the world and is designated as “critical habitat” for the endangered Palila honeycreeper, *Loxioides bailleui* (Pratt et al. 1998). Due to fires and other disturbance the ecosystem is in need of restoration, and invasive ungulates are being removed from targeted areas. Thus, understanding how abiotic and biotic conditions influence the impact of non-native herbivores on plant invasions can guide future ungulate management and restoration efforts in this critically endangered ecosystem and others where *S. madagascariensis* is a management concern.

MATERIALS AND METHODS

Study Sites

The study sites were located within the Pōhakuloa Training Area (PTA), a U.S. Department of Defense training installation, in a subalpine region between the three highest volcanoes on the island of Hawai‘i (1,300–2,600 m elevation). Mean annual precipitation is less than 400 mm and occurs primarily in the winter months (November to April). In general, soils are poorly developed due to recent deposition of substrates from volcanic sources (Rhodes and Lockwood 1995); however, our sites occur on alluvium substrates from the Pleistocene and Holocene that are relatively old for this region (Sherrod et al. 2007). We delineated two study sites, Burned and Unburned, within a community that is characterized as *Sophora-Myoporum* shrubland with grass understory; it is dominated by the trees *Sophora chrysophylla* (Māmane) and

Myoporum sandwicense (Naio) and has an understory of shrubs, grasses, and herbaceous species (Shaw and Castillo 1997). Soils of both sites are Keekee ashy loamy sand, on 0 to 6% slopes (U.S. Department of Agriculture 2016). The substrate for both sites is of Pleistocene or Holocene origin from Mauna Kea (Wolfe and Morris 1996). This community has a high value for conservation of critical habitat for the single extant population of the endangered bird *Loxioides bailleui* (Palila) (Pratt et al. 1998).

The Burned site was in a 1,300 ha area where a high-intensity wildfire occurred in August 2010. The fire was set by arson and appeared to destroy almost all of the vegetation, including mature native trees. The experimental site contained 20 individual study plots within a 100 × 150 m area centered on the location 19.734792° N, –155.504697° W. The Unburned site was of similar size and was located in an adjacent area that was not affected by the fire, centered on the location 19.731533° N, –155.507600° W. This site was 300 m from the edge of where the fire occurred and was 470 m from our Burned site. We refer to this site as “unburned,” but due to the historical presence of infrequent fires in this region there is a possibility that this site burned some time in the past (Kinney et al. 2015).

Experimental Design

We replicated the same experimental design in the Burned and Unburned site, using 20 1 m × 1 m study plots in each site. Within each site, the plots were grouped into 5 m × 5 m blocks as two plots with at least a 1 m walkway around each plot. In December 2010, five blocks in each site were contained in exclosures 1.8 m high made from heavy-wire, ungulate-resistant fencing to prevent grazing or browsing by feral goats and sheep. The other five blocks were in the open with no exclosure present. Each block was separated by 5 m, and fence treatments were randomly assigned to blocks.

We employed a *S. madagascariensis* seed addition treatment by adding 60 *S. madagascariensis* seeds to one plot in each block; the

other plot did not receive *S. madagascariensis* seeds. Seeds were added to the field plots on 12 January 2011. All plots, including plots without seeds added, were covered with coconut fiber mats 1 cm thick (North American Green, Poseyville, Indiana) to prevent seed loss from high winds. Watering was necessary due to the drought conditions present during the experiment. All plots were watered at a rate of 9.5 liters/m² after the initial seed addition and according to the following schedule: daily from 13 to 30 January 2011, three times per week from 31 January to 20 February 2011, twice per week from 21 February to 8 May 2011, and once per week from 9 May to 13 June 2011. Watering was suspended during times of rainfall.

Sampling

We sampled *S. madagascariensis* recruitment and percentage cover in each plot on 5–6 May 2011 and 28 July–3 August 2011. We measured recruitment as the number of individuals. We estimated percentage cover using a 1 m² quadrat with an internal grid containing 25 points where we used a pin flag to determine if *S. madagascariensis* was present at each of the 25 points in the quadrat. With this method, only plants that touched the sampling points in the quadrat were recorded. We ended the study and removed *S. madagascariensis* from the study sites in August 2011, when *S. madagascariensis* began to reproduce. At that time, we harvested the above-ground biomass of all plants in each plot, dried the samples at 70°C for at least 72 hr until at a constant mass, and then weighed the biomass.

We also sampled the natural seed rain to: (1) further investigate whether *S. madagascariensis* is dispersal limited in this area and (2) ensure that our experimental exclosures did not affect seed dispersal into the plots. *Senecio madagascariensis* is an annual species that sets seed continuously throughout the year as individual plants grow and mature. We collected seeds from seed traps over a 6-month period by installing one seed trap in each block on 7 February 2011. Seed funnel traps were constructed of monofilament polyester fabric [33.9 threads per cm (no. 86

mesh)] sewn into 5 cm × 15 cm bags that were attached to the bottom of a funnel, to reduce loss from predation or wind (Cottrell 2004, Thaxton et al. 2010). Traps were placed on a rebar stand in the field at a standard height of 50 cm above the ground surface to protect seeds from vertebrate seed predators (e.g., *Mus musculus*, *Rattus* sp., *Pternistis erckelii*). We collected seeds from each trap on 11 May 2011 and 8 August 2011. We identified seeds to species and counted the number of seeds of all species collected. We analyzed soil inorganic nitrate (NO₃⁻) and ammonium (NH₄⁺) at each site by collecting one soil sample from the center of each block on 31 August 2011. For analysis of NO₃⁻ and NH₄⁺, we extracted samples with a 2.0 M KCl solution and sent them for analysis at the University of Hawai'i at Hilo (UHH) Analytical Laboratory (Hilo, Hawai'i) with a Pulse Autoanalyzer III with Autosampler IV (Saskatoon, Saskatchewan, Canada).

Statistical Analysis

All data analyses were conducted in the R statistical environment (R Core Team 2015). The R package lme4 was used to analyze generalized linear models (Bates et al. 2015). All model validation procedures and diagnostics were conducted as described in Zuur and Ieno (2016). In Supplemental Appendix S1, we present the diagnostic graphs for each model used in the analyses.

Authors' Note: Supplemental materials available online at BioOne (<http://www.bioone.org/toc/pasc/current>) and Project MUSE (<http://muse.jhu.edu/journal/166>).

Comparisons among Burned and Unburned Sites

We measured the difference between soil nitrogen and *S. madagascariensis* recruitment, cover, and biomass between the Burned and Unburned sites. Low recruitment in the Unburned site and in plots where *S. madagascariensis* seeds were not added led to a heavily zero-inflated data structure as well as issues with homogeneity of variance between treatments. When *S. madagascariensis* did occur, the total count of recruits was consistently small (range was 0–8 seedlings per plot) and

the data set contained numerous zeros; therefore, we transformed the data into presence absence data. Cover data had similar problems and were also transformed into presence absence data. Both data sets were analyzed using a generalized linear model with a binomial distribution using the standard logit link function. The final sampling date (July 2011) was analyzed for recruitment data. Biomass had similar zero-inflation problems that were more difficult to handle. Biomass models consistently resulted in poor model fit and severe underdispersion; therefore, biomass data could not be statistically analyzed. Soil nitrate, ammonium, and total nitrogen were analyzed using a generalized linear model with a gamma distribution using the standard log link function. The gamma distribution was chosen for these data because the gamma distribution is appropriate for positive continuous data and provided the best model fit compared to other distributions (Zuur and Ieno 2016). All of the between-site analyses were analyzed using the same model structure: $\text{Response Variable} \sim \beta_{\text{intercept}} + \beta_2 \text{Site}$, where β is the estimate of the effect of the factor (Site) on the response variable.

Seed Rain

Seed rain of *S. madagascariensis* was too sparse to statistically analyze. To infer whether or not the fencing treatment obstructed natural seed rain into the plots, we analyzed seed rain results for the two most abundant species, *Chenopodium oahuense* and *Erodium cicutarium*. Seed counts were added from both trapping periods for a total seed count for each plot. One block from the Unburned site was omitted because the funnel disappeared during the second trapping period, leaving 10 samples from the Burned site and nine samples from the Unburned site. The model chosen for these analyses was as follows: $\text{Seed Rain} \sim \beta_{\text{intercept}} + \beta_2 \text{Site} + \beta_3 \text{Fence} + \beta_4 \text{Site} \times \text{Fence}$. Each species was analyzed separately. A generalized linear model with a negative binomial distribution using the standard log link function was selected because the negative binomial distribution is appropriate for overdispersed count data that have large variation (Zuur and Ieno 2016).

Recruitment

Low recruitment in the Unburned site led to a heavily zero-inflated data structure; therefore, we analyzed the effects of our experimental treatments only in the Burned site for recruitment. Thus, *S. madagascariensis* recruitment was analyzed using a general linear mixed effects model via restricted maximum likelihood (REML). The model used for recruitment analysis was as follows: $\text{Recruitment} \sim \beta_{\text{intercept}} + \beta_2 \text{Fence} + \beta_3 \text{Seed Addition} + \beta_4 \text{Date} + \beta_5 \text{Fence} \times \text{Seed Addition} + \beta_6 \text{Fence} \times \text{Date} + \beta_7 \text{Seed Addition} \times \text{Date} + \beta_8 \text{Block}$. Block was included as a random term.

Cover and Biomass

We were unable to statistically analyze the cover and biomass of *S. madagascariensis* across all experimental treatments due to zero-inflation, violation of assumptions, poor model fit, and models that were too complex for the data structure. The cover data set contained 65% zeroes, and the biomass data set contained 57% zeroes.

RESULTS

Site Differences

The Burned site soils had higher total N and NH_4 (Table 1, Supplemental Figure S1). *Senecio madagascariensis* recruitment, percentage cover, and biomass were higher in the Burned site compared to the Unburned site, although the differences were not statistically significant at $\alpha = .05$ [$P < .08$ (Table 1)]. The dispersion statistic was 1.05 for the recruitment and percentage cover models, indicating good model fit (Zuur and Ieno 2016). All attempted models for biomass fit poorly due to the zero-inflated data structure. Therefore, we report results for biomass as patterns only.

Seed Rain

Only eight *S. madagascariensis* seeds were collected from the Burned site, and two seeds were collected from the Unburned site; therefore, we were unable to statistically analyze

TABLE 1
Analyses between the Burned and Unburned Sites

Response Variable	Burned Site Mean	Unburned Site Mean	Estimate (SE)	P
<i>S. madagascariensis</i> seedling recruitment (no. of seedlings per plot)	1.65 (0.59)	0.3 (0.21)	−1.57 (0.88)	.073
<i>S. madagascariensis</i> abundance (% cover)	4.8 (1.89)	0.4 (0.4)	−2.09 (1.13)	.065
<i>S. madagascariensis</i> biomass (g)	25.60 (10.50)	0.66 (0.37)	***	***
Total available soil N	64.60 (24.10)	13.42 (2.63)	−1.73 (0.36)	<.005
Soil NH ₄	51.70 (23.90)	4.21 (0.82)	−2.70 (0.42)	<.005
Soil NO ₂ + NO ₃	12.92 (4.16)	9.22 (1.94)	−0.34 (0.38)	.384

Note: Estimates (SE) and *P* values are reported from the generalized linear models. A negative estimate indicates that the response variable was lower in the Unburned, compared to the Burned, site. Means ± SE are calculated for all experimental plots in each site (*N* = 20 per site for *Senecio madagascariensis* recruitment, abundance, and biomass data; *N* = 10 per site for soil nitrogen data).
*** Data could not be statistically interpreted due to heavily zero-inflated data structure.

seed rain results for *S. madagascariensis* due to the heavily zero-inflated data structure (79% zeros). *Chenopodium oahuense*, a native shrub, and *Erodium cicutarium*, a nonnative invasive forb, were the most abundant species sampled in our seed traps. There was no difference in seed rain of either species inside and outside the fenced exclosures [no significant Fence effect (*P* > .70) (Supplemental Figures S2, S3)]. Seeds of native species other than *C. oahuense* rarely occurred.

Experimental Treatment Effects

We analyzed the effect of our experimental treatments for data from the Burned site, but not the Unburned site, due to the low recruitment of *S. madagascariensis* in the Unburned site (Table 1, Supplemental Figure S4). *Senecio madagascariensis* recruitment was significantly seed limited [significant Seed Addition Effect (Table 2, Figure 1a)]. *Senecio madagascariensis* percentage cover and biomass seemed to be affected by seed addition, but we could not evaluate the statistical significance of the pattern due to poor model fit (Figure 1b).

In plots where *S. madagascariensis* was experimentally added, its recruitment was higher in unfenced, compared to fenced, treatments [significant Seed Addition × Fence interaction (Table 2, Figure 1a)]. These results suggest that once dispersal barriers were removed by adding seeds, the presence of

TABLE 2
Experimental Treatment Effects on *Senecio madagascariensis* Recruitment in the Burned Site

Factor	Estimate (SE)	P
Intercept	−0.15 (0.81)	.85
Date: July 2011	0.300 (0.86)	.73
Fenced: Open	0.300 (1.09)	.78
Seed: Added	1.900 (0.86)	.02
Fenced: Open × Seed: Added	4.000 (0.99)	<.0001
Date: July 2011 × Fenced: Open	−0.600 (0.99)	.55
Date: July 2011 × Seed: Added	−0.600 (0.99)	.55

Note: Betas (SE) and *P* values are reported from the generalized linear model. There was a significant increase in recruitment when seeds were added (Seed Addition). When seeds were added, plots that were not fenced had higher recruitment, but this effect of fencing was not apparent when seeds were not added (Fenced Open × Seed Addition).

browsing animals increased *S. madagascariensis* recruitment. In contrast, percentage cover and biomass showed a trend of lower values when herbivores were present (Figure 1b).

DISCUSSION

Dispersal Limitation

Overall we found that seed availability had the greatest impact on the recruitment of *S. madagascariensis* (Table 2, Figure 1a). It is sur-

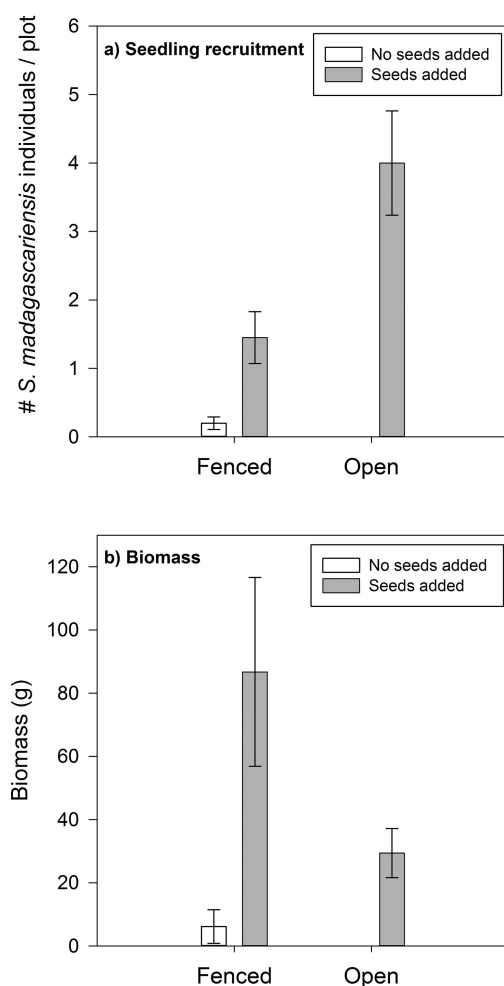


FIGURE 1. Recruitment and biomass as a function of seed addition and herbivore removal. Bars show mean number of individuals for seed addition (+/–) treatments crossed with herbivore removal treatments (fence/no fence) for (a) *S. madagascariensis* recruitment (number of seedlings) and (b) *S. madagascariensis* biomass (g). Error bars show 1 SE. Recruitment of *S. madagascariensis* was greatest when seeds were added and herbivores were present. Biomass of *S. madagascariensis* was greatest when seeds were added and herbivores were removed.

prising that *S. madagascariensis* was strongly dispersal-limited in light of its abundance in the region and wind dispersal typical of other species in the Asteraceae. It occurs in high abundance at sites downwind within 15 km of the study area, so we expected *S. madagascariensis*

to occur more abundantly in the seed rain. The areas used for this experiment occur in a large valley between Mauna Loa and Mauna Kea volcanoes, where winds are not impeded by landforms and wind speeds are high. Interpolated, 30-m wind speeds for our sites range from 22 to 25 kmph (U.S. Department of Energy 2014). These high winds may limit the ability of *S. madagascariensis* seeds to become established, and instead seeds may be blown to other areas where they are deposited. However, seeds of other species, *Chenopodium oahuense* and *Erodium cicutarium*, were captured by our seed traps. These species produce many small seeds and occur in high numbers at our sites, suggesting that it may take more time for *S. madagascariensis* to naturally invade this area from its surrounding populations.

It is also possible that invasive vertebrate seed predators could affect invasion rates (e.g., *Mus musculus*, *Rattus* sp., *Pternistis erckelii*). Our seed traps were designed to protect collected seeds from vertebrate seed predators, which can negatively influence seedling recruitment and survival and also increase seed dispersal (Cuddihy and Stone 1990, Shiels and Drake 2011). These predators are typically considered a barrier to the regeneration of native plant species in Hawai‘i; however, their potential to control or disperse *S. madagascariensis* deserves consideration and study.

Resources and Plant-Animal Interactions

Resource availability can alter invasive plant-animal interactions. The fluctuating resources hypothesis proposes that periods of high resource availability facilitate colonization (Davis et al. 2000). The resource-enemy-release hypothesis (R-ERH) expands on this idea and suggests that species adapted to high resource availability (high resource species) will be favored more by enemy release than species with slower growth that are adapted to lower resource availability (low resource species) (Blumenthal 2006). The result of the R-ERH is that enemy release and resource availability may act together to facilitate the invasion of high resource species.

We replicated our study in a Burned and Unburned area to examine how resources and disturbance may change the relationship between invasive ungulate enemies and *S. madagascariensis* invasion. Recruitment and plant biomass for *S. madagascariensis* were very low at the Unburned site and increased at the Burned site (Table 1). Native species and other nonnative species also had greater recruitment and biomass in the Burned site (E. Questad, A. Uowolo, S. Brooks, and S. Cordell, unpubl. data). This increase in invasion may be the result of the observed pulse of increased nitrogen (N) that was made available after the fire; however, our study also coincided with a period of extreme drought in the region. The relatively low recruitment at both sites suggests that drought likely had a strong, limiting effect on plant population dynamics. Even though all plots were watered during the experiment, volumetric soil water content remained low and did not exceed $0.16 \text{ m}^3/\text{m}^3$ during the time of the study, including on days with rainfall or when water was added (E. Questad, A. Uowolo, S. Brooks, and S. Cordell, unpubl. data). Plants were likely water-limited and could not fully take advantage of any soil nutrient or other resource pulses after the fire. Therefore, it is still difficult to isolate the role of resources in *S. madagascariensis* invasion from this experiment.

In our study system, *S. madagascariensis* is a fast-growing high resource species, and the native species are slower-growing low resource species. An earlier study during a year with high rainfall found that when invasive ungulates were removed from a large management area, *S. madagascariensis* cover increased (Kellner et al. 2011), similar to our finding of a trend toward increased biomass when ungulates were removed. These patterns support the role of the enemy release hypothesis in explaining *S. madagascariensis* invasion in both high and low resource conditions.

Our results further suggest that *Senecio* may experience greater intraspecific competition when ungulates are removed. In pairwise studies of competition between native and invasive plant species, intraspecific competition is often higher than interspecific competition

for invasive, but not native, species (Vilà and Weiner 2004). *Senecio madagascariensis* cover and biomass were higher in fenced treatments (Figure 1b), but *S. madagascariensis* seedling recruitment was lower in fenced treatments (Figure 1a). These differing responses to fencing may occur due to intraspecific competition (i.e., self-thinning) that is greater when herbivores are not present. As individuals grow larger in the absence of herbivores, they compete with each other and reduce the overall number of individuals in the population. This competition is absent when the seedlings are kept small by herbivory. Therefore, the overall effect of herbivores on *S. madagascariensis* is to reduce the size of plants, but increase the number of individuals. This finding contrasts with other studies in which the presence of herbivores increased intraspecific competitive interactions for invasive plant species (Steets et al. 2006, Russell and Spencer 2010). It also suggests that herbivores may alter the population growth of *S. madagascariensis* by reducing intraspecific competition, but limiting the overall size and reproductive output of individuals.

Wind

Although we did not explicitly test the effects of wind on invasion, results of this and other studies suggest that wind may play an important role in invasion dynamics in this ecosystem. Wind has substantial effects on the behavior and spread of fires across a landscape (Beer 1991, Fendell and Wolff 2001). The high winds in our study region make wildfires difficult to suppress and lead to fires extending over large areas. Wind accelerates erosion and can lead to nutrient loss, especially after a fire when high levels of erosion occur. The combination of high winds with the volcanic ash substrate in this ecosystem accelerates erosion and may lead to a depletion of topsoil, organic matter, and beneficial microorganisms from the ecosystem. Feral goats in this ecosystem spend a greater amount of time in areas protected from the prevailing winds (Cordell et al. 2016). These areas also have the most suitable microclimates for plant growth due to reduced water stress (Questad et al. 2014). Wind patterns can also strongly

affect seed dispersal and thus plant establishment and community composition. Specifically convective updrafts, turbulence, and landforms that impede wind movement are important determinants of geographic dispersal patterns for wind-dispersed seeds (Tackenberg 2003, Damschen et al. 2014). Here we found a surprisingly low number of *S. madagascariensis* seeds in the seed rain, suggesting that wind patterns in this region may not create dispersal opportunities to these sites. Thus, wind, and its interaction with landforms, fire, nutrients, ungulate behavior, and dispersal dynamics may be an important, but little-studied, force controlling plant community interactions and invasion in this ecosystem (Swanson et al. 1988).

Management Applications

The observed effects of dispersal and abiotic conditions on *S. madagascariensis* abundance have implications for managing this invasion. First, it will be important to focus *S. madagascariensis* control efforts in areas where its seed rain is high and where site conditions are conducive to its growth. Focusing control where existing populations are large and resources are readily available should be a priority. Further study of seed rain patterns surrounding existing populations could help determine additional areas for control. Domesticated goats and sheep have been used to control *S. madagascariensis* in other places where it is invasive (Sindel 2009). This practice is compatible with highly managed systems such as grazed pastures or rangeland but is less compatible in ecosystems where native species will also be negatively influenced by browsing. However, intensive control efforts either with managed ungulates or with herbicide application could be focused in areas where invasion is most likely to occur or where *S. madagascariensis* seed rain is already high.

If areas with high *S. madagascariensis* seed rain need to be fenced for conservation, fencing during a dry period may reduce the level of *S. madagascariensis* invasion. In addition, a follow-up plan to manage *S. madagascariensis* will be necessary for those areas. The release of the phytophagous moth *Secusio extensa*, whose larvae feed on leaves and strip the outer

layers of stems, for biological control of *S. madagascariensis* on Hawai'i Island is a step toward achieving control and could make it possible to remove ungulates from areas with high levels of *S. madagascariensis* invasion without increasing the spread of *S. madagascariensis* (HDOA 2008, 2013).

When the removal of feral ungulates is necessary for conservation or restoration, it may be more effective for native conservation if it occurs in an area with low *S. madagascariensis* seed rain. In such areas, explosive population growth of *S. madagascariensis* following ungulate removal is less likely to occur; therefore, there would be a lower investment needed in *S. madagascariensis* control. In fact, our study area and the saddle region surrounding it are good candidates for ungulate removal because *S. madagascariensis* seed rain is low and the conservation value of this region is high. This area is one of the last large remnants of *Myoporum-Sophora* dry forest, the critical habitat for the conservation of the endangered palila honeycreeper (*Loxioides bailleui*). Removal of feral ungulates is less likely to promote *S. madagascariensis* invasion in this region compared to other areas with greater seed rain.

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Literature Cited

- Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67:1–48.
- Beer, T. 1991. The interaction of wind and fire. *Boundary-Layer Meteorol.* 54:287–308.
- Blumenthal, D. M. 2006. Interactions between resource availability and enemy

- release in plant invasion. *Ecol. Lett.* 9:887–895.
- Cano, L., J. Escarre, K. Vrieling, and F. X. Sans. 2009. Palatability to a generalist herbivore, defence and growth of invasive and native *Senecio* species: Testing the evolution of increased competitive ability hypothesis. *Oecologia (Berl.)* 159:95–106.
- Cordell, S., E. J. Questad, G. P. Asner, K. Kinney, J. Thaxton, A. Uowolo, S. Brooks, and M. W. Chynoweth. 2016. Remote sensing for restoration planning: How the big picture can inform stakeholders. *Restoration Ecology Early View Online*.
- Cottrell, T. R. 2004. Seed rain traps for forest lands: Consideration for trap construction and study design. *BC J. Ecosyst. Manage.* 5:1–6.
- Cuddihy, L. W., and C. P. Stone. 1990. Alteration of native Hawaiian vegetation: Effects of humans, their activities and introductions. University of Hawai'i Press, Honolulu.
- Damschen, E. I., D. V. Baker, G. Bohrer, R. Nathan, J. L. Orrock, J. R. Turner, L. A. Brudvig, N. M. Haddad, D. J. Levey, and J. J. Tewksbury. 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proc. Natl. Acad. Sci. U.S.A.* 111:3484–3489.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *J. Ecol.* 88:528–534.
- Denslow, J. S. 2003. Weeds in paradise: Thoughts on the invasibility of tropical islands. *Ann. Mo. Bot. Gard.* 90:119–127.
- DeWalt, S. J., J. S. Denslow, and K. Ickes. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85:471–483.
- Erfmeier, A., L. Hantsch, and H. Bruehlheide. 2013. The role of propagule pressure, genetic diversity and microsite availability for *Senecio vernalis* invasion. *PloS ONE* 8:e57029.
- Fendell, F. E., and M. F. Wolff. 2001. Wind-aided fire spread. Pages 171–223 in E. A. Johnson and K. Miyanishi, eds. *Forest fires: Behavior and ecological effects*. Academic Press, San Diego.
- Goergen, E., and C. C. Daehler. 2001. Inflorescence damage by insects and fungi in native pili grass (*Heteropogon contortus*) versus alien fountain grass (*Pennisetum setaceum*) in Hawai'i. *Pac. Sci.* 55:129–136.
- Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecol. Lett.* 14:407–418.
- HDOA (Hawai'i Department of Agriculture). 2008. Draft environmental assessment: Field release of *Secusio extensa* (Butler) (Lepidoptera: Arctiidae), for biological control of fireweed, *Senecio madagascariensis* Poirlet (Asterales: Asteraceae), in Hawai'i. Honolulu.
- . 2013. Biocontrol moths released to fight invasive fireweed. Honolulu.
- Joshi, J., and K. Vrieling. 2005. The enemy release and EICA hypothesis revisited: Incorporating the fundamental difference between specialist and generalist herbivores. *Ecol. Lett.* 8:704–714.
- Kellner, J. R., G. P. Asner, K. M. Kinney, S. R. Loarie, D. E. Knapp, T. Kennedy-Bowdoin, E. J. Questad, S. Cordell, and J. M. Thaxton. 2011. Remote analysis of biological invasion and the impact of enemy release. *Ecol. Appl.* 21:2094–2104.
- Kinney, K. M., G. P. Asner, S. Cordell, O. A. Chadwick, K. Heckman, S. Hotchkiss, M. Jeraj, T. Kennedy-Bowdoin, D. E. Knapp, E. J. Questad, J. M. Thaxton, F. Trusdell, and J. R. Kellner. 2015. Primary succession on a Hawaiian dryland chronosequence. *PloS ONE* 10:e0123995.
- Le Roux, J. J., A. M. Wicczorek, M. M. Ramadan, and C. T. Tran. 2006. Resolving the native provenance of invasive fireweed (*Senecio madagascariensis* Poir.) in the Hawaiian Islands as inferred from phylogenetic analysis. *Divers. Distrib.* 12:694–702.
- Motooka, P., G. Nagai, K. Onuma, M. Duponte, A. Kawabata, and G. Fukumoto. 1999. Control of fireweed (*Senecio madagascariensis*). University of Hawai'i Press, Honolulu.
- Motooka, P., G. Nagai, K. Onuma, M. Duponte, A. Kawabata, G. Fukumoto, and J. Powley. 2004. Control of Madagascar

- Ragwort (aka Madagascar fireweed, *Senecio madagascariensis*). College of Tropical Agriculture and Human Resources, University of Hawai'i at Mānoa. Publ. WC-2.
- Pratt, T. K., P. C. Banko, S. G. Fancy, G. D. Lindsey, and J. D. Jacobi. 1998. Status and management of the Palila, an endangered Hawaiian honeycreeper, 1987–1996. *Pac. Conserv. Biol.* 3:330–340.
- Questad, E. J., J. R. Kellner, K. Kinney, S. Cordell, G. P. Asner, J. Thaxton, J. Diep, A. Uowolo, S. Brooks, N. Inman-Narahari, S. A. Evans, and B. Tucker. 2014. Mapping habitat suitability for at-risk plant species and its implications for restoration and reintroduction. *Ecol. Appl.* 24:385–395.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rhodes, J. M., and J. P. Lockwood. 1995. Mauna Loa revealed: Structure, composition, history, and hazards. American Geophysical Union, Washington, D.C.
- Richardson, D. M., and P. Pyšek. 2006. Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Prog. Phys. Geogr.* 30:409–431.
- Russell, F. L., and M. Spencer. 2010. Combined effects of folivory and neighbor plants on *Cirsium altissimum* (tall thistle) rosette performance. *Plant Ecol.* 208:35–46.
- Shaw, R. B., and J. M. Castillo. 1997. Plant communities of Pohakuloa Training Area, Hawaii. Fort Collins, Colorado.
- Sherrod, D. R., J. M. Sinton, S. E. Watkins, and K. M. Brunt. 2007. Geologic map of the state of Hawai'i, Sheet 8. Island of Hawai'i. In U.S. Geological Survey Open-File Report 2007-1089.
- Shiels, A. B., and D. R. Drake. 2011. Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaii? *Biol. Invasions* 13:883–894.
- Simberloff, D. 2006. Invasional meltdown 6 years later: Important phenomenon, unfortunate metaphor, or both? *Ecol. Lett.* 9:912–919.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: Invasional meltdown? *Biol. Invasions* 1:21–32.
- Sindell, B. 1989. The ecology and control of fireweed (*Senecio madagascariensis* Poir.). University of Sydney, NSW, Australia.
- . 2009. Fireweed in Australia: Directions for future research. Bega Valley Fireweed Association, Bega, NSW, Australia.
- Steets, J. A., R. S. Salla, and T. L. Ashman. 2006. Herbivory and competition interact to affect reproductive traits and mating system expression in *Impatiens capensis*. *Am. Nat.* 167:591–600.
- Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38:92–98.
- Tackenberg, O. 2003. Modeling long-distance dispersal of plant diaspores by wind. *Ecol. Monogr.* 73:173–189.
- Thaxton, J. M., T. C. Cole, S. Cordell, R. J. Cabin, D. R. Sandquist, and C. M. Litton. 2010. Native species regeneration following ungulate exclusion and nonnative grass removal in a remnant Hawaiian dry forest. *Pac. Sci.* 64:533–544.
- U.S. Department of Agriculture. 2016. Natural Resources Conservation Service soil survey for the island of Hawai'i area, Hawai'i.
- U.S. Department of Energy. 2014. Hawaii 30-meter residential-scale wind resource map (<https://windexchange.energy.gov/maps-data/161>).
- Vilà, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* 105:229–238.
- Wolfe, E. W., and J. Morris. 1996. Geologic map of the island of Hawaii. Miscellaneous Investigations Series I-2524A. U.S. Geological Survey, Reston, Virginia.
- Zuur, A. F., and E. N. Ieno. 2016. Beginner's guide to zero-inflated models with R. Highland Statistics Ltd., Newburgh, United Kingdom.