Out of the frying pan and into the fire: effects of volcanic heat and other stressors on the conservation of a critically endangered plant in Hawai'i

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Summary

Loss of local biodiversity resulting from abrupt environmental change is a significant environmental problem throughout the world. Extinctions of plants are particularly important yet are often overlooked. Drawing from a case in Hawai'i, a global hotspot for plant and other extinctions, we demonstrate an effort to better understand and determine priorities for the management of an endangered plant ('Ihi makole or *Portulaca sclerocarpa*) in the face of rapid and extreme environmental change. Volcanic heat emissions and biological invasions have anecdotally been suggested as possible threats to the species. We integrated *P. sclerocarpa* outplanting with efforts to collect geological and ecological data to gauge the role of elevated soil temperatures and invasive grasses in driving *P. sclerocarpa* mortality and population decline. We measured soil temperature, soil depth, surrounding cover and *P. sclerocarpa* survivorship over three decades. The abundance of wild *P. sclerocarpa* decreased by 99.7% from the 1990s to 2021. Only 51% of outplantings persisted through 3–4 years. Binomial regression and structural equation modelling revealed that, among the variables we analysed, high soil temperatures were most strongly associated with population decline. Finding the niche where soil temperatures are low enough to allow *P. sclerocarpa* survival but high enough to limit other agents of *P. sclerocarpa* mortality may be necessary to increase population growth of this species.

Introduction

One of the most pressing environmental issues facing the world today is the loss of biodiversity resulting from human-caused extinctions of myriad species (Ceballos et al. 2015). Plant extinctions are often overlooked but are particularly concerning because they cascade to affect other species at higher trophic levels (Humphreys et al. 2019). The islands of Hawai'i are a focal point of this issue, having recorded more plant extinctions than any other region of the world (Humphreys et al. 2019, 2020). Extinction of island plants often occurs because of their restricted range as they are confronted with abrupt environmental change, such as species introductions and land-cover conversion (MacDonald et al. 1991, Simberloff 2000, Reaser et al. 2007).

Abrupt environmental changes over space and time are common in Hawai'i. Steep gradients in soil, climate and elevation create high environmental diversity and geographically small niche habitats where endemic plants are especially vulnerable to extinction (Humphreys et al. 2019). Conditions are highly dynamic and challenging for conservation due to land-use change (Powers & Jetz 2019), introductions of invasive plants and animals (Bellard et al. 2017) and climate change (Román-Palacios & Wiens 2020), all in the face of shifting volcanic activity. Although this rich environmental diversity contributed to the evolution of many diverse, endemic species, many of those species are now threatened (Vitousek 1988).

Understanding the biophysical variables that drive a species' distribution is critical for managing threatened and endangered species, especially because most species face multiple threats. For example, such information can be used in conjunction with dispersal information (e.g., Gill et al. 2021a, 2022) and habitat distribution models (Guisan & Zimmermann 2000) to make predictions about range shifts given climate change (Fortini et al. 2013). Data representing biophysical gradients can also be used to predict the potential range of expansion by non-native species after their introduction into novel ecosystems outside their native range

Fig. 1. 'Ihi makole (*Portulaca sclerocarpa*). Photograph: Nathan S Gill, Puhimau Geothermal Area, 2017.

Table 1. Summary of hypotheses.

Potential driver variable	Hypothesized to …	Relevant literature
Invasive grass cover	Reduce abundance of *Portulaca sclerocarpa* through competition	D'Antonio et al. (1998), Cabin et al. (2002), Denslow et al. (2006), Yelenik et al. (2022)
High soil temperatures	Reduce cover and abundance of *P. sclerocarpa* and invasive grasses	D'Antonio et al. (1998), Cabin et al. (2002), Denslow et al. (2006), James et al. (2019)
Shallow soils	Increase *P. sclerocarpa* mortality	Frazier et al. (2019)
Founder identity	Increase or decrease *P. sclerocarpa* survivorship	Helenurm (1998)

(Vorsino et al. 2014, Gill & Sangermano 2016). Finally, the relationships between species and specific biophysical variables can be used to predict sites where planting or translocation efforts will be most successful based on microhabitat (Questad et al. 2014). These techniques for threatened and endangered species, however, rarely incorporate biotic interactions, such as competition from invasive species, potentially leading to spurious conclusions about how species shift given climate change (Alexander et al. 2015) or altering the utility of habitat suitability models (Yelenik et al. 2022).

Rationale and objectives

We aimed to study the relationship between an endangered plant and multiple environmental variables as a case study for understanding the relationships between species of concern, extreme environmental change and invasive species impacts. Our study also highlights a case of coordinating ongoing conservation management with research among multiple agencies by monitoring the response of individuals that were outplanted along biophysical gradients that were perceived to be influential on the species' survivorship.

'Ihi makole (*Portulaca sclerocarpa*; Fig. 1) is an endangered, low-growing succulent herb that is endemic to the Hawaiian Islands, being found only on the Island of Hawai'i and one small islet off Lāna'i (Stone et al. 1994). The species grows in relatively dry environments at >900 m above sea level (Stone et al. 1994). Previously found throughout much of Hawai'i Volcanoes National Park, the plant's population has been in sharp decline over the past several decades for reasons that have yet to be resolved. The species now occurs naturally at only two sites within Hawai'i Volcanoes National Park, and it has been outplanted at eight additional park sites. The largest population of *P. sclerocarpa* occurs at the Puhimau Thermal Area, a site with anomalously high soil temperatures, CO_2 emissions and steam vents that formed around 1936, probably in response to magmatic intrusion beneath it (Jaggar 1938, McGee et al. 2006). The Puhimau Thermal Area previously supported thousands of *P. sclerocarpa*, and over 900 were recorded there in 1994 (Pratt et al. 2011). By 2008, the population had fallen to <300 individuals (Pratt et al. 2011), and the drivers of this decline remained largely unknown. In response to continued population decline, the National Park Service started outplanting *P. sclerocarpa* at the Puhimau Thermal Area in 2017. Prior to 2017, *P. sclerocarpa* had been outplanted in a variety of other locations in the park, but survivorship of these outplantings has been extremely low (e.g., 16% after 3 years; Pratt et al. 2011). None of these prior outplanting sites exhibited volcanic heat or gas emissions.

In the face of the extreme environmental change induced by volcanic activity, as well as the biological invasion of grasses and climate change, we sought to examine how interactions between these shifting biophysical variables might influence environmental conservation efforts for *P. sclerocarpa*. We hypothesized that invasive grasses would have a negative effect on *P. sclerocarpa,* as has been shown for other native Hawaiian species (e.g., D'Antonio et al. 1998, Cabin et al. 2002, Denslow et al. 2006), and that both grasses and *P. sclerocarpa* would be negatively affected by high soil temperatures, as has been shown for a variety of grasses, including some invasive species (James et al. 2019). Thus, we suspected that it would also be possible that we might find an indirect positive effect of soil temperature on *P. sclerocarpa* due to its negative effect on grasses. We also hypothesized that shallower soils would lead to greater mortality because they would be less able to hold water in such sites, which experience seasonal drought (many native plants in the Park have been threatened by recent droughts; Frazier et al. 2019). Finally, we thought that it was possible that founder identity could affect the mortality of outplants due to genetic differences (Helenurm 1998). These hypotheses are summarized in Table 1.

Methods

Site

Puhimau Thermal Area, located near Puhimau Crater along Chain of Craters Road in the upper East Rift Zone of Kīlauea Volcano, has been an area of scientific interest since it formed *c.* 1936 when heat and gases migrated to the surface following a magmatic intrusion. The *Metrosideros polymorpha* ('ōhi'a) forest that was there died back and has since been replaced with open soils, lichens, grasses, sedges, shrubs and some herbaceous species such as *P. sclerocarpa* (Smith 1981). The dominant grass is the invasive species *Andropogon virginicus* (broom sedge). *Schizachyrium condensatum* is also present. Today, Puhimau Thermal Area is *c.* 16 ha in size with hot (as high as *c.* 200°F or *c.* 93°C), steaming soils and diffuse volcanic CO_2 emissions (McGee et al. 2006, Lewicki

et al. 2020). Soils are pahoehoe lava and are *c.* 440–660 years old (USDA & NRCS 2008), with soil depths averaging 14 cm (ranging from 4 to 27 cm) across the site.

Outplanting experiment

In partnership with the National Park Service, we outplanted 175 mature *P. sclerocarpa* in February 2017 and February 2018 from 23 known founding individuals (founders grown in a greenhouse from seed collected within Hawai'i Volcanoes National Park) in two different sections of Puhimau, spanning large gradients of soil depths (*c.* 4–27 cm) and soil temperatures (*c.* 32–66°C) due to microsite differences in heat emissions.

Surveys and data collected

Surveys and monitoring

Demographic data on *P. sclerocarpa* were compiled through surveys conducted at Puhimau in 1984, 1993, 2010 and 2011. In 1984 and 1993, precise geospatial data for individuals were not collected, but Puhimau Thermal Area was divided into 368 10-m × 10-m quadrants that were assigned unique alphanumeric labels. We georeferenced the quadrants using a known corner of a quadrant in *ArcMap* (version 10.7.1). The surveys in 1984 and 1993 assigned total *P. sclerocarpa* counts to each georeferenced quadrant, whereas later surveys tracked individuals with specific geospatial data for each plant.

From 2017 to 2021, we conducted surveys at least annually to monitor all outplants as well as all naturally recruited plants (hereafter 'wild' plants) that were still alive, although by 2017 the total population of living wild plants was down to 36 individuals from an initial count of 4322 in 1984. Besides mortality outcomes, we also obtained data on soil depth in 2017 and 2019 using a metal soil probe with increment markings depressed into the soil next to each individual *P. sclerocarpa* plant until it could be pushed no farther. When soil depth data were collected, we also collected percentage cover data of surrounding plant species and abiotic ground cover (e.g., litter, rock) by placing a 1-m × 1-m quadrat centred on the individual *P. sclerocarpa* plant and visually estimating percentage cover. Percentage cover of plants was recorded by species, but cover values for all invasive grasses were summed into a single 'invasive grass cover' metric for the final analysis. No native grasses were found in quadrats during this study.

Soil temperature

Soil temperature was manually measured with a K-type thermocouple probe systematically at 30-m spacings across Puhimau from 1996 to 1998 and again in 2019 (McGee et al. 2006, Lewicki et al. 2020). Soil temperature was measured at 5-cm depth in the 1990s and at 20-cm depth in 2019. At a site with a magmatic heat source such as Puhimau, we expect soil temperature to increase with soil depth, so we did not make any direct comparisons of temperatures measured at different depths in different decades. Rather, we intended to compare spatial patterns of soil temperatures between the two time periods. The soil temperature data measured in these surveys were interpolated by inverse-distance weighting in a geographical information system (GIS) using *ArcMap* 10.7.1. The result was a 5-m × 5-m raster grid of interpolated temperatures for each time period (Fig. 2). We used the interpolated soil temperatures to estimate soil temperature at all monitored *P. sclerocarpa* plants that survived to 2017 (211 individuals), at which time all individuals were georeferenced. We continued to track

survivorship of these individuals through 2021 (Fig. 2), noting their mortality. In addition to those that were found dead during the monitoring period, some outplanted individuals (n = 10) were not found in the most recent surveys despite repeated attempts; therefore, they are assumed dead in our analyses.

Analyses

Binomial regression

To test whether variables of soil depth, soil temperature, founder, origin (wild versus outplanted) and percentage cover of surrounding invasive grass (Table 2) affected survivorship from 2017 to 2021, we ran a binomial regression in *R* version 4.0.3 (R Core Team 2020) on the 211 *P. sclerocarpa* that were alive in 2017 and monitored through 2021. We used the *AICcmodavg* (Mazerolle 2016) package to compare corrected Akaike information criterion (AICc) scores of models incorporating different predictor variables and interactions and selected the model with the lowest AICc value (Table S1). The predictor variables from the most parsimonious model were incorporated into the model as independent variables, while the dependent variable was mortality (binary live/dead).

The 211 *P. sclerocarpa* plants consisted of 175 outplanted individuals from 23 unique founders and 36 wild individuals. Soil depth was measured adjacent to 79 of the individuals in 2017 or 2019. Percentage cover was measured for the areas surrounding 72 individuals in 2017 or 2019. A few times, soil depth or percentage cover data for the same individual were measured in both 2017 and 2019; in these cases, measurements were averaged (this happened with soil depth for eight individuals and percentage cover for 23 individuals). A separate model was generated to explore the potential effect of founder identity on outplanted *P. sclerocarpa* survivorship; wild individuals were excluded from the dataset for these models because founder information for wild plants was not known.

Piecewise structural equation modelling

If soil temperatures have a negative effect on both invasive grasses and *P. sclerocarpa* and invasive grasses also have a negative effect on *P. sclerocarpa*, it is possible that the net effect of soil temperature on the endangered species could be negative or positive depending on the relative strengths of the different interactions (Fig. 3). To help disentangle this, we used structural equation modelling to evaluate potential the causal relationships of predictor variables on *P. sclerocarpa* mortality, as well as the interactions between predictor variables. We conducted this analysis in *R* using the package *piecewiseSEM* (Lefcheck 2016) and included the predictor variables from the strongest binomial regression model of *P. sclerocarpa* mortality (invasive grass cover and soil temperature). Because we hypothesized that invasive grass cover and soil temperature would each have a direct negative effect on *P. sclerocarpa* mortality and that soil temperature would also have a direct negative effect on invasive grass cover, we structured the analysis to include *P. sclerocarpa* mortality from 2017 to 2021 as the dependent variable, invasive grass cover as an endogenous variable affecting *P. sclerocarpa* mortality and soil temperature measured in 2019 at 10-cm depth beside 53 individual *P. sclerocarpa* (rather than the interpolated values used in binomial regression) as an exogenous variable affecting both *P. sclerocarpa* mortality and surrounding invasive grass cover (Fig. 3). A generalized linear model formula and Poisson distribution were used.
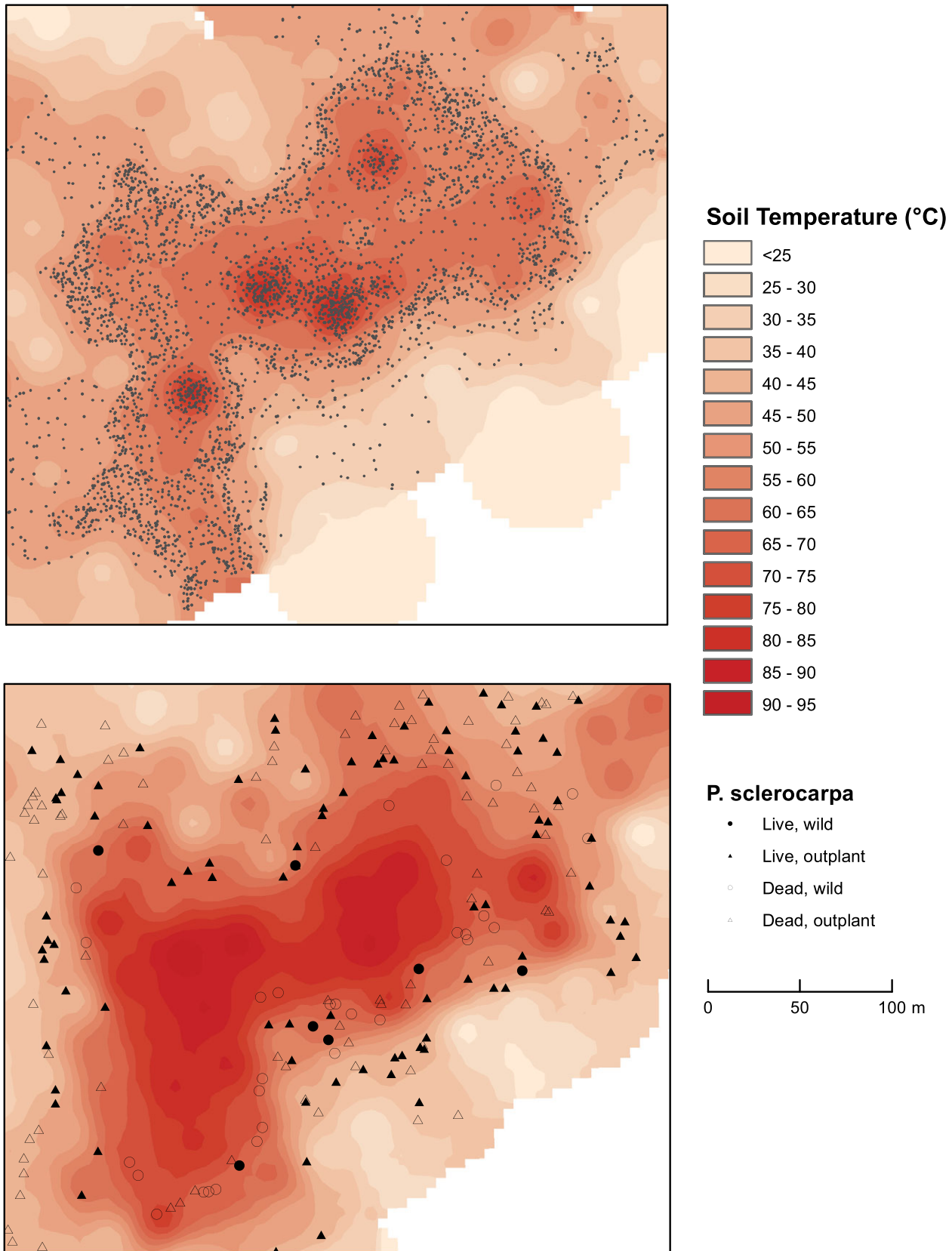
Fig. 2. Soil temperature and *Portulaca sclerocarpa* densities during historical surveys and present day (2019). *Note:* Locations of *P. sclerocarpa* have been randomized within temperature zones to protect the locations of the endangered species. Soil temperatures were interpolated from readings every 30 m taken at (a) 5-cm depth in 1996 and 1998 (McGee et al. 2006) and at (b) 20-cm depth in 2019 (Lewicki et al. 2020). Dots represent (a) naturally occurring *P. sclerocarpa* recorded in 1993 and (b) both naturally occurring and outplanted *P. sclerocarpa* recorded in 2021. Outplanting took place in February 2017 and 2018. In addition to the seven surviving wild individuals represented in (b), we know of six others (recently recruited) in the Puhimau Thermal Area; they are not pictured because their temperature zone has not been determined. Orientation indicators and graticules showing geographical coordinates are deliberately left off the map to protect the locations of the endangered species.

Table 2. Predictor variables. Five predictor variables were considered for model selection for models of *Portulaca sclerocarpa* mortality from 2017 to 2021. A total of 36 wild and 175 outplanted *P. sclerocarpa* were monitored for this analysis.

Variable	Units	Range of values	Date(s) collected
Soil depth	cm	4–27	2017, 2019
Invasive grass cover	%	0–75	2017, 2019, 2020
Interpolated soil temperature (readings at 20 cm)	°C	38.8–77.8	2019
Founder	Categorical	23 founders of outplants (wild plants: no data)	2017
Origin	Categorical	Outplanted, wild	2017

Table 3. Results of binomial regression. Results from the strongest model predicting *Portulaca sclerocarpa* survivorship with 98.42 null deviance on 71 degrees of freedom.

Variable	Estimate	Odds ratio	SE	Z-score	P-value
Temperature	−0.215	0.810	0.066	−3.255	0.001*
Grass cover	−2.23	0.800	0.087	−2.564	0.010*
Temperature × Grass cover	0.004	1.004	0.001	2.684	0.007*

*Significant at the 0.95 level.

Fig. 3. Diagram representing the structural equation model implemented. The model included *Portulaca sclerocarpa* mortality from 2017 to 2021 as the dependent variable, invasive grass cover as an endogenous variable affecting *P. sclerocarpa* mortality and soil temperature as an exogenous variable affecting both invasive grass cover and *P. sclerocarpa* mortality. Photographs: Nathan S Gill, Hawai'i Volcanoes National Park, 2017.

Results

The population abundance of wild *P. sclerocarpa* within the surveyed area of Puhimau decreased sharply over time, from 4322 individuals in 1984, to 970 individuals in 1993, to 13 confirmed living wild individuals as of September 2021 – a 99.7% decline in population size. Six of the 13 remaining wild individuals were newly recruited (and were first reported in 2021; they were not included in the analyses nor in Fig. 2). Of the 175 individuals that were outplanted at Puhimau (from 2017 to 2018), only 89 (50.9%) remained by 2021 (although this is much higher than the 16% survival rate observed 3 years after previous outplanting efforts; Pratt et al. 2011).

Interpolated soil temperatures across the Puhimau Thermal Area ranged from 18.9°C to 86.5°C in the 1990s (measured at 5cm depth) and from 19.3°C to 93.7°C in 2019 (measured at 20cm depth). Soil temperatures at wild *P. sclerocarpa* plants ranged from 30.4°C up to the maximum local temperature of 86.5°C in the 1990s (measured at 5cm depth). Soil temperatures at the locations of wild and outplanted *P. sclerocarpa* plants ranged from 38.8°C to 77.8°C in 2019, and soil temperatures farther away from *P. sclerocarpa* were up to 15.9°C hotter than any soil temperatures recorded in the 1990s, although this is probably due to the difference in the depth at which measurements were taken in different years. No *P. sclerocarpa* survived through 2021 at soil temperatures that were above 70°C in 2019 (Fig. 2 & Table S2). *Portulaca sclerocarpa* survivorship was highest (66.7%) at moderately high soil temperatures, ranging from 60°C to 70°C in 2019 (Fig. 2 & Table S2). Survival rates of the outplantings were also low (25%) in the lowest soil temperature range (<40°C), but these were the same locations where invasive grass cover was highest (>70%; Table S2).

We found the strongest binomial regression model predicting survivorship to include soil temperature, percentage invasive grass cover and their interaction (AICc 86.40; Table S1). The model found that for every degree Celsius increase in soil temperature, the likelihood of survival decreased by 19%. Similarly, for every one unit (percentage cover) increase in grass cover, the likelihood of survival decreased by 20% (Table 3). The model revealed a significant interaction between soil temperature and invasive grass cover (p = 0.007), but this interaction carried little weight, having an odds ratio of 1.004. We did not find an effect of founder on the survival of outplanted individuals (0.148 < p < 0.994 depending on founder with null deviance of 242.55 and 174 degrees of freedom), nor an effect of soil depth (p = 0.114 with null deviance of 102.53 and 73 degrees of freedom). Founder identity and soil depth were not included in the most parsimonious model.

Because soil temperature and invasive grass cover led to the strongest binomial regression model, these two predictor variables were further analysed through structural equation modelling. Soil temperature again exhibited a strong, positive effect on *P. sclerocarpa* survival (critical value 2.3677, p = 0.0179). Invasive grass cover had no detectable, direct effect on *P. sclerocarpa* mortality (critical value −0.9068, p = 0.3645). However, interpolated soil temperature also had a significantly strong, negative relationship with invasive grass cover (critical value −8.3509, p < 0.001), indicating that where soil temperatures were high (e.g., >65°C), invasive grass cover was low (Table 4).
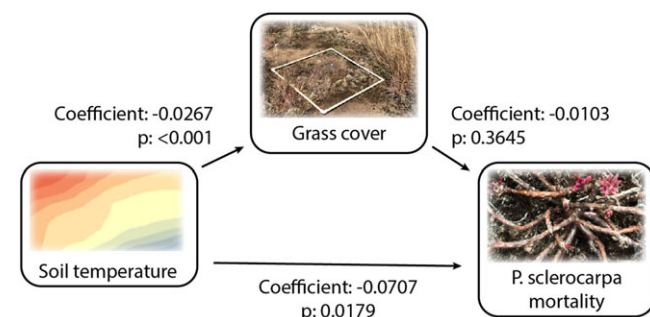
Discussion

The largest remaining population of wild *P. sclerocarpa* is in steep decline, while outplantings at the same site are also experiencing high rates of mortality over short time frames. Our study shows that high soil temperatures due to volcanic heat emissions are the most constraining factor on *P. sclerocarpa* survival from among those considered. *Portulaca sclerocarpa* survival was much higher at cooler soil temperatures, except when surrounded by >70% cover of invasive grasses. We planted *P. sclerocarpa* in very few plots with abundant invasive grass cover, limiting the power of our statistical analyses to quantitatively determine whether the grasses were a significantly limiting factor. Interestingly, soil temperature also had negative effects on invasive grass cover. Finding the 'sweet spot' where soil temperatures are low enough to allow *P. sclerocarpa* survival but high enough to decrease other constraints may increase *P. sclerocarpa* population growth in these

Table 4. Results of structural equation modelling. Soil temperature exhibited a strong, negative effect on *Portulaca sclerocarpa* survivorship, while invasive grass cover did not. Soil temperature also had a significantly strong, negative effect on invasive grass cover. No independence claims were present in the model.

Response	Predictor	Coefficient	SE	DF	Critical value	P-value
P. sclerocarpa survivorship	Soil temperature	−0.0707	0.0299	48	−2.3677	0.0179*
P. sclerocarpa survivorship	Grass cover	−0.0103	0.0113	48	−0.9068	0.3645
Grass cover	Soil temperature	−0.0267	0.0032	49	−8.3509	<0.001*

*Significant at the 0.95 level.
DF = degrees of freedom; SE = standard error.

volcanically active sites. Further research conducting tests in a controlled environment could help confirm and refine this theory.

The current study narrows in on which biophysical factors are important and which ranges of conditions support *P. sclerocarpa*. The lifespan of *P. sclerocarpa* has not been documented, although in this study we have confirmed that individuals have persisted for at least 4 years. The trends observed at Puhimau Thermal Area are reflective of other *P. sclerocarpa* outplanting sites in Hawai'i Volcanoes National Park. The only other naturally occurring population that remains in the Park today has seen high mortality rates but existent (yet slow) recruitment. Although this other population does not experience the elevated ground temperatures and CO_2 emissions that the Puhimau population does, it is adjacent to Kīlauea caldera, which has frequently been the site of eruptions and the associated release of volcanic SO_2 (Elias et al. 2018). The 28 such eruptions over the past century (most recently 1982, 2008–2018, 2020–2021, 2021–present) lasted from <1 day to *c.* 10 years (Macdonald et al. 1983, Kauahikaua & Mulliken 2020, USGS 2020, 2021), each with variably strong degassing over the course of the activity. Prevailing wind conditions in the vicinity predominantly direct volcanic fumes from the caldera away from the site where this second natural *P. sclerocarpa* population is found, indicating that volcanic gases are less likely to negatively affect plants than at sites in the direct path of degassing events. The population adjacent to Kīlauea caldera is also more barren and does not have the same prevalence of invasive grasses as Puhimau, although plant cover and soil temperature surveys near Kīlauea caldera have not been conducted to quantify these differences. Access for conducting surveys of this population has been limited by the nearby volcanic activity.

Although soil temperatures measured in the 1990s cannot be directly compared to the deeper soil temperature measurements of 2019, it is clear that the spatial pattern of soil temperatures at Puhimau Thermal Area has shifted over the last three decades. The locations of the hottest soil temperatures today are different from those in the 1990s, although we do not know how recently or quickly soil temperatures increased, and there may be a lag between these increased soil temperatures and the mortality of the plants. The distribution of *P. sclerocarpa* over the soil temperature gradient has shifted over the last three decades; although the plants used to occupy locations ranging from 19.3°C all the way up to the maximum temperature recorded at Puhimau, *P. sclerocarpa* now achieves >55% survivorship only in a middle temperature range (60–70°C – which is still high compared to soil temperatures without volcanic activity). Some of the plants survive at the low end of the soil temperature spectrum, but these cooler soils are often the same microsites where invasive grass abundance is now high. Our interpretation is that *P. sclerocarpa* may have found a niche where they can escape from other limiting factors in areas where high soil temperatures are intolerable for the grasses, but as volcanic heat emissions have continued to shift, some of these microsite

conditions have become intolerably hot for *P. sclerocarpa* as well. No microsite apparently had soils too hot for *P. sclerocarpa* 30 years ago, but that is no longer the case.

Invasive grass effects on *P. sclerocarpa* may also vary by site or ontogenetically. Prior data from a different site, Kalanaokuaiki Pali, where *P. sclerocarpa* was planted with and without invasive grass, showed no difference in survival but higher growth rates after 1 year when planted with invasive grasses (Pratt et al. 2011). Kalanaokuaiki Pali has higher air temperatures and is somewhat drier than Puhimau, and it is possible that under more stressful conditions grasses could act as nurse plants and facilitate the species via shade (Callaway & Walker 1997, Gill et al. 2020). A study from a geothermal area in Sonoma County, California, found that *Dichanthelium lanuginosum* var. *thermale*, a rare thermophilic grass that needs high soil temperatures to germinate, was also growing in areas with the same invasive grass as found in our study, *A. virginicus* (Pavlik & Enberg 2001). In that case, however, *A. virginicus* could only occupy sites where geothermal activity had lessened, while the native grass thrived on hotter soils. The rare native grass was not in refuge on hot soils (i.e., only being there because there was no invasive competitor) but because the soil facilitated its germination. This underlies why understanding the interacting mechanisms within a system will help predict outcomes for species of concern.

Invasive grasses are not the only non-native plants at the Puhimau Thermal Area. *Portulaca pilosa*, another *Portulaca* species (introduced to Hawai'i from the coastal plains of the southeastern USA), is abundant at Puhimau (based on anecdotal observations), while the population of its relative is in steep decline. Researchers are able to distinguish *P. sclerocarpa* from *P. pilosa* primarily through the colouration of their flowers (white on *P. sclerocarpa* and purple on *P. pilosa*). The impact of the introduced species on *P. sclerocarpa* is unknown (Stone et al. 1994). One possibility that has not been mentioned in the literature or explored through research to date is whether hybridization of the two species may be contributing to the lack of *P. sclerocarpa* recruitment. It is also possible that *P. pilosa* puts competitive pressure on *P. sclerocarpa* if the two species compete for the same niche. This has not been explicitly tested, but the species co-occur throughout Puhimau. However, in our dataset, *P. pilosa* was only present in 17 of 72 quadrats (23.6%) where we measured percentage cover of plant species. When present, *P. pilosa* accounted for an average cover of 4.6% within each quadrat, and its percentage cover or presence/absence was not found to be a significant explanatory variable for *P. sclerocarpa* mortality (p = 0.142 for cover, p = 0.158 for presence). Finally, it is possible that introduced rodents may be eating seed capsules and thus lowering seed set and recruitment (Pratt et al. 2011), as has been shown for other endangered species in Hawai'i (Shiels & Drake 2011, Pender et al. 2013, Gill et al. 2018).

Although invasive species pose threats to native biodiversity (Simberloff 2005), addressing the effect of a single invasion on

its own may have little impact on the recovery of native plants when other stressors are at play (Gill et al. 2018), possibly including other interacting invasive species (Simberloff & Von Holle 1999, D'Antonio et al. 2017, Yelenik et al. 2020, 2022, Gill et al. 2021b). Our findings have refined our understanding of the factors contributing to the success and demise of *P. sclerocarpa*, although other factors may also be at play, such as the influence of *P. pilosa*, possible seed predation by (introduced) small mammals, loss of pollinators or dispersers (Pratt et al. 2011) or a change in soil microbiota or chemistry due to altered plant communities. It is possible that invasive grasses have a direct competitive influence on *P. sclerocarpa* or an indirect effect such as providing habitat for small mammals (which predate *P. sclerocarpa* seeds). Alternatively, they could co-occur with soil microbiota or other (e.g., chemical) properties of the soil substrate that affect *P. sclerocarpa*. Management of valued plant species that are approaching extinction in the wild may benefit from efforts to identify which biophysical factors constrain success while treating multiple threats holistically rather than in isolation (Dávalos et al. 2014, Bernardo et al. 2020, Yelenik et al. 2020). This presents a challenge because scientific enquiry often relies on the isolation of single variables; yet, for example, a study of multiple threats to four rare species in a New York forest found that the single and combined effects of stressors were species-specific (Dávalos et al. 2014). Research that places the influence of isolated variables in the broader context of multiple potential threats can accelerate arrival at a fuller understanding of a threatened species' needs (D'Antonio et al. 2017, Bernardo et al. 2020). Such an approach is important for informed decision-making in the face of extreme environmental change.

Conclusion

Among those environmental conditions we analysed, very high (>70°C) soil temperature was the primary factor associated with high rates of *P. sclerocarpa* mortality. Invasive grass cover was not a significant predictor of mortality, but both invasive grass cover and *P. sclerocarpa* mortality were high in the few plots where soil temperatures were relatively cool. Invasive grasses were also highly constrained by hot soil temperatures. Further research would be useful to determine whether invasive grass cover might be associated with *P. sclerocarpa* mortality directly (e.g., through competition) or indirectly (e.g., microbiome, other soil properties besides temperature, habitat for small mammals), as well as what other factors are limiting *P. sclerocarpa* survival and recruitment in Puhimau Thermal Area and other locations. Until further information is determined, we expect that *P. sclerocarpa* planted in soil temperatures ranging from 60°C to 70°C (measured at 20 cm deep) will have the highest rate of survival. These soils appear cool enough to allow for moderate *P. sclerocarpa* success while also being hot enough to limit invasive grass cover (or other unidentified factors limiting *P. sclerocarpa* survival at the fringes of the geothermal area). Although it would represent a great work, it would be useful for additional research of imperilled plant recovery to consider both thresholds of tolerance and interactions of constraints. Although plant extinctions are accelerating in the face of multiple threats around the globe, this study demonstrates how the monitoring and analysis of population declines and the fates of outplants can reveal important hierarchies and relationships between plant species of concern and multiple (potentially interacting) environmental stressors.

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