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Mapping habitat suitability for at-risk plant species and its implications for restoration and reintroduction

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Abstract. The conservation of species at risk of extinction requires data to support decisions at landscape to regional scales. There is a need for information that can assist with locating suitable habitats in fragmented and degraded landscapes to aid the reintroduction of at-risk plant species. In addition, desiccation and water stress can be significant barriers to the success of at-risk plant reintroduction programs. We examine how airborne light detection and ranging (LiDAR) data can be used to model microtopographic features that reduce water stress and increase resource availability, providing information for landscape planning that can increase the success of reintroduction efforts for a dryland landscape in Hawaii. We developed a topographic habitat-suitability model (HSM) from LiDAR data that identifies topographic depressions that are protected from prevailing winds (high-suitability sites) and contrasts them with ridges and other exposed areas (low-suitability sites). We tested in the field whether high-suitability sites had microclimatic conditions that indicated better-quality habitat compared to low-suitability sites, whether plant-response traits indicated better growing conditions in high-suitability sites, whether the locations of individuals of existing at-risk plant species corresponded with our habitat-suitability classes, and whether the survival of planted individuals of a common native species was greater in high-suitability, compared to low-suitability, planting sites. Mean wind speed in a high-suitability field site was over five times lower than in a low-suitability site, and soil moisture and leaf wetness were greater, indicating less stress and greater resource availability in high-suitability areas. Plant height and leaf nutrient content were greater in high-suitability areas. Six at-risk species showed associations with high-suitability areas. The survival of planted individuals was less variable among high-suitability plots. These results suggest that plant establishment and survival is associated with the habitat conditions identified by our model. The HSM can improve the survival of planted individuals, reduce the cost of restoration and reintroduction programs through targeted management activities in high-suitability areas, and expand the ability of managers to make landscape-scale decisions regarding land-use, land acquisition, and species recovery.

Key words: *dryland; endangered; LiDAR; microtopography; outplant; threatened species; water stress.*

Introduction

The conservation of species at risk of extinction requires the ability to make decisions at landscape to regional scales. Restoring habitat, managing biological invasions, and mitigating other risks to sensitive populations all depend on the capacity to observe characteristics of ecosystems throughout large areas and make management decisions across the geographic range of threatened populations. In many cases, a lack of appropriate data at large scales limits the ability to make decisions in a landscape or regional context.

Traditionally, remote sensing has provided useful data for large-scale decision making and planning, such as land-use land-cover mapping from Landsat satellite imagery (Turner et al. 2003). More recently, remote sensing has achieved the high spatial resolution and physical accuracy needed to model smaller habitat

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features important for many organisms (e.g., individual trees, microtopography of stream channels [Lefsky et al. 2002, Turner et al. 2003, Vierling et al. 2008, Bergen et al. 2009]). Recent developments in airborne light detection and ranging (LiDAR) enable measurements of topography and the three-dimensional structure of vegetation at high spatial resolution and throughout large areas. Typical applications of these data to conservation problems include the use of three-dimensional vegetation structure data to understand forest structure and the habitat requirements of wildlife species (Dubayah et al. 2000, Lefsky et al. 2002, Turner et al. 2003, Vierling et al. 2008, Hudak et al. 2009). LiDAR-derived topographic data are less commonly used in conservation, and have been most often applied to mapping habitat suitability for aquatic species in wetlands and river channels (Jones 2006, James et al. 2007, Hogg and Holland 2008, McKean et al. 2008, Knight et al. 2009). Here, we use topographic measurements from airborne LiDAR to examine habitat suitability for 11 species of threatened and endangered plants on the Island of Hawaii.

A lack of suitable habitat is the major barrier to the recovery of the more than 100 000 plant species thought to be at risk of extinction (Pitman and Jorgensen 2002, Godefroid et al. 2011, Maschinski and Haskins 2012). The two primary conservation actions for these species are to restore suitable habitat areas so that extant populations can expand and to reintroduce individuals to restored or protected areas. The success rates of reintroduction projects are variable, and low success is often due to a lack of suitable habitat, the very cause of decline (Godefroid et al. 2011, Drayton and Primack 2012). Thus, a major challenge to reintroduction success is finding suitable habitats in fragmented and degraded landscapes.

Habitat quality and microsite conditions are key drivers of plant establishment, growth, survival, and population persistence in reintroduction projects (Bottin et al. 2007, Godefroid et al. 2011, Kaye 2011, Maschinski and Haskins 2012). In particular, microclimatic conditions influence early life stages of germination and establishment, which are the most critical life history phases for regeneration, i.e., the *regeneration niche* (Grubb 1977, Maschinski et al. 2012). For example, local topography influences solar radiation, soil water retention, and temperature that alter where plants can regenerate and persist.

Identifying the optimal conditions for regeneration and survival is especially important in arid or seasonal ecosystems, where water availability limits plant growth (Guerrant 2012). Desiccation, one of the primary barriers to the successful establishment of reintroduced plants, is common in these ecosystems (Helenurm 1998, Godefroid et al. 2011). Over 40% of all at-risk plant species occur in dry or rocky habitats where low water availability is a barrier to recovery (Kew Royal Botanic Gardens 2010), including the highly endangered drylands where we work in Hawaii (Dobson et al. 1997). Reintroduction programs have had limited success in many drylands due to a low probability of establishment and high levels of plant mortality (e.g., Cordell et al. 2008). Often planting areas are arbitrarily or opportunistically selected without consideration of microclimatic gradients. Thus, identifying areas with high-quality conditions for reintroduction can significantly improve plant survival and reproduction (Bottin et al. 2007, Godefroid et al. 2011, Maschinski et al. 2012).

We propose that, in dryland ecosystems, topography may be an important landscape feature for reintroduction planning, and planting activities may have the greatest success in topographic depressions where soil and water accumulate and where plants are protected from desiccating winds. Topographic lowlands typically have greater soil depth, organic matter, and water availability compared with uplands (e.g., Abrams et al. 1986, Knapp et al. 1993, Burke et al. 1999, Nippert et al. 2011), leading to greater plant heights and annual net primary productivity in lowlands, where soil conditions are more favorable for plant growth (Knapp et al. 1993, Nippert et al. 2011). In drylands, topographic position affected the survival of an endangered plant species and the success of native plant restoration by reducing stressful conditions (Biederman and Whisenant 2011, Nicole et al. 2011, Simmons et al. 2011).

However, knowledge of the importance of microtopography for plant growth and survival has not been formally incorporated into landscape planning for restoration or the management of at-risk species. In fact, the spatial resolution of most readily available topographic data is too coarse to model microtopographic features that could be used for restoration and reintroduction. Here, we develop topographic models from LiDAR data as a powerful tool for enhancing landscape planning for native restoration and at-risk plant species reintroduction. We identified habitat suitability for restoration and reintroduction on the basis of topography for a 49 000-ha dryland landscape in Hawaii. Our habitat-suitability models identify topographic depressions that are protected from prevailing winds (high-suitability sites) and contrast them with ridges and other exposed areas (low-suitability sites). First, we test whether sites predicted to have high suitability harbor conditions that are high-quality habitat for at-risk plant species. Second, we test whether wild populations of at-risk plant species were more likely to occur in areas designated as high suitability compared to areas designated as low suitability. Third, we test whether our suitability designations (low vs. high) predicted survival of a reintroduced common native species. We show that our habitat-suitability model has the potential to increase the survival and performance of reintroduced native and at-risk species, to reduce variability among reintroduction sites, and is likely to be a critical landscape-level planning tool to assist the recovery of species in dryland ecosystems.

Methods

Study area

We developed a topographic habitat-suitability model (HSM) for the Pohakuloa Training Area (PTA) in Hawaii, USA. PTA covers over 49 000 ha of a subalpine region between three volcanoes on the Island of Hawaii (1300–2600 m elevation). Mean annual precipitation is low (<400 mm) and soils are poorly developed due to recent deposition of substrates from volcanic sources (Rhodes and Lockwood 1995). Fifteen federally listed threatened and endangered plant species occur at PTA, and several of these species only exist in the wild at this site (Shaw 1997).

High-resolution surface cover mapping

The Carnegie Airborne Observatory (CAO) Beta system was used to map PTA on 7 January 2008 (Asner et al. 2007). The CAO-Beta instrument package included a small-footprint, high-power LiDAR scanner that mapped the position and elevation of the ground surface and vegetation. The LiDAR sub-system was configured to record the locations of up to four reflecting surfaces for every emitted laser pulse at 1.1-m laser spot spacing. Horizontal and vertical accuracy of the LiDAR system were provided by Asner et al. (2007), and are ~15 cm. To quantify ground elevation, LiDAR ranging measurements were processed to identify laser pulses that penetrated vegetation and reached the ground surface. These points were then used to model the elevation of the ground (DEM) at 2.2-m spot sampling distance.

Topographic-suitability modeling

We used the DEM to create our two criteria variables for classifying the suitability of areas for plant reintroduction. The criteria were (1) the descending or ascending quality of the site and (2) the degree of protection from prevailing winds. We distinguished descending and ascending local topography by subtracting DEM values from the mean within an ~50-m window (23 pixels) centered on each focal pixel. If elevation within a given pixel is greater than the window's mean, the focal location has a positive value and is ascending. A location has a negative value and is descending if the focal pixel is less than the mean. We classified negative values as suitable.

We used long-term records of monthly diurnal wind direction from remote automatic weather stations at PTA (National Interagency Fire Center; data *available online*)[10] to quantify exposure to prevailing winds and found that the prevailing wind direction was 67.5°. Next, we used shaded relief modeling to calculate the degree of exposure of each pixel in the DEM to prevailing wind patterns. Shaded relief is typically used to simulate the appearance of natural light on a DEM from a defined azimuth and elevation above the horizon. We used a 3 × 3 pixel window, an azimuth of 67.5°, and an elevation of 6° to emulate the degree of exposure to prevailing winds. When applied to the azimuth of wind direction, the resultant image has pixels with brightness values ranging continuously from 0 to 1. Areas that are protected from prevailing winds have low brightness, and areas that are directly exposed have high brightness. We classified pixels with values less than 0.05 as suitable.

We created binary raster layers on the basis of each criterion with a score of 1 if the condition was true and a score of 0 if false. The binary criteria layers were combined to develop a map of our HSM with three suitability classes: no criteria met (pixel value = 0; low suitability, LS), one criterion met (pixel value = 1; moderate suitability, MS), and both criteria met (pixel value = 2; high suitability, HS). Field observations confirmed that areas coded as high suitability typically corresponded with leeward topographic depressions, and areas with low suitability corresponded with ridges and areas with exposure to prevailing winds.

Microclimate conditions of suitability classes

We explored microclimate differences among suitability classes by delineating six pairs of HS and LS plots in an open *Dodonaea viscosa* shrubland habitat at PTA. We used the HSM and a GPS-enabled tablet PC to find plots in the field that were identified as HS and LS. HS and LS plots were paired together by proximity (<300 m) to control for geographic variability. One pair of plots was 30 × 230 m per plot and was designated for intensive measurements of wind speed, air temperature, relative humidity, and soil moisture. We installed a weather station in March 2010 in each plot that logged measurements of air temperature, relative humidity, and wind speed every minute (Onset Computer Corporation, Pocasset, Massachusetts, USA). We established three permanent sampling areas across each plot for measuring soil water potential every four to six weeks in each subplot from November 2010 to August 2011 using soil psychrometers (Wescor, Logan, Utah, USA). We lacked replication for statistical analysis of these intensive measurements and display the results graphically.

We used the remaining five pairs of plots, which were 8 × 45 m each, for more extensive sampling of leaf wetness and soil nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^3). We installed four Decagon leaf wetness sensors and one data logger in the center of each plot, placing sensors in randomly selected compass directions (Decagon Devices, Pullman, Washington, USA). The data logger recorded measurements every 10 minutes from 28 June 2011 to 31 January 2012. We collected two soil samples from each plot in late August/early September 2011, collected 5 m in from opposite sides of a central transect, for analysis of inorganic nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}). NO_3^- and NH_4^+ samples were

[10] http://www.wrcc.dri.edu/cgi-bin/rawMAIN.pl?hiHPTA

extracted with a 2.0 mol/L KCl solution and sent for analysis at the University of Hawaii-Hilo (UHH) Analytical Lab (Hilo, Hawaii, USA) with a Pulse Autoanalyzer III with Autosampler IV (Pulse Instrumentation, Saskatoon, Saskatchewan, Canada). PO_4^{3-} samples were air-dried for at least 48 hours and sent to Brookside Laboratories (New Knoxville, Ohio, USA) for analysis with the Bray I test. We analyzed differences among suitability classes in soil nutrients with a paired samples Wilcoxon signed ranks test performed in SPSS 20 (IBM 2011).

Plant functional traits across suitability classes

We measured plant functional traits associated with plant growth and performance (plant height, specific leaf area, and leaf nutrients) of five common plant species in the open *Dodonaea* shrubland ecosystem: native shrubs *D. viscosa* and *Chenopodium oahuense*; native C_4 grass *Eragrostis atropioides*; nonnative, invasive C_4 grass, *Pennisetum setaceum*; and nonnative, invasive forb, *Senecio madagascariensis*. Functional trait measurements were taken from five healthy adult individuals of each species in each of the 10 paired 8 × 45 m plots that were designated for extensive sampling (see *Microclimate conditions of suitability classes*) from 16 June to 14 July 2011.

We measured plant height by recording the distance between the base of the plant and the top of the youngest fully expanded leaf. Specific leaf area (SLA, cm^2/g) was measured using standard methods on three relatively young, but fully expanded leaves per plant (Cornelissen et al. 2003). We collected 20 relatively young, but fully expanded leaves per plant for nutrient analyses of N (N_{leaf}), P (P_{leaf}), and C (C_{leaf}). Samples were oven-dried for at least 48 hours at a constant temperature of 70°C, ground with a Wig-L-Bug (Crescent, Elgin, Illinois, USA) and sent to UHH Analytical Lab for analysis. N_{leaf} and C_{leaf} were determined through combustion on a Costech 4010 elemental combustion system (Costech Analytical Technologies, Valencia, California, USA). P_{leaf} was determined by dry ashing (500°C for 5 h) of ~0.25g of sample and re-suspending in 0.5 mol/L HCl, followed by measurement of P concentrations on a Varian Vista MPX ICP OES (Agilent Technologies, Palo Alto, California, USA).

We analyzed differences in functional trait measures with a general linear model (GLM) that included a random blocking term for each pair of plots, species as a random factor, suitability class as a fixed factor, and the species × suitability interaction term. SLA data were log-transformed to improve normality and homogeneity of variance. If the species × suitability class interaction term was significant, we used a Tukey posthoc test to compare differences among suitability class within each species. GLM analyses were performed in Minitab 15 (Minitab 2007).

Distribution of threatened and endangered populations across suitability classes

We used randomization tests to evaluate how the location of existing threatened and endangered plants corresponded with our HSM for 11 threatened and endangered species. The randomization tests evaluated whether the observed locations of individuals from each population were different from a null distribution of 10 000 simulated populations. The location data for the analysis were recorded by the Center for Environmental Management of Military Lands (CEMML). In 2007, CEMML began annual surveys of existing threatened and endangered plant populations at PTA to record GPS locations for individual plants for monitoring purposes. Staff walked parallel transects through high-priority habitat and recorded locations of plants with Garmin GPS 72 units (Garmin, Olathe, Kansas, USA). They used the average function on the GPS to maximize spatial accuracy and recorded the number of plants at each location. Each year, new plant locations were added to the database and plant locations were removed if the plants there were confirmed to be dead. Species with small populations of several hundred individuals or fewer were comprehensively censused each year by recording the fate of all known individuals and recording new recruits. The result of this monitoring effort was a GIS shape file showing the known locations of individuals of all species surveyed with a high level of spatial accuracy.

We evaluated whether the location of existing threatened and endangered plants corresponded with our HSM for 11 threatened and endangered species. We used the GIS layers from the CEMML surveys updated through 2009. In addition, we obtained GIS shape files based on climate envelope modeling of the hypothesized geographic distribution of each species (Price et al. 2007). We used randomization tests to evaluate whether the observed locations of individuals from each population were different from a null distribution based on complete spatial randomness. We did this by generating 10 000 simulated populations for each species. Each simulated population contained the same number of plants as the population census for that species and was constrained by the geographic distribution of the species at PTA determined through climate envelope modeling (Price et al. 2007). This analysis allowed us to determine if a species was associated with higher or lower class values, independent of broader scale climate and substrate effects, which we controlled for by using the climate envelope for each species. At each iteration of the simulation, we extracted the topographic-suitability index value from the location of each simulated individual (LS = 0, MS = 1, HS = 2). We compared the mean suitability class value across all known plant locations with the distribution of mean values from the simulated populations. If the mean of known plants falls outside the 95% confidence interval, there is an

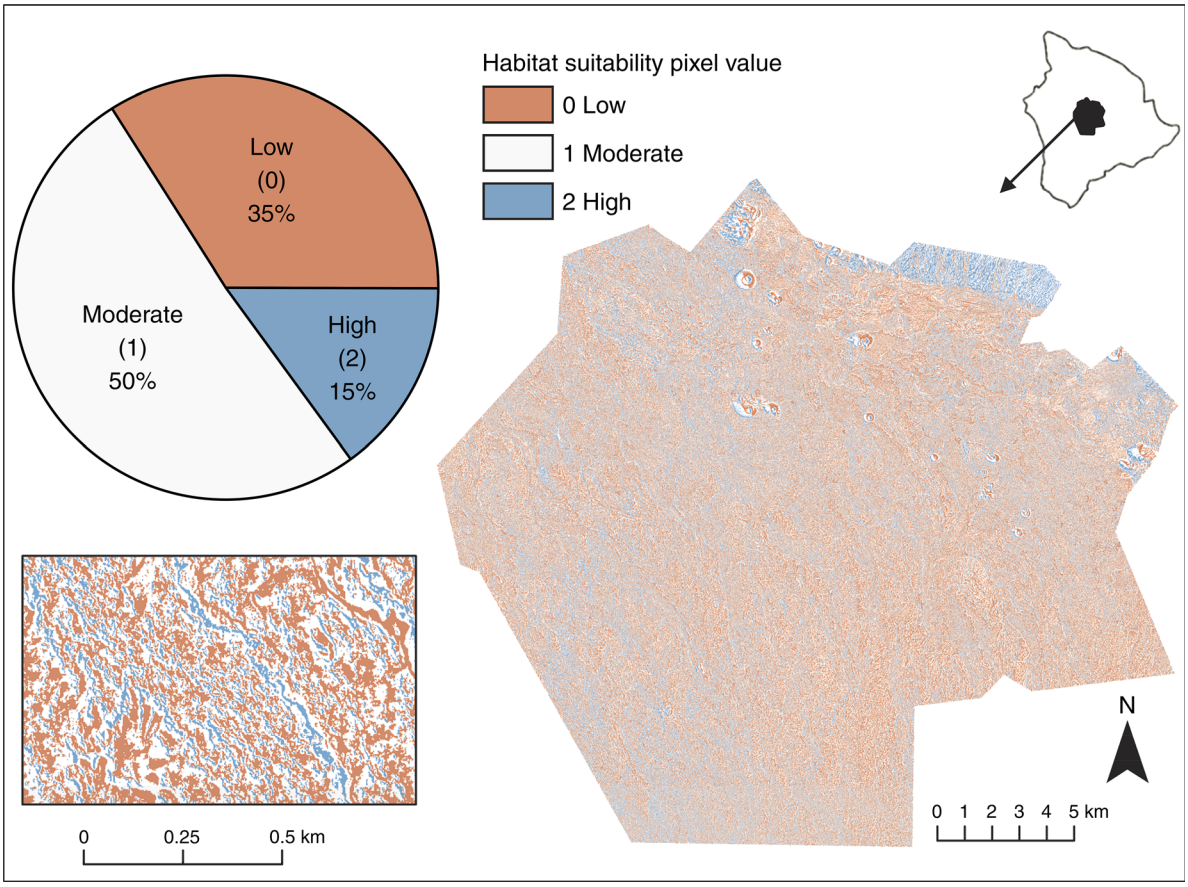

FIG. 1. Habitat-suitability model map for Pohakuloa Training Area (PTA), Hawaii, USA. PTA is located on Hawaii Island and is 49 000 ha in size (inset). We based habitat-suitability classes on descending local topography and protection from prevailing winds to model areas with the optimal conditions for plant growth and survival. Pixel values are integers ranging from 0 (low suitability) to 2 (high suitability). The pie chart shows that 35% of the landscape of PTA had pixel values of 0, 50% had pixel values of 1, and 15% had pixel values of 2. The inset in the lower left shows a closer view of an area within PTA and illustrates a typical distribution pattern of the suitability classes at this site.

association of the species with either higher or lower suitability sites.

CEMML also manages a reintroduction program for threatened and endangered plant species at PTA and maintains a GIS layer of areas that represent each planting site. We overlaid this GIS layer over our HSM to examine the habitat-suitability values of existing planting sites.

Survival of common native outplants across suitability classes

We began a preliminary study in order to determine if habitat suitability affects the outcome of planting efforts. We used seed collected from our field site to propagate and plant seedlings of *D. viscosa*, a common native shrub, in three HS and three LS areas. The 4.5 × 4.5 m planting areas were located in the pair of sampling plots designated for intensive measurements (see *Microclimate conditions of suitability classes*) and were separated by at least 10 m. We planted 20 equally spaced individuals in a grid in each area on 4 and 5 April 2011. We recorded the survival of all plants in Summer 2011 (13 July 2011), Fall 2011 (29 September and 12 October 2011), and Winter 2012 (16, 21, and 23 February 2012). Because of our limited sample size, we analyzed the data separately for each sampling period with a *t* test in Minitab 16 that compared the proportion of plants surviving in HS and LS areas (Minitab 2010). In order to test whether higher habitat suitability reduced variability in survival among plots, we calculated the coefficient of variation (CV) of survival among the three plots in each suitability class in each sampling period (i.e., one CV for each suitability class from each date, $n = 3$ plots). We used a paired *t* test to compare the CVs between HS and LS plots.

RESULTS

The landscape of PTA had 35% of its area in LS (pixel value = 0), 50% in MS (pixel value = 1), and 15% in HS (pixel value = 2). The class value of all pixels was 0.80 ± 0.01 (mean ± SE), indicating overall low habitat suitability as defined by our model (Fig. 1). The

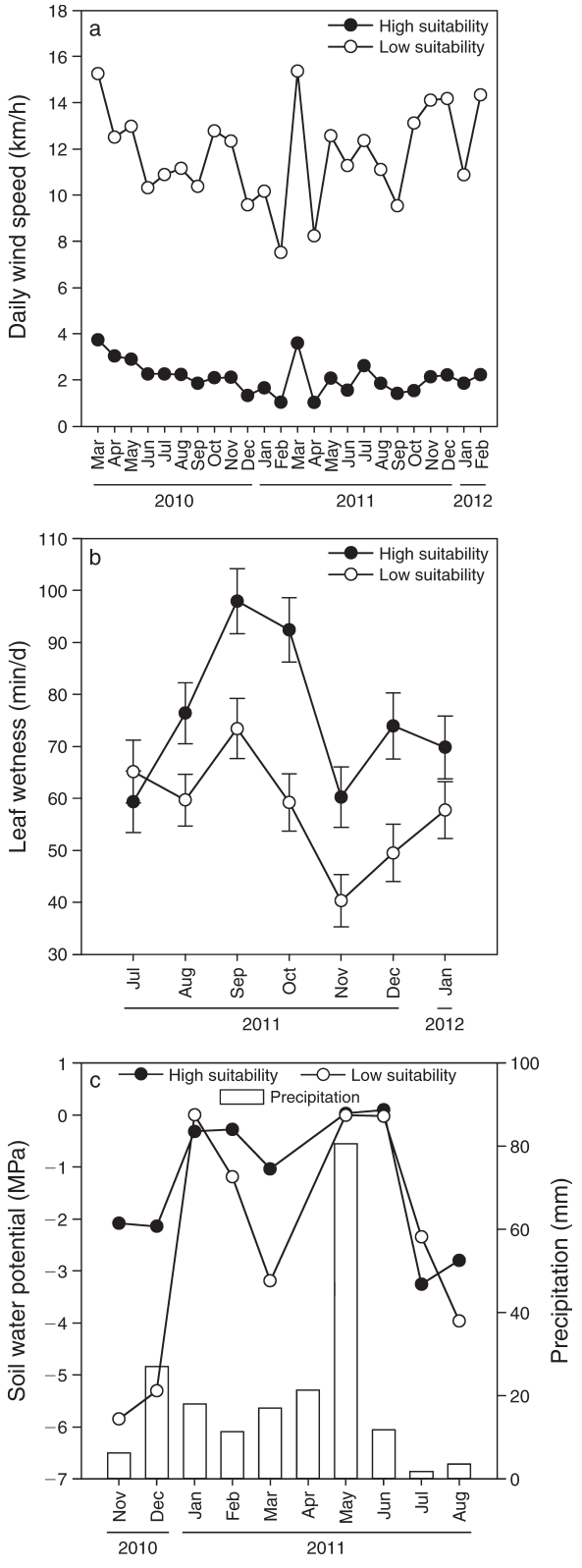

FIG. 2. Microclimate conditions in high- and low-suitability areas. (a) Average daily wind speeds were higher and more variable in the low-suitability, compared to the high-suitability, plot. In both plots, average wind speeds were highest in May and November and lowest in February. (b) The number of minutes per day with measurable leaf wetness was higher in high-suitability relative to low-suitability plots. Values are means ± SE. Leaf wetness differences between the suitability classes were greatest in October during the onset of winter rains and the least in July during the dry season, where leaf wetness was almost identical between the classes. Leaf wetness was highest in the early morning and evening hours with almost negligible leaf wetness measured in both sites between the hours of 08:00 and 14:00. (c) Soil water potential (MPa) was generally higher in the high-suitability, compared to the low-suitability, plot. Each point is a mean of three permanent sampling locations. More negative values indicate drier soil conditions. Bars show total monthly precipitation measured at the site.

distribution of classes was similar across substrates of different ages, and HS areas exist across the landscape. The areas currently used by land managers for threatened and endangered species reintroduction had a median pixel value of one and mean pixel value of 0.82. This mean pixel value is similar to the mean of all pixels, indicating that locations used for current reintroductions are not statistically different from a random sample of the landscape.

Microclimate

Our analysis of microclimatic data indicated differences between suitability classes in conditions that can influence plant growth and performance, with LS sites consistently windier (Fig. 2a), drier (Fig. 2b, c), and relatively deprived of nutrients. Wind speed in the LS plot was over five times higher than in the HS plot (11.8 ± 0.4 and 2.1 ± 0.1 km/h, respectively; Fig. 2a). Similarly, maximum gust speed in the LS plot was 66.4 ± 1.8 km/h compared to 38.7 ± 1.8 km/h in the HS plot. The number of minutes per day with measurable leaf wetness was higher in HS plots (76 ± 5.6 min) relative to LS plots (58 ± 4.0 min; Fig. 2b). The LS plot had more negative water potentials for six of the seven dates measured, indicating less water available to plants. The differences between classes were especially large during dry periods (Fig. 2c). Soil nutrient results were consistent with higher-quality soil conditions in HS, compared to LS, plots. Values for NO_3^- (HS, 18.43 ± 11.29 μg/g dry soil; LS, 13.77 ± 7.34 μg/g dry soil), NH_4^+ (HS, 5.09 ± 1.78 μg/g dry soil; LS, 4.64 ± 1.12 μg/g dry soil), and PO_4^{3-} (HS, 24.4 ± 7.16 ppm; LS, 12.7 ± 2.45 ppm) were higher in HS, compared to LS plots. However, differences between classes were not statistically significant ($P > 0.5$).

Plant functional traits

The difference in plant height between suitability classes was greatest for the native shrub *D. viscosa* (significant suitability class × species interaction; Table 1, Fig. 3a). *D. viscosa* shrubs in HS plots were more than 50% taller than shrubs in LS plots (Fig. 3a). Specific leaf area (SLA) varied among species, but not among HS and LS plots (Table 1).

TABLE 1. Test statistic (F) and significance (P) are reported for general linear models of plant functional traits.

	Block			Species			Suitability class			Suitability class × species			
Plant trait	F	df	P	F	df	P	F	df	P	F	df	P	R^2
Plant Height	7.67	4, 231	***	8.05	4, 231	*	3.02	1, 231	0.157	10.19	4, 231	***	0.654
ln(SLA)	1.01	4, 260	0.404	63.50	4, 260	***	0.00	1, 260	0.977	0.95	4, 260	0.435	0.519
Leaf N	4.72	4, 229	***	13.60	4, 229	*	11.31†	1, 229	*	5.17	4, 229	***	0.634
Leaf P	11.45	4, 229	***	174.99	4, 229	***	178.71†	1, 229	***	0.09	4, 229	0.986	0.359
Leaf C	8.17	4, 229	***	120.97	4, 229	***	0.05	1, 229	0.828	2.40	4, 229	0.051	0.844

* $P < 0.05$; ** $P < 0.01$; *** $P \leq 0.001$.

† The significant suitability class effect for leaf N and P indicates higher nutrient content in high suitability, compared with low suitability, plots.

N_{leaf} was greater in HS than in LS plots for all species (significant suitability class effect; Table 1; Fig. 3b), but the proportional differences among classes varied among species (significant suitability class × species interaction; Table 1, Fig. 3b). The native shrub *C. oahuense* had the highest N_{leaf} among all species in both HS and LS plots, and had greater N_{leaf} in HS plots (Fig. 3b). The invasive forb *S. madagascariensis* also had a large difference in N_{leaf} between classes (Fig. 3b). N_{leaf} did not differ significantly among classes for the other species measured ($P \geq 0.05$; Fig. 3b).

P_{leaf} was greater in HS plots (0.107% ± 0.004%) than in LS plots (0.090% ± 0.003%) among all species (significant suitability class effect; Table 1), differed among species, and there was not a significant suitability class × species interaction. Most of the variation in C_{leaf} was explained by differences among species (significant species main effect; Table 1).

Association of threatened and endangered species

We found significant associations between the location of plants and habitat-suitability classes for eight of the 11 species we analyzed. Six species were associated

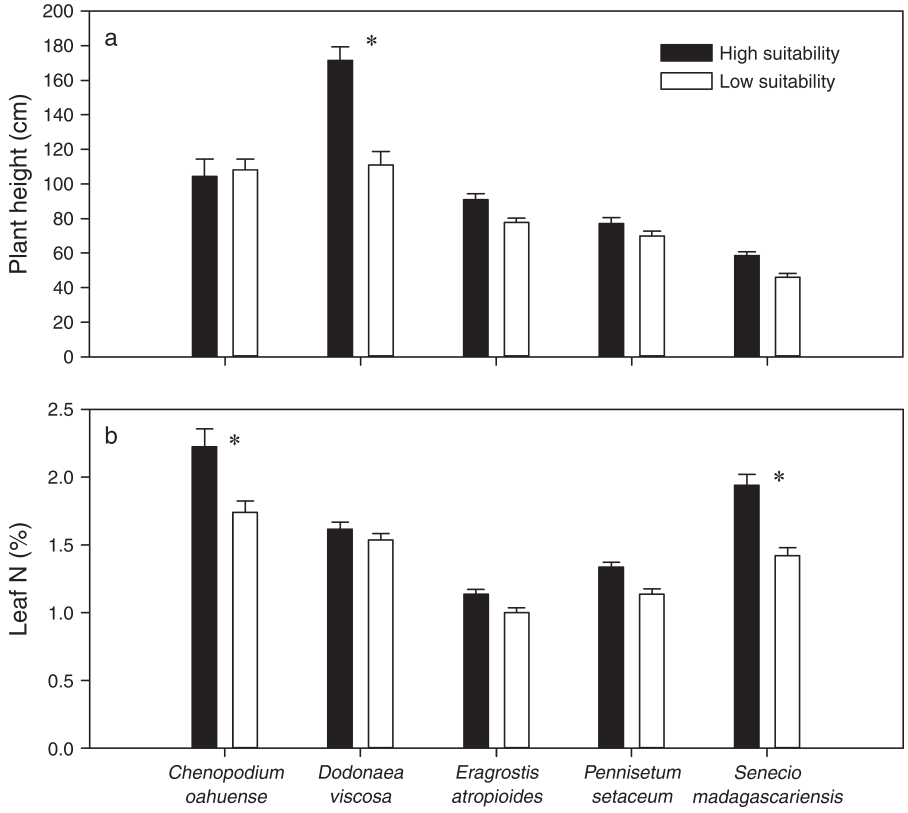

FIG. 3. Plant functional traits of dominant species among suitability classes. Species are native shrubs *C. oahuense* and *D. viscosa*, native grass *E. atropioides*, invasive grass *P. setaceum*, and invasive forb *S. madagascariensis*. (a) Plant height and (b) leaf N varied among species and among suitability classes. Asterisks indicate significant differences among suitability classes within each species (Tukey test, $P < 0.05$). Error bars show +SE.

TABLE 2. Results of habitat-suitability analysis for existing at-risk species.

Species	Number of individuals	Suitability value of known plants	95% CI of suitability values from simulated populations	Direction of habitat association
Haplostachys haplostachya	11 373	0.9719	0.7542–0.7759	higher*
Hedyotis coriacea	175	0.7257	0.6743–0.8457	no association
Neraudia ovata	41	0.2927	0.5122–0.8537	lower*
Portulaca sclerocarpa	65	0.7231	0.5846–0.8615	no association
Silene hawaiiensis	2 730	0.8048	0.7498–0.7938	higher*
Silene lanceolata	14 607	0.9393	0.7406–0.7594	higher*
Solanum incompletum	154	1.0260	0.6558–0.8377	higher*
Spermolepis hawaiiensis	5 367	0.7593	0.7339–0.7650	no association
Stenogyne angustifolia	2 533	1.1283	0.7165–0.7619	higher*
Tetramolopium arenarium	871	0.5465	0.6349–0.7118	lower*
Zanthoxylum hawaiiense	619	0.7868	0.6801–0.7738	higher*

Notes: We report the mean suitability class value across all known plant points and the 95% confidence interval (CI) of the mean suitability class values of 10 000 simulated populations. All species are listed by the US Fish and Wildlife Service as endangered except *Silene hawaiiensis*, which is listed as threatened. Six species showed an association with higher valued classes, and two species showed an association with lower valued classes. Three species did not show an association.

* $P < 0.05$ for association of the species with either higher or lower classes.

with higher valued classes, and two species were associated with lower valued classes (Table 2). The density of all threatened and endangered plants increased with habitat suitability (Fig. 4).

Native outplant survival

There was a trend toward a higher proportion of surviving planted *D. viscosa* in HS plots, compared to LS plots, in July 2011 (HS, 0.93 ± 0.04; LS, 0.78 ± 0.10; one-tailed t test, $t = 1.36$, $P = 0.15$), Fall 2011 (HS, 0.85 ± 0.06; LS, 0.57 ± 0.20; one-tailed t test, $t = 1.33$, $P = 0.16$), and Spring 2012 (HS, 0.80 ± 0.08; LS, 0.57 ± 0.20; one-tailed t test, $t = 1.07$, $P = 0.20$). The CV of survival averaged over all dates was significantly lower in HS (0.12 ± 0.02), compared to LS (0.49 ± 0.13) plots (paired t test, $t = 3.22$, $P = 0.04$).

DISCUSSION

Our approach of spatially modeling topographic habitat suitability can inform plant reintroduction and restoration programs in dryland ecosystems. The high spatial resolution of our data made it possible to model topographic features that are important to the establishment and growth of small, low-statured plants; and the extensive nature of remote sensing data allow for large-scale analysis useful for planning at the landscape level. Further, our field analysis of the HSM provided several lines of evidence that support its use to guide restoration and reintroduction programs. High-suitability habitats had (1) more favorable microclimate conditions important for regeneration, (2) plants that showed greater growth and resource capture through measured functional traits, and (3) lower variability in survival rates of planted *D. viscosa* seedlings. The HSM can improve restoration success by guiding planting activities to areas of the landscape with favorable microclimates that reduce plant stress and decrease variability in survival among planting locations.

Water stress is the primary barrier to plant growth and survival in this and other dryland ecosystems, and the sites that we identified as high suitability had microclimatic conditions associated with reduced water stress. Annual precipitation is low (<400 mm) and the porous volcanic substrate does not store water for long periods following rain. In addition, wind speeds are high with gusts typically from 60 to 90 km/h, which create conditions of high evaporative demand for plants. During several periods, soil moisture and leaf wetness of high-suitability areas were greater than low-suitability areas. Periods of higher leaf wetness are possibly associated with moisture inputs from fog, which can be a significant source of water during dry conditions (Dawson 1998, Liu et al. 2004, 2010). The dramatic decline in wind speeds in the high-suitability site may be one of the most effective ways our model can reduce water loss through transpiration (Fig. 2a). This reduc-

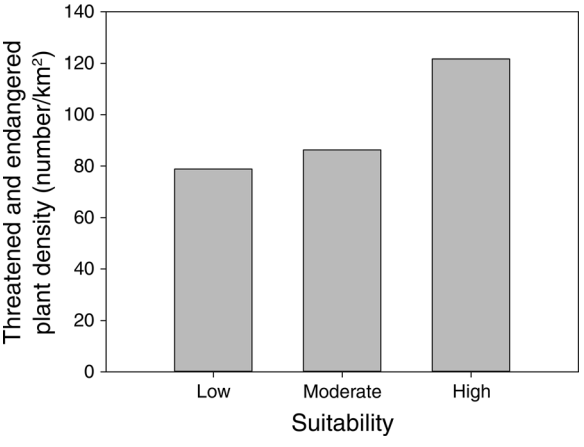

FIG. 4. Density of threatened and endangered plants in each topographic-suitability class. Data are total number of federally listed threatened and endangered plants recorded at PTA divided by the total area of each suitability class at PTA.

tion in transpiration stress may be why other studies have found higher restoration and reintroduction success on the leeward sides of topographic features (Pipoly et al. 2006, Biederman and Whisenant 2011, Simmons et al. 2011). We can significantly reduce wind-related water stress by using the HSM to position reintroduced plants in highly suitable sites that are protected from prevailing winds by existing topographic features.

Our analyses of plant responses to the HSM further support the use of this approach to guide reintroduction efforts. The functional traits of plants we measured in the field indicated that high-suitability sites support greater plant growth and performance. Plant functional traits represent the evolved attributes of species, ecologically driven trade-offs, and the effect of species on ecosystem processes (Lavorel and Garnier 2002). They are often measured to indicate differences in life-history trade-offs among species (e.g., competition–colonization trade-offs between growth and seed size); however, they may also indicate responses to environmental gradients (Lavorel and Garnier 2002, McGill et al. 2006). We observed greater N_{leaf} and P_{leaf} averaged over all species in high-suitability, compared with low-suitability, sites, which may reflect higher soil nutrient availability. The height of three species was greater in high-suitability, compared with low-suitability, sites, suggesting that these species have greater resource acquisition and productivity in high-suitability areas (Weiher et al. 1999). Six of the existing populations of threatened and endangered plant species had individuals that were associated with higher-suitability sites, and more threatened and endangered plants occurred in high-suitability areas (Fig. 4). The preliminary results from our experimental planting of *D. viscosa* seedlings showed less variability in survival of planted individuals among plots in high-suitability areas and a trend toward greater survival in high-suitability sites. Together, these results provide strong support for using the HSM to guide plant restoration and reintroduction efforts.

Management implications

LiDAR is an important tool for mapping habitat suitability for at-risk species. Its high spatial resolution (i.e., small ground sampling distance) allows for mapping small features of the landscape that are important to many organisms (e.g., soil depressions, heterogeneity of forest canopy structure). The large spatial extent of remote sensing data provides insight across significant portions of the range of many species and generates data useful for conservation decisions at landscape scales. Most applications of LiDAR in this manner use data of vegetation structure to map habitat quality for terrestrial wildlife species or to understand forest stand structure more generally (Dubayah et al. 2000, Lefsky et al. 2002, Turner et al. 2003, Vierling et al. 2008, Hudak et al. 2009).

The most similar LiDAR analysis to our study linked the species richness of a tropical forest community to terrain elevation and curvature (Wolf et al. 2012). Species richness was greater at lower elevations and in concave, compared to convex, terrain features (Wolf et al. 2012). These features generally indicate areas with greater soil moisture in this ecosystem (Daws et al. 2002), suggesting that plant diversity was greater in areas with greater soil moisture. This finding is in accordance with our results of greater soil water potential and plant resource acquisition in topographic depressions.

Several studies have used LiDAR topographic data to model three-dimensional features in aquatic ecosystems (Jones 2006, James et al. 2007, Hogg and Holland 2008, Knight et al. 2009). Jones (2006) used LiDAR topography and orthoimagery to model habitat suitability for salmon restoration planning and concluded that the cost of restoration projects could be reduced by using their data to identify suitable areas and minimize the need for field inspections. Our habitat-suitability model (HSM) can also be used in a similar way to minimize costs of plant reintroduction projects. In addition, our study is the first to our knowledge to employ LiDAR in the context of native plant restoration.

The HSM can redefine habitat restoration and at-risk plant reintroduction programs by providing a set of quantitative, spatially explicit tools to increase the success of planting efforts. Variability in survival rates among planting sites is currently a major challenge to reintroduction projects, including those at our study site (Godefroid et al. 2011). The significant reduction in variability (lower CV) that we observed in the survival of *D. viscosa* outplants and the trend toward greater overall survival in high-suitability areas supports the use of the HSM to overcome this challenge. *D. viscosa* is the most commonly used native species in habitat restoration plantings due to its importance as a dominant species in this ecosystem, its capacity to grow fairly quickly, and its ability to withstand some fires. Thus, we are optimistic that our HSM can improve the success of native habitat restoration activities.

The current survival rate of threatened and endangered outplants at PTA is highly variable among species and sites (15–73%; K. Kawakami, *unpublished data*). Outplanting sites at PTA are arbitrarily selected, and had relatively low suitability values. We expect an increase in survival if our HSM technology is employed; however it is not yet clear how broadly we can apply this HSM across species. The two herbaceous species we tested (*Portulaca sclerocarpa* and *Spermolepis hawaiiensis*) did not show an association with our habitat-suitability classes. The six species that were associated with higher-suitability areas are perennial woody plants. It is possible that the HSM will be most useful for reintroduction activities for woody species, but further study is needed to determine how individual species will respond. However, an increase in survival of any species

that results from using the HSM would help reduce the costs of reintroduction programs.

An additional benefit of the HSM is the improved ability to make management decisions at landscape scales. The management of at-risk species in most ecosystems is extremely expensive and labor intensive. Management activities such as fire suppression, removal of nonnative herbivores, and control of invasive plant species are often more expensive to maintain than planting programs because they require a large up-front investment of labor and materials and constant maintenance. Management is also challenging in areas like PTA that are large and difficult to access due to having few roads, rough terrain, and military training activities. The HSM can be used to select regions of the landscape with a large amount of high-suitability habitat for intensive, expensive, management activities. It can also help managers identify nearby parcels for acquisition or conservation easements that may have a high value for threatened and endangered species recovery and mitigation activities. Therefore, this tool will be especially effective in regions that are difficult to access due to their remote location or lack of infrastructure.

We believe this modeling approach will be useful in many other areas, especially in other dryland ecosystems. However, a DEM with high spatial resolution ($\leq$2.5 m) is necessary for modeling fine-scale microtopographic features that are important for plant growth. Our DEM was derived from airborne LiDAR measurements from the CAO, which are not widely available, and the cost of airborne LiDAR data acquisition can be limiting. Satellite data sources now exist that that may provide some degree of precision for mapping topography at high resolution (1–5 m). Stereographic DEMs from satellites such as WorldView-2 are globally available, so they can be used to generate HSMs anywhere in the world. Sensors flown on lightweight unmanned aerial vehicles could also provide a cost-effective method to generate DEMs with high spatial resolution (Anderson and Gaston 2013). As these technologies develop and become cost effective, they offer the possibility of expanding the HSM tool to other regions with active reintroduction programs.

We are excited by the potential to use the HSM in other critical conservation areas. We have explored numerous lines of evidence that all support our initial hypothesis that topographic depressions that are protected from wind are more favorable habitats for plant growth and regeneration. Our study is unique in that we combine a remote modeling approach with extensive field measurements of microclimate conditions and plant functional traits, and a planting experiment. The HSM should be field validated in a similar way if it is used in other locations, and we hope that if other managers adopt this approach, recovery efforts for at-risk plant species will have greater success.

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