Received: 17 August 2021 | Revised: 17 March 2022 | Accepted: 18 March 2022

DOI: 10.1002/eap.2690

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

The role of microtopography and resident species in post-disturbance recovery of arid habitats in Hawai‘i

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Funding information
Department of Defense; National Science Foundation (NSF)

Handling Editor: Elisabeth Huber-Sannwald

Abstract

Habitat-suitability indices (HSI) have been employed in restoration to identify optimal sites for planting native species. Often, HSI are based on abiotic variables and do not include biotic interactions, even though similar abiotic conditions can favor both native and nonnative species. Biotic interactions such as competition may be especially important in invader-dominated habitats because invasive species often have fast growth rates and can exploit resources quickly. In this study, we test the utility of an HSI of microtopography derived from airborne LiDAR to predict post-disturbance recovery and native planting success in native shrub-dominated and nonnative, invasive grass-dominated dryland habitats in Hawai‘i. The HSI uses high-resolution digital terrain models to classify sites' microtopography as high, medium, or low suitability, based on wind exposure and topographic position. We used a split-plot before-after-control-impact design to implement a disturbance experiment within native shrub (*Dodonaea viscosa*) and nonnative, invasive grass (*Cenchrus clandestinus*)-dominated ecosystems across three microtopography categories. In contrast to previous studies using the same HSI, we found that microtopography was a poor predictor of pre-disturbance conditions for soil nutrients, organic matter content, or foliar C:N, within both *Dodonaea* and *Cenchrus* vegetation types. In invader-dominated *Cenchrus* plots, microtopography helped predict cover, but not as expected (i.e., highest cover would be in high-suitability plots): *D. viscosa* had the greatest cover in low-suitability and *C. clandestinus* had the greatest cover in medium-suitability plots. Similarly, in native-dominated *Dodonaea* plots, microtopography was a poor predictor of *D. viscosa*, *C. clandestinus*, and total plant cover. Although we found some evidence that microtopography helped inform post-disturbance plant recovery of *D. viscosa* and total plant cover, vegetation type was a more important predictor. Important for considering the success of plantings, percent cover of *D. viscosa* decreased while percent cover of *C. clandestinus* increased within both vegetation types 20 months after disturbance. Our results are evidence that HSIs based on topographic features may prove most useful for choosing planting sites in harsh habitats or those

already dominated by native species. In more productive habitats, competition from resident species may offset any benefits gained from "better" suitability sites.

KEYWORDS
Cenchrus clandestinus, degraded habitats, disturbance, *Dodonaea viscosa*, grassland, Hawai'i, invasive species, plant competition, restoration, shrubland, soil resources

INTRODUCTION

Topography affects resources across the landscape and this can be important for plant dynamics (Ettema & Wardle, 2002; Nippert et al., 2011). The depth and composition of soil can change based on slope position because organic matter may naturally increase at the bottom of a slope due to erosion and gravity, leading to higher nutrient content and greater water-holding capacity (Dwyer & Merriam, 1981; Schimel et al., 1985). Similarly, topography can influence wind exposure, thus soil moisture (Questad et al., 2014), and a plant's position relative to dominant winds can factor into evaporation and plant stress (Defossé et al., 1997; Ma et al., 2004). Indeed, various studies have found that topographic position can lead to differential plant growth and resource uptake, including greater foliar nutrient concentrations (Abrams et al., 1986; Knapp et al., 1993; Questad et al., 2014). For these reasons, it has been suggested that topographic position can play a large role in restoration success, particularly in arid environments (Defossé et al., 1997; Ma et al., 2004; Questad et al., 2014).

Complications with using topographic indices to guide restoration, however, may arise because topographic positions that benefit native species may also benefit undesired and highly competitive nonnative, invasive species (Huston, 2004; Levine, 2000; Yelenik et al., 2017). How soil resources ultimately affect restoration depends on the relative benefit gained from resources by native versus undesired invasive species (here, we define invasive species as nonnative species that are likely to cause economic and/or environmental harm) and whether or not previously established invaders exert competitive suppression (i.e., priority effects). For example, higher soil moisture in topographic depressions will benefit newly colonizing or planted native species if the existing dominant species obtain less benefit from moist soil than the target native plant (Blumenthal et al., 2003; Corbin & D'Antonio, 2004). In cases where the undesired, established invasive species obtain greater relative benefit from resources, the priority effects of resident invasive species may need to be reduced enough to release the target natives (Fukami, 2015; Hess et al., 2019; Young et al., 2005). Testing the response of an array of native and invasive species to topographic characteristics while manipulating the priority effects of the established invaders will help elucidate the importance of considering topography prior to native species restoration.

Disturbances, which are common in degraded habitats (e.g., grazing, fire, military training), as well as restoration programs that clear invasive species, can disrupt priority effects and make resources temporarily available (Davis et al., 2000). An increase in resource availability immediately following a disturbance may allow native species enough time to recover in the face of simultaneously recovering invasive species especially if natives are planted at larger size classes than seedlings in order to give them a competitive advantage (D'Antonio et al., 2017; Young et al., 2005). The strength of priority effects can also be influenced by resource availability (Kardol et al., 2013), leading to interactions between native recovery and microsite topography. In more resource-rich environments, for example, new species may have shorter windows to successfully colonize open sites after disturbance (Symons & Arnott, 2014), making probability of native survival lower. As such, clearing invasive species may not be enough to successfully increase dominance of native species during restoration projects in resource-rich microsites (D'Antonio et al., 2017).

We explore how microsite topography affects native and invasive species recovery and native species outplant success following disturbance in native-dominated and invader-dominated habitats. We used a habitat-suitability classification index that was based on microsite topography, previously developed to delineate suitable planting sites for rare and endangered species in drylands on Hawai'i Island (Questad et al., 2014). This non-species-specific index makes use of high-resolution LiDAR (light detection and ranging) to classify the suitability of microsites based on wind exposure and topography, both of which can alter resource availability and plant water relations. Hereafter, we use the term "microtopography" to refer to this specific combination of wind exposure and topography. Questad et al. (2014) found that high habitat-suitability sites had lower wind speeds and maintained higher soil moisture and higher leaf wetness than low-suitability sites within native *Dodonea*-dominated shrublands of Hawai'i. They used this approach to develop

a microtopographic habitat-suitability index (HSI) to aid restoration efforts and to guide planting of native threatened and endangered species. Notably, they found that high-suitability sites resulted in taller native outplants with greater leaf nutrient content and improved survivorship of native outplants. Their study, however, did not explicitly incorporate biotic interactions into the HSI, primarily because it was a very arid environment with patchy resident vegetation into which managers were planting threatened and endangered species. In a more productive habitat, however, it is possible that high-suitability sites could benefit other species, leading to a negative, competitive effect on planted native species.

Our goal was to ask whether the Questad et al. (2014) habitat-suitability index predicted site characteristics (e.g., soil moisture and nutrients) and native plant performance when there was a resident community. We evaluated the utility of the Questad et al. (2014) HSI within native *Dodonaea viscosa*-dominated vegetation type, as well as an invasive *Cenchrus clandestinus*-dominated vegetation type, both of which are common within high-elevation dryland habitats of Hawai'i. *Dodonaea viscosa*-dominated plant communities tend to be more patchy (more open spaces), suggesting that competitive interactions are less likely to shape community dynamics than *C. clandestinus*-dominated plant communities, which tend to have continuous cover. *Cenchrus clandestinus* and other invasive grasses have also been shown to reduce recruitment, survival, and growth of native Hawaiian woody species, including *D. viscosa* (Denslow et al., 2006; McDaniel & Ostertag, 2010; Yelenik et al., 2022), leading us to hypothesize that biotic interactions would be important to consider with the HSI to predict restoration outcomes in this habitat. In addition, we evaluated the ability of the Quested et al. (2014) HSI to predict post-disturbance plant regrowth and native outplant success within habitats dominated by invasive and native plants.

Following Questad et al. (2014), we hypothesized that high-suitability plots would have greater resources available to plants than medium- and low-suitability plots. In addition, we hypothesized that recovery of naturally recruiting or planted native species in a *D. viscosa*-dominated plant community would be greatest in high-suitability sites. We also hypothesized, however, that invasive *C. clandestinus*-dominated sites would have the greatest recovery of the invasive grass, which can resprout from rhizomes and favors high-nutrient sites (Colman & O'Neill, 1978), in high-suitability sites, leading to competitive interactions and low recruitment and lower survivorship and growth of outplanted native species.

Specifically, we ask (1) Does the Questad et al. (2014) HSI microtopography index correlate with plant growth, soil moisture, soil nitrogen, and foliar nitrogen levels within native and invader-dominated habitats prior to disturbance? (2) Does microtopography influence post-disturbance plant recovery within native and/or invader-dominated habitats? And (3) does microtopography influence native outplant survival within native- and/or invader-dominated habitats?

METHODS

Study area

We conducted this study within the The Keʻāmuku Maneuver Area (KMA), a 9227-ha parcel that was added to the Army Pōhakuloa Training Area (PTA) on Hawai'i Island in 2006. Prior to its acquisition, this property was owned by the Parker Ranch since ~1847, but cattle grazing may have started earlier (Bergin, 2004). The property was purchased by the military, and cattle grazing was phased out in 2009. Since that time, portions of the parcel have been grazed by introduced feral ungulates such as domestic goats (*Capra aegagrus hircus*) domestic sheep (*Ovis aries*), mouflon sheep (*O. orientalis*), and their hybrid (Army Garrison-Hawaii, 2010). Ungulates were not excluded from the study area, but in general are in low abundance within the military area due to active hunting. We did not observe any direct ungulate damage during the experiment.

In general, the KMA is a dry landscape that is prone to stochastic heavy rainfall events (Kellner et al., 2011). It consists primarily of nonnative, invasive perennial grasslands dominated by *Cenchrus clandestinus* (kikuyu grass), *C. setaceus* (fountain grass), *C. ciliaris* (buffel grass), or *Melinis repens* (Natal redtop grass) with some scattered native shrublands (dominated by *Dodonaea viscosa* but also includes native shrub *Sida fallax*) and native grassland (dominated by the perennial *Erogrostis atropioides*) areas. The noxious pasture weed *Senecio madagascariensis* can be found throughout the area. Non-disturbed "reference communities" are not available in this arid landscape, but recent evidence points to later successional communities being a mix of native shrubs and grasses dominated by *D. viscosa* and *E. atropioides* with scattered trees (Kinney et al., 2015).

Underlying substrates are volcanic Andisols (Medial, amorphic, isothermic Humic Haplustands), ranging from 11,000 to 64,000 years old on Laupahoehoe lava flows (Sherrod et al., 2007). Our experimental plots were in areas dominated by the invasive grass *C. clandestinus* or the native shrub *D. viscosa* that were relatively close together (within ~17 km). Henceforth, we refer to *C. clandestinus*- and *D. viscosa*-dominated plots as

vegetation types and refer to them as "*Cenchrus* plots" and "*Dodonaea* plots," respectively, as shorthand terms that include all of the species in the plots. Mean annual temperatures were similar (though statistically different) between the *Cenchrus* (14.8°C + 0.23; mean ± SE) and *Dodonaea* (14.1°C + 0.06) plots. Mean annual rainfall was slightly higher in *Cenchrus* plots (mean ± SE for $n = 5$ plots: 612.5 ± 11.38 mm year^{-1}) than *Dodonaea* plots ($n = 5$ plots: 576.36 ± 1.72 mm year^{-1}) plots (Giambelluca et al., 2013). *Dodonaea* plots were ~150–200 mm year^{-1} wetter in terms of rainfall than sites used by Quested et al. (2014), whose habitat-suitability model we base this study on, with some similarity in species composition.

Habitat suitability index (HSI) and microtopography

To explore the relationship between microtopography and restoration success we used a similar approach to that outlined in Questad et al. (2014). We generated the KMA HSI (Appendix S1: Figure S1) using measurements from airborne LiDAR acquired by the National Center for Airborne Laser Mapping (NCALM, Houston, TX). We produced a 1-m resolution Digital Terrain Model (DTM), where each pixel represents a 1 × 1 m area, and classified microtopography by analysis of the DTM based on two modeling criteria that were developed and tested at PTA (Questad et al., 2014). Leeward position quantifies the degree to which a given location is protected from prevailing winds. Descending topography characterizes local depressions where soil and water can accumulate.

We used shaded-relief modeling to calculate the degree of exposure of each pixel in the DTM to prevailing wind patterns. Shaded relief is typically used to simulate the appearance of natural light on a DTM from a user-defined azimuth and elevation above the horizon. Computing shaded-relief models for sunlight requires knowing the direction of the sun, and the elevation above the horizon of the sun. Using shaded relief to model wind patterns requires the input of the same parameters. We used the direction of prevailing winds (110.5°) as the direction parameter and a low elevation (6°) for the elevation parameter. Low elevation values approximate the wind blowing over the ground surface. When applied to the azimuth of wind direction, the resultant image has pixels with brightness values ranging continuously from 0 to 1. There is low brightness in areas that are protected from prevailing winds and high brightness in areas that are directly exposed. Values <0.05 were classified as suitable.

Descending topography describes an area that is lower than the average elevation of areas in its local neighborhood (e.g., in a depression), whereas ascending topography describes an area that is higher (e.g., on top of a ridge). We distinguished descending and ascending topography by subtracting DTM values from the mean within the local neighborhood of a focal pixel. We set the neighborhood size to a 20-m radius window 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. Negative values were classified 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 microtopography map with three "suitability" categories: no criteria met (pixel value = 0; "low suitability"), one criterion met (pixel value = 1; "medium suitability"), and both criteria met (pixel value = 2; "high suitability"). In other words, the HSI output is categorizing pixels as one of three categories (0, 1, or 2). Field observations confirmed that areas coded as high suitability corresponded with leeward topographic depressions and areas with low suitability were ridges and areas with high wind exposure.

This microtopography map (Appendix S1: Figure S1), generated from the KMA digital terrain model, provided a high-resolution map of areas with topographic depressions that also provided protection from the wind across the study area and can be indicative of favorable conditions for native plant restoration (Questad et al., 2014). According to the microtopography index, the KMA landscape contained 51% low-suitability, 19% medium-suitability, and 30% high-suitability habitats.

Plant communities, soils, and disturbance recovery rates

We used a split-plot BACI (before, after, control, impact) design to implement a disturbance experiment across the three microtopography categories defined by the HSI. We established one 20 × 10 m plot in each of the three microtopography suitability classes (low, medium, and high) for both the native *Dodonaea* and the invasive *Cenchrus* vegetation types, at five replicate sites each. This approach led to a total of 30 plots (15 *Dodonaea* plots and 15 *Cenchrus* plots). Plots were chosen to be at least 100 m apart and in areas with comparatively high percent cover of the target vegetation type (by observation). The *Dodonaea* and *Cenchrus* vegetation types were spatially distinct from each other, but all sites fell within 17 km of each other.

To ask if microtopography correlates with soil resources and plant nutrient status we collected plant

foliar and soil samples in June 2014. For plant foliar samples, newly expanded leaves of the focal species (*D. viscosa* and *C. clandestinus*) were collected within each plot. Foliar samples were taken from three different plants, evenly spaced across the 200-m^2 plots. Leaves were bulked for each plot, dried at 70°C for at least 48 h, ground with a Wiley Mill, and sent to the University of Hawai'i at Hilo (UHH) Analytical Lab for percent carbon and nitrogen analysis (Costech Elemental Analyzer). A 4 cm diameter × 10 cm depth soil core was used to collect three soil samples, which were bulked per plot. Cores were taken at roughly regular intervals across the 200-m^2 plot under the focal species. Samples were air dried and sieved to 2 mm, at which point a subsample was ground and sent to the UHH Analytical Lab for percent carbon and nitrogen analysis (Costech Elemental Analyzer). Remaining soil samples were used to determine percent organic matter (OM) by mass lost via combustion at 500°C for 24 h.

Prior to initiating a disturbance, we also quantified percent cover of vegetation and substrate using a point-intercept method (Mueller-Dombois & Ellenberg, 1974). Two transects spanning the 20-m length of each plot were placed at regular intervals (starting at 3 and 7 m along the 10 m long edge) and a point-frame was used to drop pins every 20 cm along each transect. The first plant species encountered was recorded and the total number of "hits" for that species was divided by the total number of possible points along the two transects (200) to give an estimate of percent cover. Substrate (soil, litter, rock) was recorded if no plants were encountered and we lumped these into "bare ground" for analyses. We also lumped herbaceous legume species, which included *Medicago lupulina*, *Medicago polymorpha*, *Melilotus alba*, *Melilotus indica*, and *Trifolium* species as their cover was low and they are in the same functional group. In addition, we counted the number of *D. viscosa* and *Sida fallax* individuals, both of which are early successional, native woody shrubs likely to be found in disturbances, within each plot and binned them into four height categories (0–0.5, >0.5–1, >1–2, >2 m). Initial percent cover and shrub count data were acquired in June 2014.

In July 2014, we randomly selected one 10 × 10 m half of each 20 × 10 m plot to be disturbed (Appendix S1: Figure S2). The front-end loader of a Bobcat was used to move vegetation and a fine layer of topsoil. Debris was left inside of the treatment subplot. There were often scattered, remnant live shrub stems or grass roots that resprouted, although this seemed more common for *C. clandestinus* than *D. viscosa*. Following the disturbance, we re-established the two initial 20-m transects for use during all subsequent monitoring. While pre-disturbance percent cover monitoring was done using point-intercept sampling only, post-disturbance monitoring included a combination of point-intercept and quadrat sampling. Point-intercept sampling was done in July 2014 prior to disturbance, and again in March 2016, to complete the BACI sampling design. Quadrat sampling was conducted during all post-disturbance sampling efforts, but not prior to disturbance.

We monitored vegetation response to disturbance within 10 × 10 m treatment subplots every 4–5 months from October 2014 through March 2016. This monitoring was done by placing 1-m^2 quadrats at four regularly spaced intervals along each of the transects used to collect point-intercept cover data. Quadrat sampling was conducted in order to capture a time series of fine scale seedling dynamics that would not be captured with point-intercept data. Percent cover of all species within each quadrat was estimated independently by two observers and averaged. Total cover of all species and substrates summed to 100% within each quadrat.

In addition to point-intercept and quadrat sampling, we counted all shrubs, including recently established individuals, within each plot during all visits (pre- and post-disturbance) and assigned each to one of five height categories (0–5, 5–10, 10–30, 30–100, >100 cm). Shrub and seedling density were quantified for *D. viscosa* and *S. fallax* within each plot during all visits.

Finally, we monitored post-disturbance soil moisture at 5- and 20-cm depths every hour over 653 consecutive days using soil moisture sensors (Meter Group 10HS, Pullman, WA) and a data logger (Meter Group EM50, Pullman, WA). We monitored soil moisture in all disturbed and undisturbed *Dodonaea* and *Cenchrus* sites at two suitability levels (high and low). We chose high- and low-suitability plots because previous data suggest that these would be the most different suitability levels for plants over time (Questad et al., 2014).

Native species outplanting

To test whether microtopography and disturbance altered the success of native restoration plantings, we used two species that are common within the area: the native shrub *D. viscosa* and the native perennial bunchgrass *E. atropioides*. We chose these species because they were dominant in different parts of KMA, and we were interested in whether species with similar life history traits (*E. atropioides*), versus different life history traits (*D. viscosa*), would be more or less likely to survive in invasive grass (*C. clandestinus*)-dominated areas.

Seeds were collected close to planting sites and germinated in Sunshine Mix #4 (SunGro Horticulture, Agawam, MA) at a greenhouse facility of the USDA

Forest Service in Hilo, Hawai'i. Once seedlings were established, they were transferred to 7-cm diameter, 25-cm deep seedling tubes with the same soil mix and allowed to grow for 6 months. Seedlings had roots extending the length of the tubes at the time of outplanting. We planted five seedlings of each species (*D. viscosa* and *E. atropioides*) in each of our disturbed and undisturbed plots in October 2014. These were watered twice a week for 1 month to ensure transplant success, and thereafter were not watered. Outplant survivorship was assessed in November 2014, February, June, and November 2015, and March 2016.

Statistical analyses

To determine whether initial foliar and soil properties differed across vegetation types and microtopography index values, we used an information theoretic criterion (AIC) approach to evaluate four models for each foliar and soil property (foliar carbon to nitrogen ratio, soil percent organic matter (OM), percent soil moisture, soil carbon to nitrogen ratio). For each soil property, we developed three linear models incorporating the effects of (1) vegetation type, (2) microtopography index value, (3) the additive effects of vegetation type and microtopography. All models were optimized using maximum likelihood and assumed the response variable had a Gaussian distribution, consistent with the continuous nature of the measurements for each soil property. For each soil property, the three models were evaluated against a null model, which did not incorporate any covariates. Models with lower AIC values than the null model provide a more parsimonious explanation of the response variable. The larger the difference between AIC values, the more important an explanatory variable would be. All analyses were conducted in R (R Core Team, 2020). Models were developed using the lme4 package (Bates et al., 2015), and AIC model evaluations were conducted using the AICcmodavg package (Mazerolle, 2016).

In order to ask how continuously monitored soil moisture varied across microsites, vegetation types, and disturbance regimes, we developed linear mixed models using soil moisture as a response variable. *Dodonaea*- and *Cenchrus*-dominated plots were considered independently, and models were developed for the effects of microtopography, disturbance, and their additive effects. All models included nested random effects of time and plot, to account for the temporal nature of continuous soil moisture monitoring, as well as any plot specific variation. These four models were then compared to a null model using AIC and model-averaged parameter estimates were deemed significant in the direction of their sign when 95% confidence intervals (CI) did not overlap zero. This was done for both wet and dry periods within *Dodonaea* and *Cenchrus* dominated plots. Dry is the default climate condition in this region so we chose a rainfall threshold to determine wet periods. A day was included in the analysis of the "wet" period if there was at least 10 mm of precipitation in the previous 4 days, while days with <10 mm of precipitation during that time were included in the "dry" period analyses. To facilitate modeling, we randomly selected 100 soil moisture readings from wet and from dry periods within each subplot.

Next, we asked whether pre-disturbance percent cover of dominant species (native shrub *D. viscosa* or invasive grass *C. clandestinus*) as well as total plant cover differed as a function of microtopography. To do this, we developed linear mixed models for percent cover of all plants (TotalPlantCover), as well as percent cover of native *D. viscosa* and invasive *C. clandestinus*. To account for the spatial association of 10 × 10 m subplots (ultimately paired control and treatment subplots), we models incorporated a fixed effect of microtopography and a random effect of plot for each response variable. Parameters were deemed significant according to the sign if 95% Wald CI did not overlap zero.

We also developed linear models to ask whether pre-disturbance native shrub seeedling density (*D. viscosa* and *S. fallax*) varied as a function of microtopography within the *Dodonaea* and *Cenchrus* vegetation types. Native shrub seedlings were quantified as the number of shrubs of each species that were ≤100 cm tall. Prior to disturbance, shrub counts were conducted across each plot, without regard to control and treatment subplots, and counts were converted to density (stems per m^2) prior to being used as a response variable in linear models to identify the effect of HSI. Parameters were deemed significant according to the sign if 95% Wald CI did not overlap zero.

To understand the relative importance of microtopography and vegetation type for plant recovery, we quantified the change in cover that was due to disturbance by subtracting the change in percent cover within control sites from the change in cover within disturbed sites $[(\text{Disturbed}_{\text{AFTER}} - \text{Disturbed}_{\text{BEFORE}}) - (\text{Control}_{\text{AFTER}} - \text{Control}_{\text{BEFORE}})]$. As such, the resulting "relative change in cover" was indicative of the effect that disturbance had on disturbed plots relative to control plots. This BACI analysis of "relative change in cover" was conducted using the point-intercept data collected during the initial pretreatment site visits in June 2014 and the final posttreatment visits in March 2016. A negative relative change in cover is evidence that disturbance

resulted in less cover in disturbed plots than was found within the control plots, while a positive change in cover suggests an increase within disturbed plots relative to paired control plots. The relative change in cover was calculated for total plant cover and percent cover of both the native *D. viscosa* and the invasive *C. clandestinus* within each vegetation type. Each of these response variables was used to develop a set of four (generalized linear models) glms, wherein we compared the relative effects of biotic (vegetation type), abiotic (microtopography), and their additive effects (mixed: vegetation type +- microtopography), with a null model using AIC. We used the same approach to ask if changes in the number of native *D. viscosa* and *S. fallax* shrubs (≤100 cm tall) could be explained by vegetation type and/or as a function of microtopography.

While we quantified percent cover within each plot using the two different methods (point-intercept sampling and quadrat sampling; see *Plant communities, soils, and disturbance recovery rates* for more details), these metrics were not combined for any of the analyses presented herein. Because the point-intercept sampling data were collected during the pre-disturbance visit, as well as the final post-disturbance visit, these estimates were used for all BACI analyses. The quadrat sampling data were only collected during post-disturbance sampling visits and were used for an observational picture of post-disturbance cover over time (Appendix S1: Figures S3 and S4).

To explore the effects of microtopography and vegetation type on outplant survival, we used survivorship analysis (glm with exponential distribution, and a log link estimation method, JMP 10 software) to analyze survivorship of seedlings planted in different vegetation types. The two native seedling species (*D. viscosa* and *E. atropioides*) were analyzed separately with vegetation type, microtopography, and disturbance as model effects.

RESULTS

Microtopography and pre-disturbance conditions

We predicted that plots with high-suitability microtopography would have greater resources available to plants than medium- and low-suitability plots. In contrast to our prediction, the top model for foliar C:N included vegetation type, but not microsite (Tables 1 and 2). While foliar C:N was greater within *D. viscosa* leaves than it was in those of *C. clandestinus* within their respective plots, soil C:N values were similar across vegetation types leading the top model for soil C:N to be the null model. Soil organic matter, however, was higher in *Cenchrus* than *Dodonaea* soils. Soil moisture was the only variable affected by microsite, with the top model including the additive effects of vegetation type and microsite. Soil moisture, in contrast to expectations that it would be greatest in high-suitability plots, was greater in medium-suitability plots than in high- or low-suitability plots for vegetation types. Soil moisture was also slightly higher in *C. clandestinus* than *D. viscosa* plots (Tables 1 and 2).

Patterns of plant cover within the different microtopography categories did not consistently match expectations that percent cover would be greatest in high-suitability plots (Figure 1). In *Dodonaea* plots, models showed a positive association between HSI and *D. viscosa* (estimate = 3.05, lower CI = −3.03, upper CI = 9.13); however, 95% CI overlapped zero, suggesting these patterns did not significantly differ (Table 3). Similarly, though *C. clandestinus* showed a negative relationship with HSI within *Dodonaea*-dominated plots (estimate = −0.25, lower CI = −2.64, upper CI = 2.14), cover did not decline significantly. Neither *D. viscosa* seedling density nor *S. fallax* seedling density were influenced by microtopography within *Dodonaea* plots prior to disturbance (Table 3).

In invasive grass dominated *Cenchrus* plots, counter to expectations, total plant cover was higher in medium-suitability plots (99.5%) than it was in high- (94.1%) or low- (90.9%) suitability plots. Prior to disturbance, patterns of total plant cover were largely driven by *C. clandestinus* itself, which had 71% cover in medium-suitability as opposed to 36% and 25% in high- and low-suitability plots, respectively (Figure 1). An increasing HSI was negatively associated with *D. viscosa* cover, as well as *D. viscosa* seedling density (Table 3). Native shrub *D. viscosa* seedlings also showed variation among HSI in *Cenchrus* plots prior to disturbance with the greatest densities in low-suitability sites (0.34 m^{-2}), followed by high- (0.07 m^{-2}) and medium-suitability sites (0.01 m^{-2}). Native *S. fallax* shrub seedling density was similar across HSI.

Effects of microtopography and disturbance on soil moisture

Following experimental disturbance, continuously monitored soil moisture varied widely during the study period (0.071–0.254 m^3 m^{-3}) and exhibited complex relationships with habitat type, microtopography, and disturbance (Table 4 and Figure 2). The top models during wet and dry periods within *Dodonaea* sites included the additive effects of microtopography and disturbance. In both cases, soil moisture was higher in

TABLE 1 Foliar and soil nutrient content summary within *Dodonaea viscosa* and *Cenchrus clandestinus* plots.

Vegetation type and suitability	Foliar C:N	Soil OM (%)	Soil moisture (%)	Soil C:N
D. viscosa ('a'ali'i)				
High	38.61 ± 2.19	18.59 ± 0.55	10.42 ± 0.96	10.42 ± 0.19
Medium	40.75 ± 2.22	19.20 ± 0.63	12.07 ± 1.05	10.26 ± 0.24
Low	37.60 ± 1.74	19.80 ± 1.60	9.95 ± 0.59	11.39 ± 0.91
C. clandestinus (kikuyu grass)				
High	24.13 ± 1.11	23.32 ± 2.18	12.47 ± 1.80	10.57 ± 0.38
Medium	23.04 ± 1.76	27.76 ± 2.68	17.84 ± 1.31	11.56 ± 0.51
Low	22.26 ± 0.50	24.25 ± 2.68	12.31 ± 2.18	10.21 ± 0.35

Note: Values (mean ± SE) are shown foliar carbon to nitrogen ratios (C:N) of the dominant species within each vegetation type, and soil properties within high-, medium-, and low-suitability plots prior to disturbance. Soil properties include soil moisture, soil organic matter (OM), and C:N ratio.

TABLE 2 Akaike information criterion corrected for sample size (AIC_c) model summary results evaluating the effects of vegetation type, microsite index, and an additive model, against a null model for each foliar and soil property.

Parameter and model	*K*	AIC_c	ΔAIC_c	Wt.	Cum. wt.	LL
Foliar C:N						
Vegetation	3	168.32	0.00	0.88	0.88	−80.70
Vegetation + microsite	5	172.22	3.91	0.12	1.00	−79.86
Null	2	219.30	50.99	0.00	1.00	−107.43
Microsite	4	224.18	55.87	0.00	1.00	−107.29
Soil OM (%)						
Vegetation	3	176.81	0.00	0.85	0.85	−84.95
Vegetation + microsite	5	180.42	3.61	0.14	0.99	−83.96
Null	2	186.87	10.05	0.01	1.00	−91.21
Microsite	4	190.74	13.92	0.00	1.00	−90.57
Soil moisture (%)						
Vegetation + microsite	5	162.77	0.00	0.78	0.78	−75.13
Vegetation	3	166.02	3.26	0.15	0.93	−79.55
Microsite	4	168.39	5.63	0.05	0.98	−79.40
Null	2	170.11	7.35	0.02	1.00	−82.83
Soil C:N						
Null	2	96.36	0.00	0.69	0.69	−45.96
Vegetation	3	98.79	2.43	0.21	0.90	−45.93
Microsite	4	100.76	4.40	0.08	0.98	−45.58
Vegetation + microsite	5	103.61	7.24	0.02	1.00	−45.55

Note: Model evaluation results include the number of parameters (*K*), Akaike information criterion corrected for sample size (AIC_c), change in AIC_c relative to the top model (ΔAIC_c), model weight (Wt.), cumulative weight (Cum. wt.), and the model log likelihood (LL).

high-suitability sites and lower in disturbed sites, although the pattern was stronger during wet periods. Soil moisture at 5 cm depth showed an increase with HSI in *Dodonaea*-dominated plots, but no association with HSI in *Cenchrus*-dominated plots. Similarly, soil moisture at 5 cm depth decreased after disturbance within *Dodonaea*-dominated plots, but not within *Cenchrus*-dominated plots. At *Cenchrus* sites, the top model during dry periods also included the additive effects of microtopography and disturbance, although the effects were negative in both cases and 95% CI had an upper boundary of zero. During wet periods, however, there was no effect of microtopography or disturbance on soil moisture at *Cenchrus*-dominated sites.

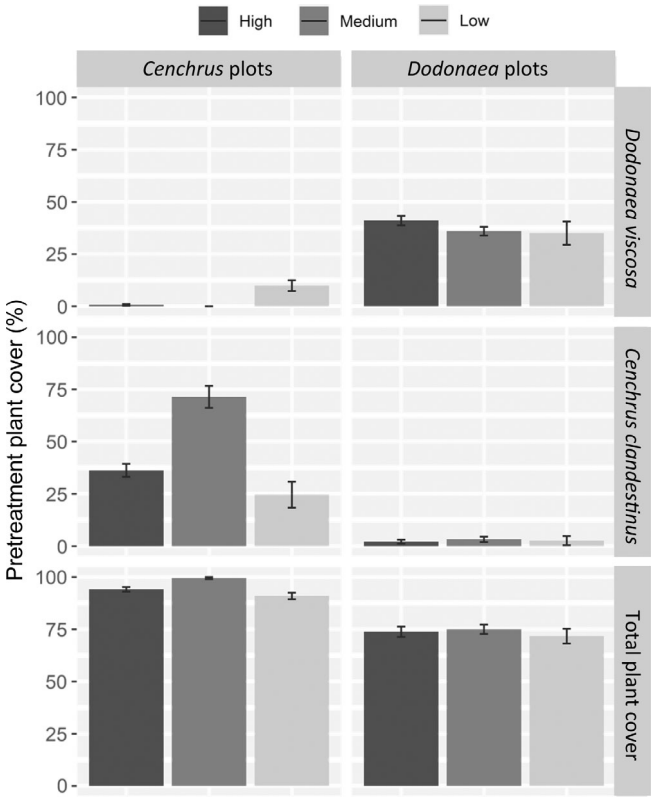

FIGURE 1 Total plant cover and cover of the dominant species within *Dodonaea* and *Cenchrus* plots. Percent cover was taken before disturbance within low-, medium-, and high-suitability plots at five replicated sites for each plant type. Bars represent mean ± SE.

TABLE 3 Model results for the effect of microtopography on pretreatment percent cover and seedling (≤2 cm tall) density.

Response variable	*N*	Effect of microtopography estimate
Dodonaea viscosa plots		
D. viscosa cover	30	3.05 (−3.03, 9.13)
C. clandestinus cover	30	−0.25 (−2.64, 2.14)
Total cover	30	1.05 (−3.44, 5.54)
D. viscosa density	15	0.32 (−3.45, 4.09)
S. fallax density	15	−0.01 (−0.04, 0.03)
Cenchrus clandestinus plots		
D. viscosa cover	30	−4.65 (−7.10, −2.20)*
C. clandestinus cover	30	5.80 (−8.78, 20.38)
Total cover	30	1.60 (−0.96, 4.16)
D. viscosa density	15	−0.14 (−0.22, −0.05)*
S. fallax density	15	−0.03 (−0.13, 0.08)

Note: Models of percent cover account for the spatial arrangement of treatment and control subplots (10 × 10 m, $N = 30$) by incorporating a random effect of plot into linear mixed models. In contrast, seedling density was quantified across whole plots (20 × 10 m, $N = 15$) without respect to future treatment assignment so models do not incorporate random effects. The effect of microtopography on each response variable is reported using the parameter estimates and associated 95% confidence intervals (lower CI and upper CI). Parameter estimates indicate association between the response variable and increasing suitability based on microtopography, as such a positive estimate indicates a positive relationship between a response variable and increasing habitat-suitability indices. An asterisk indicates that 95% confidence intervals (CI) do not overlap zero.

Effects of microtopography and disturbance on plant recovery

Overall, disturbance resulted in increased cover of the invasive *C. clandestinus* and decreased cover of the native *D. viscosa* (Appendix S1: Figure S2), but each species response varied across vegetation type and, to a lesser extent, microtopography (Table 5 and Figure 3). The top model for change in *D. viscosa* cover included vegetation type, but not microtopography, and carried 98% of the model weight. Disturbance had a general negative effect on *D. viscosa* cover though this effect was stronger in the *Dodonaea* vegetation type, which lost about 28% cover as compared to *Cenchrus* plots, which lost about 9% cover. We found a similar pattern for total plant cover, wherein *Cenchrus* plots lost almost 4% total cover and *Dodonaea* plots lost almost 20% cover due to disturbance. In contrast, the top model explaining the relative difference in recovery between the disturbed and control plots for the *C. clandestinus* cover was the null model, which carried 45% of the model weight. Neither microtopography nor vegetation type helped to explain patterns of recovery for this species.

When focusing on the effects of microtopography, total plant cover within *Dodonaea* plots showed similar patterns of recovery after disturbance across all three microtopography categories (Appendix S1: Figure S3). Despite this, percent cover of *D. viscosa* was notably lower than it was in control plots by 20 months posttreatment (Figure 4), with high-suitability plots experiencing the largest declines relative to paired control plots (−37.8% ± 2.42%) and low-suitability plots experiencing the smallest declines (−18.40% ± 6.21%). These declines corresponded with an overall increase in bare ground within plots of all suitability categories. In contrast, *C. clandestinus* showed increased cover within disturbed *Dodonaea* plots relative to associated controls for all microtopography categories. Notably, *C. clandestinus* cover returned to pre-disturbance levels within 3 months post-disturbance within both *Dodonaea* (Appendix S1: Figure S3) and *Cenchrus* (Appendix S1: Figure S4) plots, with the slowest recovery within high-suitability *Dodonaea* plots.

Similar to patterns of percent cover, *D. viscosa* recruitment was influenced by vegetation type to a greater

TABLE 4 AIC_c results for the effects of microtopography and disturbance on post-disturbance soil moisture at 5 cm depth within *Dodonaea* and *Cenchrus* plots during wet and dry periods.

Plot type	Estimate (lower CI, upper CI)	Top models	*K*	AIC_c	ΔAIC_c	AIC_c wt.	LL
Wet period (5 cm depth)							
Dodonaea	Microtopography: 0.082 (0.077, 0.086) Disturbance: −0.012 (−0.017, −0.008)	Microtopography + disturbance	6	−5052.01	0.00	1.00	2532.03
		Microtopography	5	−5026.22	25.79	0.00	2518.13
		Disturbance	5	−4175.36	876.65	0.00	2092.70
		Null	4	−4167.41	884.60	0.00	2087.71
Cenchrus	Microtopography: 0.004 (−0.004, 0.013) Disturbance: 0.002 (−0.007, 0.010)	Null	4	−3441.33	0.00	0.45	1724.67
		Microtopography	5	−3440.29	1.04	0.27	1725.16
		Disturbance	5	−3439.47	1.86	0.18	1724.75
		Microtopography + disturbance	6	−3438.43	2.90	0.11	1725.24
Dry period (5 cm depth)							
Dodonaea	Microtopography: 0.064 (0.061, 0.067) Disturbance: −0.045 (−0.048, −0.042)	Microtopography + disturbance	6	−7085.09	0.00	1.00	3549.01
		Microtopography	5	−6406.09	679.88	0.00	3208.06
		Disturbance	5	−5914.74	1171.23	0.00	2962.39
		Null	4	−5551.01	1534.96	0.00	2779.52
Cenchrus	Microtopography: −0.005 (−0.008, 0.000) Disturbance: −0.004 (−0.008, 0.000)	Microtopograpy + disturbance	6	−6667.54	0.00	0.57	3339.79
		Microtopography	5	−6666.06	1.48	0.27	3338.05
		Disturbance	5	−6664.16	3.38	0.10	3337.09
		Null	4	−6662.83	4.71	0.05	3335.42

Note: Results include model averaged parameter estimates and 95% confidence intervals (lower CI, upper CI) for the effects of microtopography and disturbance on soil moisture. All models included nested random effects of time and plot. AIC_c, corrected Akaike information criterion; AIC_c wt., corrected Akaike information criterion weight; LL, model log likelihood.

extent than microtopography (Table 6). Within *Dodonaea* plots, *D. viscosa* seedlings showed a recruitment pulse for all suitability categories (Appendix S1: Figure S3), but recruitment was only higher relative to controls within medium (1.46 ± 1.11 stems m^{-2}) and low-suitability (1.71 ± 0.36 stems m^{-2}) plots (Figure 3). Models of *S. fallax* recruitment were not improved by including vegetation type or microtopography. Although the greatest recruitment for this species was found in low-suitability *Cenchrus* plots (0.58 ± 0.51 stems m^{-2}), post-disturbance recruitment was similar within control and treatment plots across all microtopography categories for both vegetation types (Appendix S1: Figure S3).

Microtopography, disturbance, and native species restoration

For outplanted *D. viscosa* and *E. atropioides* seedlings, we found no effect of disturbance on seedling survival (Figure 5, *D. viscosa* seedlings, vegetation type effect, $\chi^2 = 21.83$, $p < 0.001$; disturbance effect, $\chi^2 = 1.01$, $p = 0.316$; microtopography effect, $\chi^2 = 8.35$, $p = 0.015$; *E. atropioides* seedlings, vegetation type effect, $\chi^2 = 30.49$, $p < 0.001$; disturbance effect, $\chi^2 = 0.26$, $p = 0.609$; habitat-suitability effect, $\chi^2 = 15.32$, $p < 0.001$). However, there was an effect of both vegetation type and microtopography on seedling survival (Figure 5). Namely, seedlings of both species showed less than half the survival in medium-suitability *Cenchrus* plots than any other dominant vegetation/suitability combination. As noted above, medium-suitability plots had greater total plant cover after disturbance (averaging 99.4% cover) than high- (94.0%) or low- (88.7%) suitability plots.

DISCUSSION

Microtopography can influence soil depth, soil composition (Dwyer & Merriam, 1981), and water-holding capacity (Schimel et al., 1985), thereby influencing patterns of plant growth and species composition (Ettema & Wardle, 2002; Nippert et al., 2011). Within Hawai'i, microtopography has been shown to influence native outplant success and resource availability in some arid habitats. Questad et al. (2014) identified a microtopography gradient that correlated

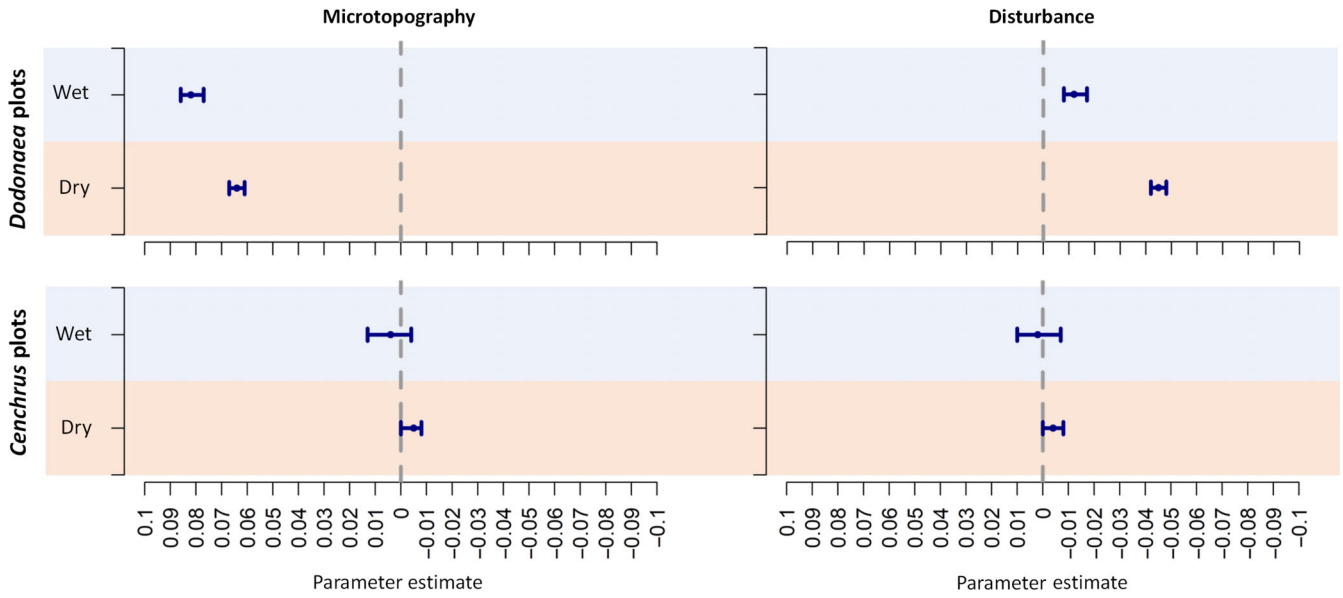

FIGURE 2 Parameter estimates (points) and 95% confidence intervals (error bars) derived from generalized linear mixed models exploring the effects of habitat-suitability indices and disturbance on continuously monitored soil moisture at 5 cm depth.

with soil moisture, leaf wetness, plant height, leaf nutrient content, and native outplant survival within arid *D. viscosa*-dominated habitats. Despite this, our results suggest that other processes may override these patterns, even within similar *D. viscosa*-dominated habitats. In particular, highly productive sites, where cover returns quickly after a disturbance, benefit undesired invasive species as much or more than desired native species, leading to a net negative impact via competition on native seedlings (D'Antonio et al., 2017; Huston, 2004; Levine, 2000). This dynamic highlights the importance of measuring the impact of site quality and disturbance on focal species as well as more common and/or invasive species to ascertain longer term outcomes.

Microtopography and abiotic resources

Although Questad et al. (2014) showed that their HSI incorporating microtopography was correlated with soil and plant resources, wherein high-suitability plots showed greater soil moisture, leaf wetness, leaf N, and phosphorus, we did not find similar patterns within nearby *Dodonaea* or *Cenchrus* plots. In contrast, our study showed that the only resource that related to microtopography prior to disturbance was soil moisture, and while high-suitability habitats had greater soil moisture than low-suitability habitats, soil moisture was the greatest within medium-suitability plots. One possible explanation for the differences between these findings is that our pre-disturbance data within medium-suitability plots relied on only a single time point, which may have been an anomaly. Unfortunately, we only measured soil moisture within medium-suitability plots during the pre-disturbance visit, and automated time-series soil moisture data with data loggers were not collected within medium-suitability plots after disturbance. Alternatively, high soil moisture in medium plots could be in part due to the topographic-suitability criteria for this model: plots that have both (1) leeward-facing microsites that are (2) in descending topography were classified as high-suitability plots. Plots that met only one of these two criteria were classified as medium suitability. Thus, flat sites, which are not in descending topography are considered medium suitability (Questad et al., 2014). It is possible that such "flat" topography sites have deeper soils due to surrounding topography, run-off, and drainage of silt and organic matter. That medium-suitability plots in the *Cenchrus* vegetation type had slightly higher organic matter content and nitrogen is consistent with the idea that these sites are acting as resource sinks for the surrounding area. In addition, deeper soils, especially in young, volcanic or rocky substrates can lead to higher resource availability for plants per unit area (Bi et al., 2003; Huenneke et al., 1990).

Importantly, automated time-series soil moisture data in high- and low-suitability plots showed complex relationships between plant community and disturbance. Soil moisture in the *Dodonaea* plots was significantly higher in high-suitability areas across both wet and dry time periods (Table 4 and Figure 3). Soil moisture within *Dodonaea*

TABLE 5 AIC_c results comparing generalized linear models of the effects of disturbance on % cover (Δdisturbed − Δcontrol).

Cover type	Estimate (lower, upper)	Model	*K*	AIC_c	ΔAIC_c	Wt.	Cum. wt.	LL
Dodonaea viscosa	Microtopography: −1.92 (−7.94, 4.09) Plot type *Cenchrus*: −8.87 (−18.46, 0.72) Plot type *Dodonaea*: −27.60 (−37.19, −18.01)	Biotic	3	246.03	0.00	0.75	0.98	−115.29
		Mixed	4	248.28	2.25	0.24	0.99	−113.89
		Null	2	256.07	10.04	0.00	1.00	−121.35
		Abiotic	2	259.52	13.49	0.00	1.00	−121.34
Cenchrus clandestinus	Microtopography: 4.45 (−0.11, 9.01) Plot type *Cenchrus*: 11.96 (−0.78, 24.7) Plot type *Dodonaea*: 8.03(−4.71, 20.77)	Null	2	264.40	0.00	0.45	0.45	−129.98
		Abiotic	2	264.95	0.55	0.34	0.80	−130.25
		Biotic	3	266.53	2.13	0.16	0.96	−129.80
		Mixed	4	269.06	4.66	0.04	1.00	−129.73
Total plant cover	Microtopography: −0.24 (−5.50, 5.03) Plot type *Cenchrus*: −3.78 (−11.4, 3.83) Plot type *Dodonaea*: −19.72 (−27.33, −12.10)	Biotic	3	237.50	0.00	0.79	0.79	−115.29
		Mixed	4	240.17	2.67	0.21	0.99	−115.28
		Null	2	247.14	9.64	0.01	1.00	−121.35
		Abiotic	2	249.93	12.44	0.00	1.00	−122.75

Note: We evaluated models incorporating vegetation type (biotic), microtopography as quantified by habitat suitability indices (abiotic), and a combination of the two (mixed) against a null model. Models were developed for the effects of disturbance on *D. viscosa*, *C. clandestinus*, and total plant cover. A positive model averaged estimate (estimate) indicates a positive effect of disturbance on the response variable, while a negative estimate suggests a negative effect. Estimates whose 95% confidence intervals (lower, upper) do not overlap zero suggest a strong effect. AIC_c, corrected Akaike information criterion; Cum. wt., cumulative weight; and the LL, model log likelihood.

plots was lower within disturbed, open plots, as well as within low-suitability microtopography plots. One possible explanation for these differences is that high rainfall patterns may lead to lower incident light and lower overall temperatures, thus less evaporation, than during dry periods. In addition, during the dry period it may be that existing vegetation in undisturbed control plots was able to capture water via fog or condensation, or to lower evaporation rates from the soil surface as compared to open, disturbed plots (Barbosa et al., 2010; Breshears et al., 1998; Fischer et al., 2009). Similar to these results, complex relationships between soil water evaporation under canopies versus open habitats have been shown to shift through the growing season based on rainfall patterns and soil temperature (Breshears et al., 1998).

In contrast with the patterns found at *Dodonaea* plots, *Cenchrus* plots showed little effect of disturbance or microtopography on soil moisture (Table 4 and Figure 3). Although the top model during dry periods included the additive effects of microtopography and soil moisture, all four models carried some of the model weight, and parameter estimates included zero. *Cenchrus* plot soils generally had higher organic matter content, which may have helped to retain soil moisture for longer even under dry conditions, possibly helping to explain the different findings for soil moisture. In addition, *Cenchrus* plots quickly returned to similar levels of plant cover after disturbance, likely due to the ability of *C. clandestinus* to quickly resprout from roots. While *D. viscosa* was also seen resprouting, this was rarer and less vigorous than the invasive grass. Thus, while disturbance was similar between species, their differential life history strategies strongly influenced the impacts of this disturbance. This quick recovery may have reduced the overall effect of disturbance on continuously monitored soil moisture.

Microtopography, disturbance, and dominant vegetation types

Our results suggest that indices of microtopography such as the KMA HSI may not be consistently useful across different vegetation types or even universally within a vegetation type, either for predicting current vegetation or the success of planting native species. Contrary to our expectations, neither *Dodonaea* nor *Cenchrus* dominated plots exhibited the expected relationship with microtopography prior to disturbance: highest cover in high-suitability plots. Pre-disturbance *Dodonaea* plots did not show an effect of habitat suitability on total plant cover, *D. viscosa* cover, seedling density, plant regrowth, or native outplant survival. In contrast, HSI influenced pre-disturbance cover within *Cenchrus* plots, but total plant cover was greatest in medium-suitability, rather that high-suitability plots. The fact that we did not find an effect of microtopography on outplant success was surprising given its effectiveness at predicting successful native species planting locations in *D. viscosa* sites nearby, albeit in a drier climate (Questad et al., 2014). Thus, the influence of microtopography on restoration outcomes may

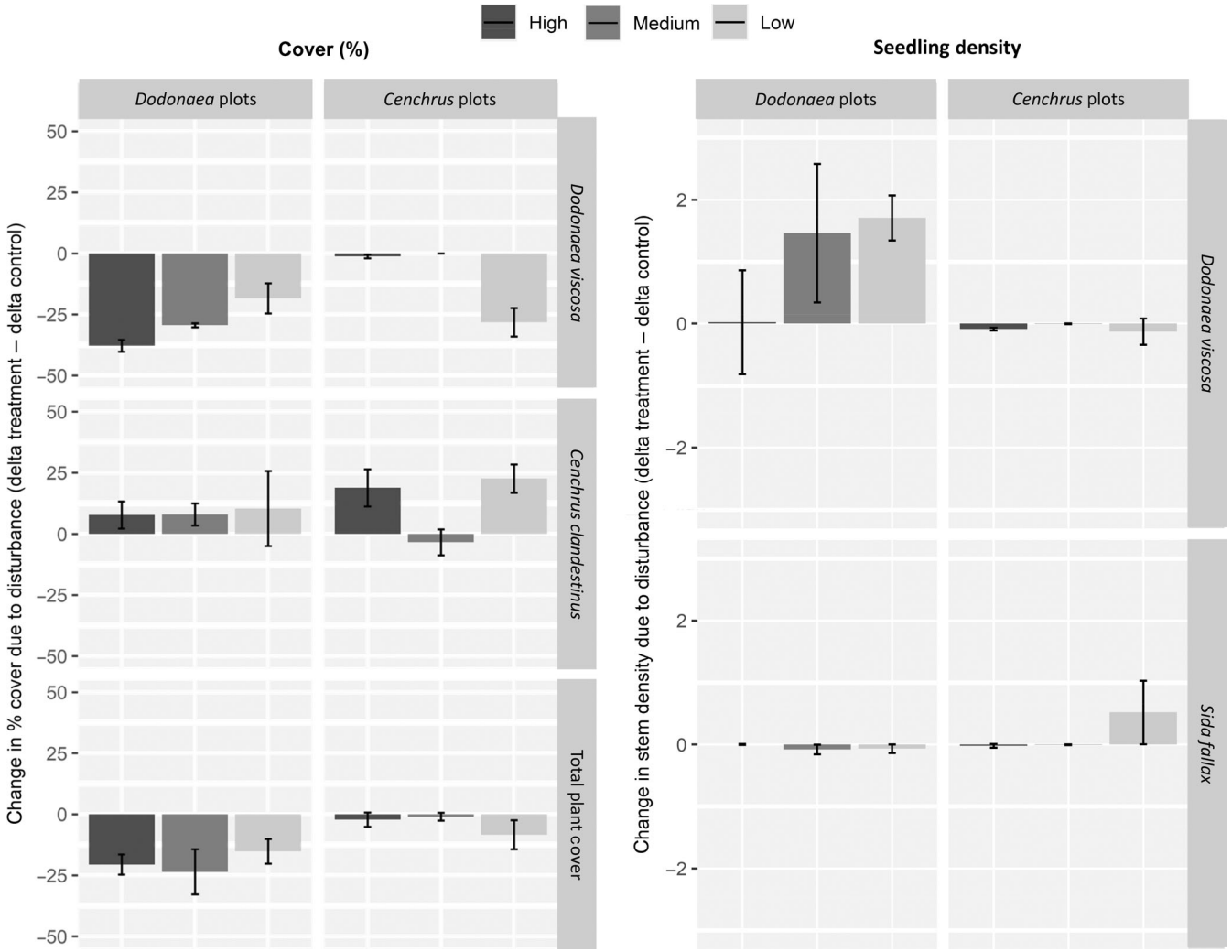

FIGURE 3 Change in percent cover and native seedling density resulting from disturbance of *Dodonaea*- and *Cenchrus*-dominated plots. Percent cover is presented for native *D. viscosa*, nonnative *C. clandestinus*, herbaceous cover, and total vegetation cover, which is the complement to bare ground. Native seedling density is presented for *D. viscosa* and *Sida fallax*. Bars represent the mean ± SE relative change in cover between disturbed and control plots (Δdisturbed − Δcontrol). Bars below the zero line indicate a decline in percent cover resulting from disturbance 20 months after treatment, while those above indicate an increase in cover relative to control plots over that time period. Note that total plant cover is the complement of bare ground, which is not presented in this figure.

vary greatly across, and even within, dominant vegetation types. Importantly, it may be most useful in harsher, native-dominated locations where abiotic factors exert the most control on plant survival and productivity, such as in the Questad et al. (2014) sites.

It is unclear what led to the initial differences between the two dominant vegetation types included in this study (i.e., invasive grass vs. native shrub dominated). It is possible that the native shrub *D. viscosa* was dominant in remnant areas that had not experienced the same historical levels of disturbance as areas dominated by *C. clandestinus*. That *C. clandestinus* cover increased in *Dodonaea* plots after disturbance is evidence that repeated disturbance may lead to an increase in cover of this invasive grass, which is well known to reduce native plant success in Hawai'i (McDaniel & Ostertag, 2010; Yelenik, 2017). Anthropogenic landscapes often contain a mosaic of different, overlapping land use and disturbance histories that lead to heterogeneous vegetation patterns (Adler et al., 2001; Julie Sloan Denslow, 1980). It is also possible that underlying heterogeneity in soils led to vegetation differences. According to USGS maps (Sherrod et al., 2007), all *Cenchrus* and *Dodonaea* plots were on the same substrate age and soil type. It should be noted, however, that these were very coarse categories; therefore, it is still plausible that unmeasured substrate differences led to vegetation patchiness. Indeed, soil properties (rockiness, depth, aggregate properties, etc.) are highly variable over relatively small

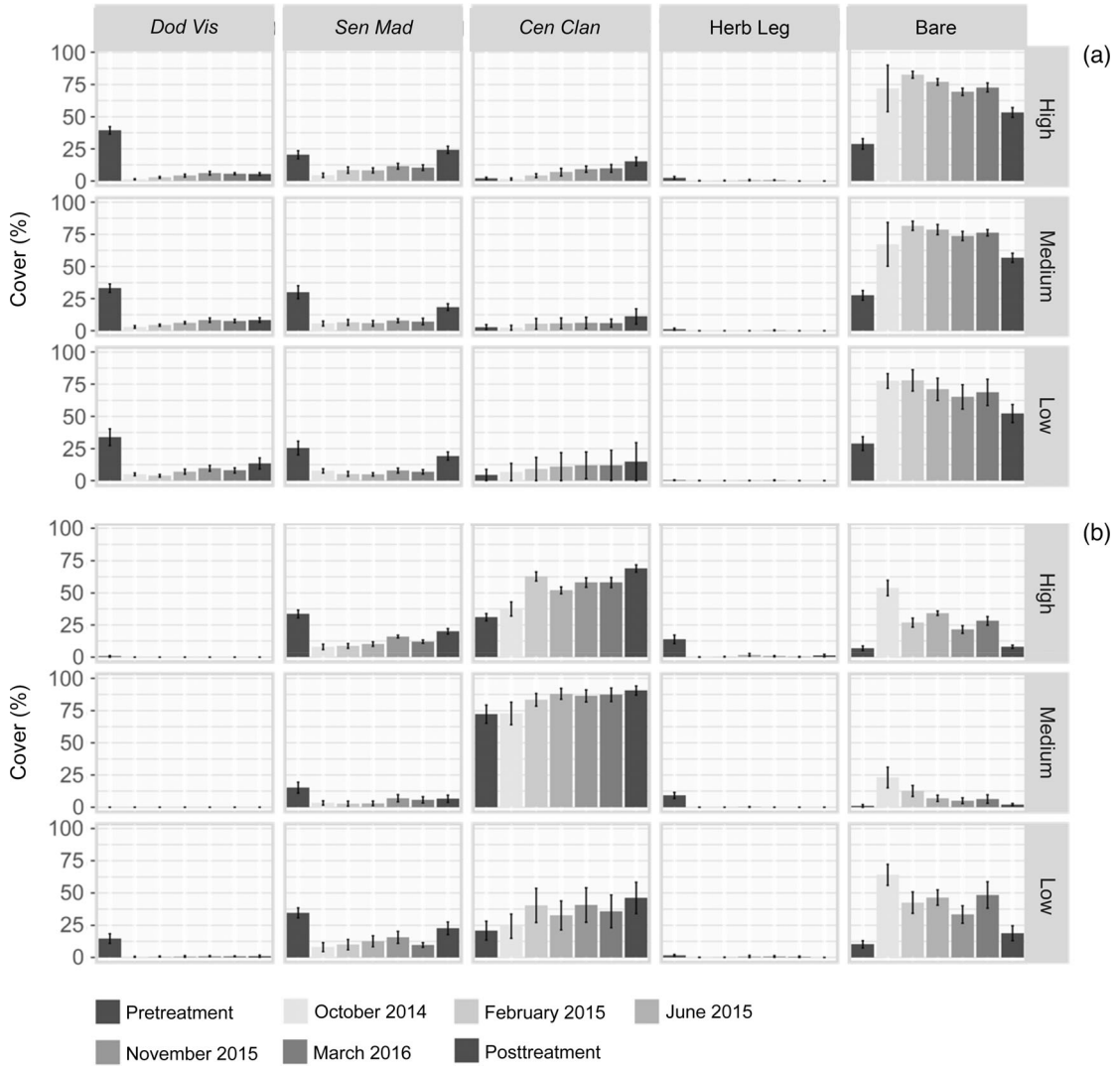

FIGURE 4 Percent cover of *Dodonaea viscosa* (Dod Vis), *Senecio madagascariensis* (Sen Mad), *Cenchrus clandestinus* (Cen Cla), herbaceous legumes (Herb Leg), and bare ground (Bare) in (a) *D. viscosa*-dominated and (b) *C. clandestinus*-dominated plots during all visits. Figure shows mean ± SE percent cover estimated from point-intercept data (black: pre-disturbance and post-disturbance) and quadrat data (grayscale). In March 2016, data were collected using both methods to account for potential differences. They are both plotted here for reference (March 2016 from quadrat data and post-disturbance from point-intercept data). When compared directly, quadrat data were highly correlated with point-intercept data ($r^2 = 0.88$) but had a slight positive bias (+3%).

spatial scales, and this variation can affect plant community dynamics particularly in semiarid ecosystems (Maestre & Cortina, 2002; Valentin et al., 1999).

Microtopography, disturbance, and biotic interactions

While few plant-based habitat suitability indices incorporate biotic interactions with resident communities (Guisan & Thuiller, 2005; Hirzel & Le Lay, 2008), our work is evidence that they play an important role. Importantly, habitat type had a strong influence on *D. viscosa* cover following disturbance, while microtopography was less important. Similarly, in the invasive grass (*C. clandestinus*) vegetation type, competition from resident plant communities seemed to negate any benefit native outplants may have gained from "better" habitat suitabilities. In the most productive, medium-suitability plots, *C. clandestinus* regrowth, largely due to vigorous post-disturbance resprouting, was fast enough that plots had returned to pre-disturbance cover within three months. Presumably because of this invasive grass regrowth and competition, outplanted native seedlings (*D. viscosa* and *E. atropioides*) incurred the highest mortality in medium *Cenchrus* plots. These results suggest that restoration practitioners would benefit from exercising caution in using microtopographic indices that rely

TABLE 6 AIC_c results comparing linear models of the effects of disturbance on stem density of two native plants *Dodonaea viscosa* and *Sida fallax*.

Cover type	Estimate (lower, upper)	Model	*K*	AIC_c	ΔAIC_c	Wt.	Cum. wt.	LL
D. viscosa	Microtopography: −0.35 (−1.00, 0.31) Plot type *Cenchrus*: 0.27 (−1.02, 1.56) Plot type *Dodonaea*: 1.41 (0.12, 2.70)	Biotic	3	107.89	0.00	0.48	0.48	−50.48
		Mixed	4	108.51	0.62	0.35	0.83	−49.45
		Null	2	110.65	2.76	0.12	0.95	−53.10
		Abiotic	2	112.59	4.70	0.05	1.00	−54.07
S. fallax	Microtopography: −0.03 (−0.20, 0.14) Plot type *Cenchrus*: 0.24 (−0.16, 0.65) Plot type *Dodonaea*: 0.03 (−0.38, 0.44)	Null	2	45.03	0.00	0.36	0.36	−20.29
		Abiotic	2	45.34	0.40	0.30	0.66	−20.49
		Biotic	3	45.96	0.93	0.23	0.89	−19.52
		Mixed	4	47.34	2.31	0.11	1.00	−18.87

Note: We evaluated models incorporating vegetation type (biotic), microtopography as quantified by habitat-suitability indices (abiotic), and a combination of the two (mixed) against a null model. The response variable in each case represents the relative change in density between disturbed and control plots over time (Δdisturbed − Δcontrol). A positive model averaged estimate (estimate) indicates a positive effect of disturbance on the response variable, while a negative estimate suggests a negative effect. Estimates whose 95% confidence intervals (lower, upper) do not overlap zero suggest a strong effect. AIC_c, corrected Akaike information criterion; Cum. wt., cumulative weight; and the LL, model log likelihood.

solely on topographic variables when the resident vegetation is known to constrain native species success, as invasive grasses are well understood to do across Hawai'i (Cabin et al., 2002; D'Antonio et al., 2017; Denslow et al., 2006; Yelenik, 2017).

That resident communities can interact with habitat suitability to drive community assembly was also seen in the pre-disturbance plant communities. The native shrub *D. viscosa* was only found in low-suitability *Cenchrus* plots before disturbance, and this was the only suitability that native shrubs recruited into after disturbance within invasive grass dominated plots. This pattern was perhaps due to the lower invasive species cover and regrowth/resprouting rates resulting in weaker competitive interactions in low-suitability *Cenchrus* plots, which tended to have greater bare ground both before and after disturbance. Resources that lead to high productivity in native species often have similar effects on invasive species (Questad et al., 2014; Stohlgren et al., 2003). Indeed, many native species such as *D. viscosa* have been shown to benefit from greater resources such as soil N, water, and light (Cabin et al., 2002; Vitousek & Farrington, 1997; Yelenik et al., 2017), and *C. clandestinus* growth rates have been shown to increase with soil moisture and nutrients (Colman & O'Neill, 1978). However, if the invasive species are able to take up resources more quickly and achieve higher growth rates than natives, then increased resource availability can lead to decreased native growth indirectly due to competitive effects from the invasive species (Blumenthal et al., 2003; Daehler, 2003). That *C. clandestinus* is rhizomatous and can vigorously resprout after disturbance surely helped it quickly take up resources and exert high competitive pressure on both naturally regenerating and planted native species. Low-habitat-suitability sites, then, may be acting as "refugia" from competition for slower growing native shrubs, similar to serpentine outcrops in California grasslands acting as refugia from invasive grasses due to sub-prime growing conditions (Huenneke et al., 1990). Put together, this provides evidence that low-suitability sites in *C. clandestinus*-dominated habitats will potentially be the most successful for active restoration efforts unless invasive species management co-occurs with restoration activities.

Management implications

Non-species-specific HSIs based on microtopography, such as the one discussed in this study, may prove most useful for choosing planting sites in dryland or other harsh habitats, such as those found in Questad et al. (2014). In more productive habitats, however, competition from resident species may offset any benefits gained from "better" suitability sites. On the other hand, microtopography could be used in invasive-dominated landscapes to target low-suitability sites for planting. In this case, however, it seems simpler to choose sites with lower invasive grass cover than make use of airborne LiDAR, which requires specialized knowledge for post-processing and interpretation. More generally, our results provide evidence that other indices of habitat suitability, including species range projections, should consider the role of resident dominant vegetation type in model outputs (Guisan & Thuiller, 2005; Hirzel & Le Lay, 2008). This will be particularly important for predicting plant range shifts with climate change (Alexander et al., 2015), as species of interest may be

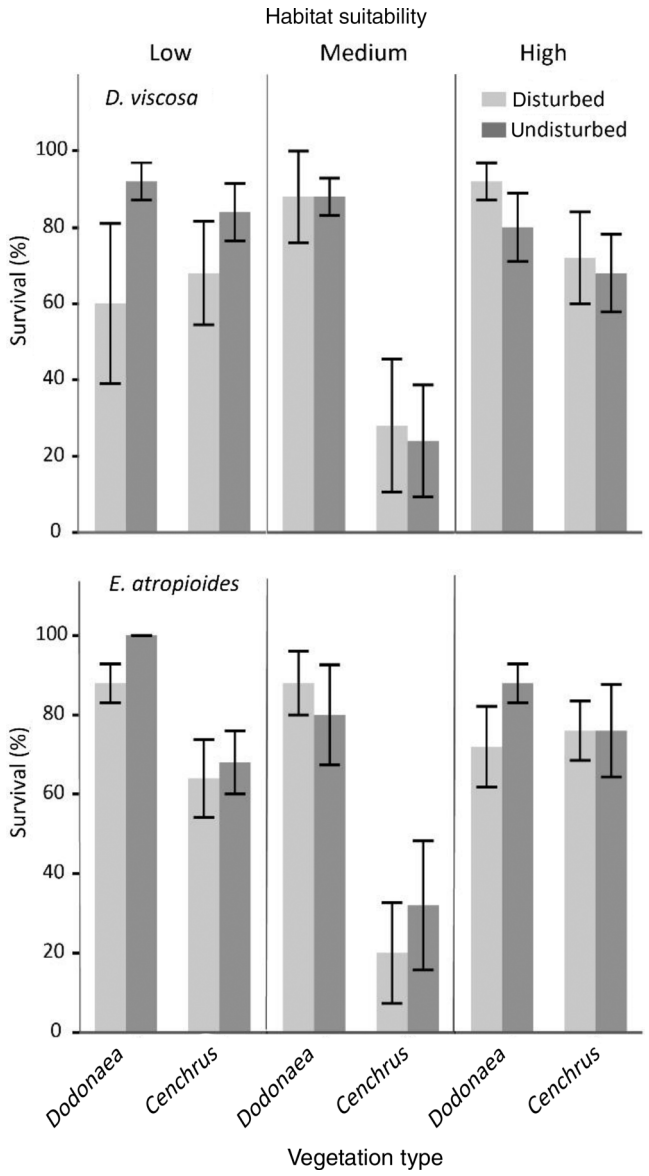

FIGURE 5 Survival of *Dodonaea viscosa* and *Erogrostis atropioides* seedlings after 20 months in different vegetation types, habitat suitabilities, and disturbance regimes. Bars represent mean ± SE.

predicted to overlap with highly competitive invasive species. Incorporating biotic interactions into such indices will help to more accurately predict important future conservation areas or target areas for invasive species removal if they are predicted to be important for threatened and endangered species in the future (Gillson et al., 2013; Keith et al., 2008).

ACKNOWLEDGMENTS

We acknowledge that our fieldwork took place in the ahupua'a of Waikoloa, Waimea, Pu'uanahulu, Ka'ohe Mauka, in the moku of Hāmākua and Kohala, and on the mokupuni of Hawai'i, which is the ancestral, traditional, and contemporary lands of the Hawaiian people. Kai'ena Bishaw, Jim Crisp, Shayna McCarthy, and Amanda Uowolo helped with fieldwork. Jonathan Stock and Linda Pratt helped develop the proposal and Paul Berkowitz helped with GIS-related data analysis. The manuscript was improved by comments from Jim Jacobi, Lucas Fortini, and two anonymous reviewers. Peter Peshut helped with site access and logistics. Funding was provided by the Department of Defense and an internship was provided for M. Victoria by UH Hilo's Pacific Internships Program for Exploring Science (PIPES, NSF Grant No. 1005186). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this publication should not be construed to represent any official USDA determination or policy.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Yelenik & Rose, 2022) are available from U.S. Geological Survey ScienceBase: https://doi.org/10.5066/P9NDWVCH.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Yelenik, Stephanie, Eli Rose, Susan Cordell, Michelle Victoria, and James R. Kellner. 2022. "The Role of Microtopography and Resident Species In Post-Disturbance Recovery of Arid Habitats in Hawai'i." *Ecological Applications* e2690. https://doi.org/10.1002/eap.2690