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RESEARCH ARTICLE

Nonperiodic grassland restoration management can promote native woody shrub encroachment

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Woody species encroachment is increasingly displacing grasslands, negatively impacting regional plant richness and reducing economic productivity from grazing. Although intermediate disturbance has been found to reduce woody species encroachment and maximize species diversity, ecological restoration can often lead to many small, infrequent disturbances. These small disturbances may not be strong enough to limit woody encroachment, and instead may promote invasion. Drought may slow encroachment, but adjustments in key functional traits may allow for persistent woody invasion. *Baccharis pilularis* is a woody shrub native to western North America, but has been shown to have higher recruitment following nonperiodic disturbances and be invasive in native grasslands. To address the extent of woody invasion following limited restoration actions, I quantified natural *B. pilularis* recruitment and cover at an invaded coastal California grassland in plots after experimental restoration (singular planting and nonnative species control efforts) and extreme drought conditions (60% rain exclusion) 6 years posttreatment. For traits, I measured *B. pilularis* specific leaf area, major vein length per unit area, leaf thickness, and lobedness 4 years posttreatment and stem diameter 5 years posttreatment. Native shrub encroachment by *B. pilularis* was higher in restored plots compared to nonrestored plots, which had zero recruitment. Drought reduced *B. pilularis* recruitment but not cover and resulted in adjustments in leaf thickness and major vein length per area. Results suggest that planting and other singular restoration activities (i.e. invasive species control) in coastal grasslands can cause small, infrequent disturbances that promote native woody shrub encroachment.

Key words: ***Baccharis pilularis*, drought-net, intermediate disturbance hypothesis, manual restoration, restoration disturbance, woody species invasion**

> **Implications for Practice**
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> - Infrequent restoration activities such as singular planting or weeding efforts can create small disturbances that facilitate woody invasion by *Baccharis pilularis*.
> - Establishment of periodic disturbance regimes may prevent woody encroachment of restored California grasslands to shrub and woodlands if the underlying management goal is to preserve grassland habitats.
> - Restoration of drier microhabitats may limit woody recruitment, but management may still be needed to prevent woody invasion because the invading *B. pilularis* population that establishes, achieves similar cover to the invading population not experiencing drought.

Introduction

Globally, native woody species can become invasive and encroach into historic grasslands (McBride & Heady 1968; Ghersa et al. 2002; Stevens et al. 2017). Woody encroachment has accelerated in past years due to altered disturbance regimes and increased atmospheric nitrogen deposition (Van Auken 2009), but is an increasing management concern (Archer & Predick 2014; Fogarty et al. 2020) because it locally displaces grassland habitats with high conservation values (Ford & Hayes 2007; Stevens et al. 2017). Loss of grassland habitat reduces economic returns from grazing (Zarovali et al. 2007; Anadón et al. 2014) and decreases regional plant species richness (Van Auken 2009; Ratajczak et al. 2012) which can negatively impact higher tropic levels that rely on diverse plant hosts (Coppedge et al. 2001; Beal-Neves et al. 2020).

Woody species are better able to establish during wet periods (Williams et al. 1987; Archer 1990; Browning et al. 2008) and can persist into drier years if their taproots grow deep enough (Van Auken 2009). Until recently, habitat conversion of grasslands into shrublands or woodlands were often prevented by historic disturbance regimes (Van Auken 2009; Stevens

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et al. 2017). Historic disturbance regimes were typically implemented by indigenous tribes through prescribed burns (Anderson 2007) and can limit woody invasion (DeSantis et al. 2011). Many grasslands were also previously grazed by now-extirpated or extinct ungulates which also helped to abate woody shrub invasion (Wigand 2007). As previous research has found moderate disturbance is required to maintain grasslands and maximize species diversity (Hobbs & Huenneke 1992; Peterson & Reich 2008; Mayor et al. 2012), the intermediate disturbance hypothesis (Connell 1978), may provide a fitting framework to describe grassland community dynamics. In fact, this may be the theoretical basis for grazing programs and annual mowing that historically employed by land managers and restoration practitioners in grasslands globally (Tälle et al. 2016).

Habitat type conversion occurs when a habitat surpasses a threshold that causes the system to be converted to a different ecosystem (Beisner et al. 2003). Protecting grasslands in California from habitat conversion is a strong conservation priority because they support high levels of herbaceous diversity that are not often present in temperate shrub or woodlands (Ford & Hayes 2007). For example, a survey from California grasslands found that just 13 remnant grasslands harbored more than 40% of state's total native plant diversity, along with several rare and endangered species of concern (Schiffman 2007). California native grasslands previously encompassed 25% of the state, but only 1% of native grasslands have not been strongly affected by land development or species invasions since European colonization (Jantz et al. 2007). Historic and large reductions of native grasslands indicate that restoration will be needed for future habitat recovery. However, similar to many other regions in the world, woody species encroachment has been documented to be increasing in California for nearly a century (McBride & Heady 1968; Williams et al. 1987; Laris et al. 2017).

Studies from both Texas and South Africa suggest that extended droughts may constrain and potentially reverse woody species encroachment (Twidwell et al. 2014; Case et al. 2020). In Australia, woody species encroachment was found to be slowed, but not reversed by extreme drought (Zeeman et al. 2014). More research is needed to understand how woody species and grasslands in California will respond, because it is expected that rainfall will become more spatially and temporally variable, portending longer and more extreme droughts (Swain et al. 2018). Increased temporal variability in rainfall will lead to less available water for plant use (Loik et al. 2004), and potentially slow woody species encroachment (Twidwell et al. 2014; Zeeman et al. 2014; Case et al. 2020). Functional traits may be especially useful in understanding the mechanisms that potentially halt woody invasion during drought (Cadotte et al. 2015; Luong et al. 2021). For example, wood density, which is negatively related to stem diameter (Chave et al. 2009; Markesteijn et al. 2011), can support higher drought tolerance through cavitation resistance (Hacke et al. 2001) and help explain woody encroachment during drought, while key leaf traits are often related to resource acquisition and drought tolerance (Sack & Scoffoni 2013; Cadotte et al. 2015; Pérez-Harguindeguy et al. 2016).

Ecological restoration attempts to enhance degraded ecosystems through common practices such as nonnative species removal and reintroductions (via planting and seeding) of native species (Gann et al. 2019). Planting efforts and nonnative species removal often lead to small-scale soil disturbances (D'Antonio & Meyerson 2002). Disturbed open spaces freed from nonnative species removal are often recolonized during secondary invasions of fast growing, unplanted native or nonnative species with high reproductive output (Zavaleta et al. 2001; Pearson et al. 2016). Although intermediate disturbance such as periodic burning, grazing, or mowing may serve to improve species richness in restored grasslands (Connell 1978; Hobbs & Huenneke 1992), restoration often focuses limited resources solely on the removal of the most noxious nonnative species and ignore most other plants (Holl & Howarth 2000; Pearson et al. 2016). Newly bared ground may effectively provide open habitat for fast-growing shrubs to invade during ideal years (Tyler et al. 2007; Pierce et al. 2017). A common native woody invader in California, *Baccharis pilularis* DC., was previously found to establish better when nearby nonnative annual grasses were removed (da Silva & Bartolome 1984) and found to frequently encroach into California coastal grasslands (McBride & Heady 1968).

Reestablishing historic disturbance regimes is another growing restoration practice, but past evidence indicates that temporally limited restoration actions can promote native and nonnative woody invasion in open grassland habitat (Hobbs & Mooney 1985; Laris et al. 2017; Abella et al. 2020; Hopkinson et al. 2020). Abella et al. (2020) and Hopkinson et al. (2020) both found that singular prescribed fires without additional maintenance promoted woody invasion. In pampa grasslands, researchers found that singular small- and large-scale experimental disturbances led to increased recruitment of woody tree species in mesic conditions, but not consistently for drier plots (Mazía et al. 2019). Peltzer and Wilson (2006) found that extreme weather events could also result in disturbances that promotes woody species invasion. Laris et al. (2017) found that *B. pilularis* recruited heavily after mechanical removal of nonnative species. Mechanical removal is a common method used for invasive species control in restoration (Stromberg et al. 2007) and therefore may indicate at very least that some restoration activities can facilitate grassland woody invasion.

I was interested in the role that key restoration actions (singular planting and seeding) and drought had in influencing native woody shrub encroachment in grasslands by *B. pilularis* because of stark visual differences in *B. pilularis* cover observed 4 years posttreatment (Fig. S1). To test this, I took advantage of experimental plots at a coastal grassland in Santa Cruz, California, U.S.A. that were exposed to extreme drought, and previously restored experimentally though native species outplanting (Luong et al. 2021). I measured leaf functional traits (specific leaf area, major vein length per unit area, lobedness, and thickness) 4 years posttreatments and quantified the average stem diameter and abundance of *B. pilularis* 4- and 5-year posttreatment, and cover and recruitment 6-year posttreatment. I predicted that increase woody species encroachment (higher abundance of *B. pilularis*) would be promoted by singular restoration actions and be curtailed by drought. I hypothesized that *B. pilularis* would exhibit leaf trait adjustments that help explain its persistence through drought.

Methods

Study Site

The study was completed at the University of California Younger Lagoon Reserve (YLR) in Santa Cruz, California, U.S.A. The climate is characterized as Mediterranean with wet, cool winters and hot, dry summers. The area was historically utilized for cattle grazing and row crop agriculture before becoming a reserve in 1986. Legacy effects persist and the site is dominated by invasive species, notably *Avena barbata* Pott ex Link (Poaceae), *Festuca perennis* (L.) Columbus & J.P Sm. (Poaceae), *Bromus diandrus* Roth (Poaceae), *Medicago polymorpha* L. (Fabaceae), *Cirsium vulgare* (Savi) Ten. (Asteraceae), *Geranium dissectum* L. (Geraniaceae), and *Raphanus sativus* L. (Brassicaceae) with some native species, such as *Baccharis pilularis* (Asteraceae), *Erigeron canadensis* L. (Asteraceae), and *Elymus triticoides* Buckley (Poaceae).

Experimental Design

I utilized previously constructed rain exclusion (drought) shelters designed using a standardized protocol in 2015 as a part of the International Drought Experiment. Structures exclude 60% of incoming precipitation to simulate a 1-in-100-year drought after 5 years. These structures have been shown *in situ* induce drought with minimal nontarget effects, although they were documented to minimally reduce photosynthetically active radiation (PAR) and increase nighttime temperature by about 0.6°C (Loik et al. 2019). Rain exclusion plots were trenched and lined with 6-mil plastic to 50 cm depth to inhibit lateral water flow. The research plots are 3 × 3 m with a 0.5-m buffer around all edges resulting in a total 4 × 4 m area for each plot (Fig. 1). Plots were placed at least 1 m after accounting for buffer areas. Drought-induced reduction of soil moisture in these plots were confirmed in a previous field study with METER Environmental volumetric soil moisture probes (Luong et al. 2021). Standing biomass was removed via mowing from the research area and interstitial buffer areas prior to demarking twenty 4 × 4 m plots for the experiment. There was a full drought × restoration factorial design with five replicates for each treatment: (1) no experimental restoration and no drought (control; Fig. S1A); (2) experimental restoration only (Fig. S1B); (3) drought only (Fig. S1C); and (4) drought and experimental restoration (Fig. S1D). Plots were placed in an invaded annual grassland on area with visually similar vegetation, typically consisting of nonnative annual grasses and forbs, to avoid potential effects of site heterogeneity.

Experimental restoration included plantings that were previously installed as part of an ongoing experiment established in 2016 using a standard grid that was prerandomized (Luong et al. 2021). Because the original restoration experiment had different research goals, the planting design included three woody species to better assess the community level effect of drought on experimental restoration (Luong et al. 2021). The three woody species from the planting palette commonly occur in coastal sage scrub habitat that may naturally disperse into nearby grasslands, but are not often quick growing or invasive (Ford & Hayes 2007), unlike *B. pilularis* (McBride & Heady 1968), so they were not analyzed as encroaching woody natives. The 12 species were (Table S1) collected in 2015 from local reference sites and were grown in the UC Santa Cruz Jean H. Langenheim Greenhouses for about 3 months in "cone-tainer pots" (107 mL; Ray Leach—Stubby Cell Classic) in Pro-Mix Potting Soil Mix (Pro-Mix) prior to out-planting in January 2016. After planting, all nonnative plants were removed from restoration treatments manually with small hand tools once in January 2016 and a final time in April 2016. Buffer areas between plots were maintained through annual spring mowing,

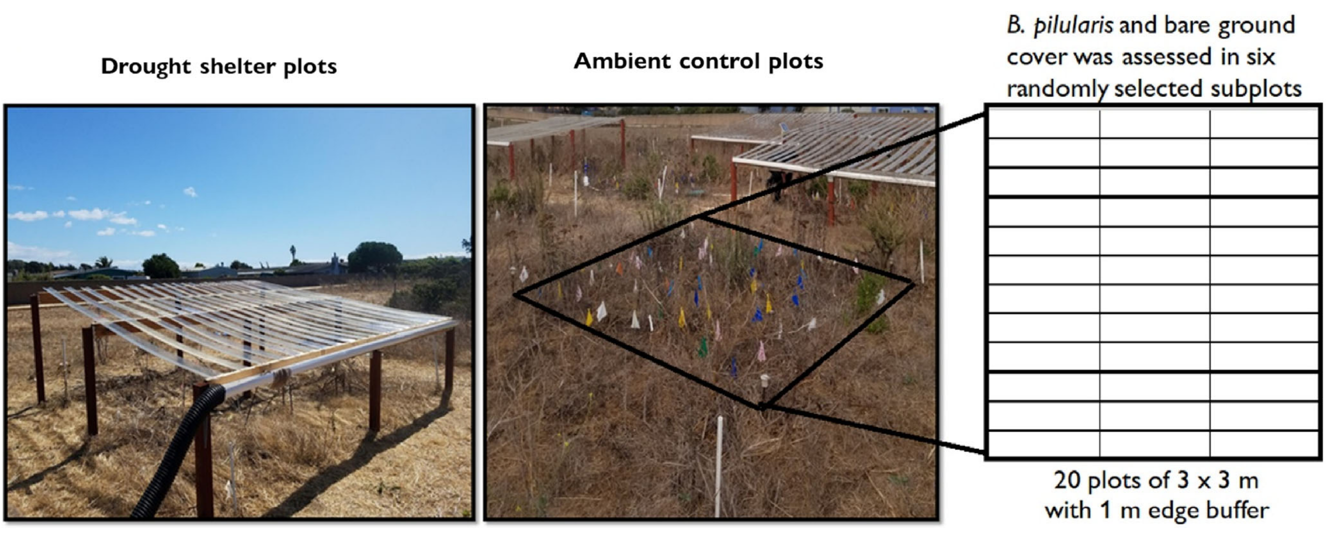

Figure 1. A photograph of the experimental design and *Baccharis pilularis* cover sampling methods. Drought plots exclude 60% of incoming rainfall. Ambient rainfall plots had no climate manipulations. *B. pilularis* and bare ground cover were assessed in six randomly selected subplot within 3 × 3 m plots with 1 m buffers around all edges.

but no other restoration activities were conducted on experimental plots after April 2016.

Data Collection

I assessed the cover of *B. pilularis* in 2021, the sixth year after planting, by estimating its relative cover to the nearest 5% within six 0.25-m^2 quadrats on each plot (Fig. 1). I also estimated the cover of bare ground within quadrats. I counted the total number of *B. pilularis* individuals within each plot in 2019 and 2020 (fifth and sixth year postplanting). I quantified leaf functional traits from five *B. pilularis* per plot in 2019, 4 years after initial treatments, and stem diameter for every individual in 2020. I collected leaves from up to four *B. pilularis* per plot to assess key functional traits and sampled two leaves per individual to account for variability. Leaves sampled were west facing, fully expanded, undamaged and three levels below the apical meristem on a given branch. Using standardized protocols, I measured specific leaf area (SLA), leaf thickness, major vein length per unit area (VLA), stem diameter, and leaf lobedness because they are related to plant hydraulics or water use (Hacke et al. 2001; Sack & Scoffoni 2013; Cadotte et al. 2015; see Pérez-Harguindeguy et al. 2016 for more detail on trait measurements). SLA is correlated with relatively high investments in structural leaf defenses and increased leaf lifespan. Major VLA of leaves can increase drought resistance by providing redundant pathways for hydraulic transport (Sack & Scoffoni 2013). However, increased VLA can also increase water requirements (Lambers et al. 2008), especially if the veins are not reticulated with minor vein networks. Leaf area and perimeter were measured using ImageJ software (Schneider et al. 2012). Leaf thickness was measured with a digital micrometer and is a proxy for higher mesophyll resistance against water movement through the leaf. Similar to VLA, the leaf thickness may have a mixed response to drought. Increased thickness can support more chloroplast and photosynthesis thereby increasing water demand (Lambers et al. 2008) but can also increase mesophyll resistance to water loss (Kröber et al. 2015). Higher leaf lobedness can effectively decrease the leaf air boundary layer increasing potential for cooling via convection and conduction (Lambers et al. 2008).

SLA was calculated as the ratio of fresh leaf area by oven-dried mass. VLA was quantified by measuring primary and secondary veins from fresh leaf scans using ImageJ and was standardized via fresh leaf area. Leaf lobedness was calculated as leaf perimeter squared divided by π and leaf area (Cadotte et al. 2015; Luong et al. 2021). Due to restrictions for in-person laboratory work from COVID-19, I was not able to collect and process leaf traits past year four (2019).

Analyses

All analyses were completed in R Statistical Software V 4.0.2 (R Core Team 2020) with base functions and the *plyr* and *ggplot2* packages (Kassambara et al. 2020; Wickham 2020). Data were tested for parametric assumptions prior to using *t*-tests, analysis of variance (ANOVA) or generalized linear models (GLMs). For count data, sampling year was included as a random effect. VLA was slightly nonparametric so I used a log-based transformation to meet statistical assumptions for a *t*-test, then back-transformed these data for visualization. No other measurements required transformation. Prior to analyzing functional traits, I averaged the values of the two collected leaves from the same individual. I then took the average of all measured individuals to calculate the mean at the plot level. All data were analyzed at the plot level ($n = 5$).

Results

The invading native shrub, *Baccharis pilularis* had higher abundance ($F = 20.1$, $df = 1$, $p < 0.001$) and cover ($F = 140$, $df = 1$, $p < 0.001$) on restored plots compared to unrestored control plots, which had no *B. pilularis* (Fig. 2). Drought resulted in lower individual *B. pilularis* counts on drought plots

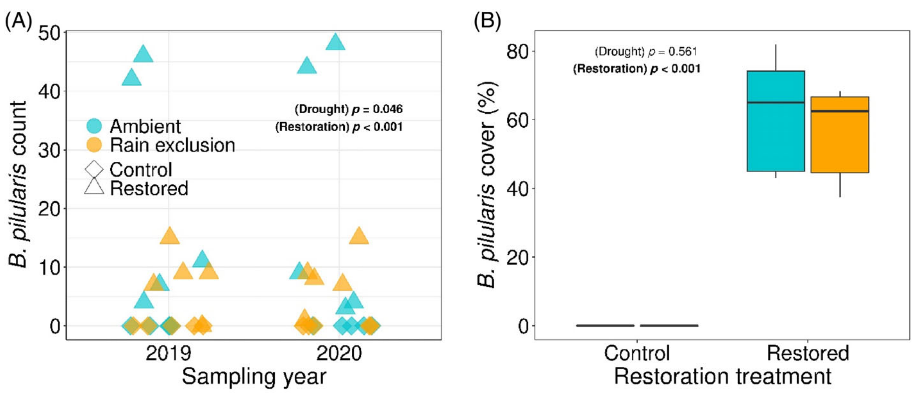

Figure 2. (A) Comparison of *Baccharis pilularis* counts 2019–2020. Points represent the count of *B. pilularis* in a given plot. (B) *B. pilularis* cover in 2021 for restored and nonrestored plots experiencing ambient (blue) or drought (orange) conditions. Boxes represents the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers. *p* values are presented within figures for drought and restoration treatments after respective text labels.

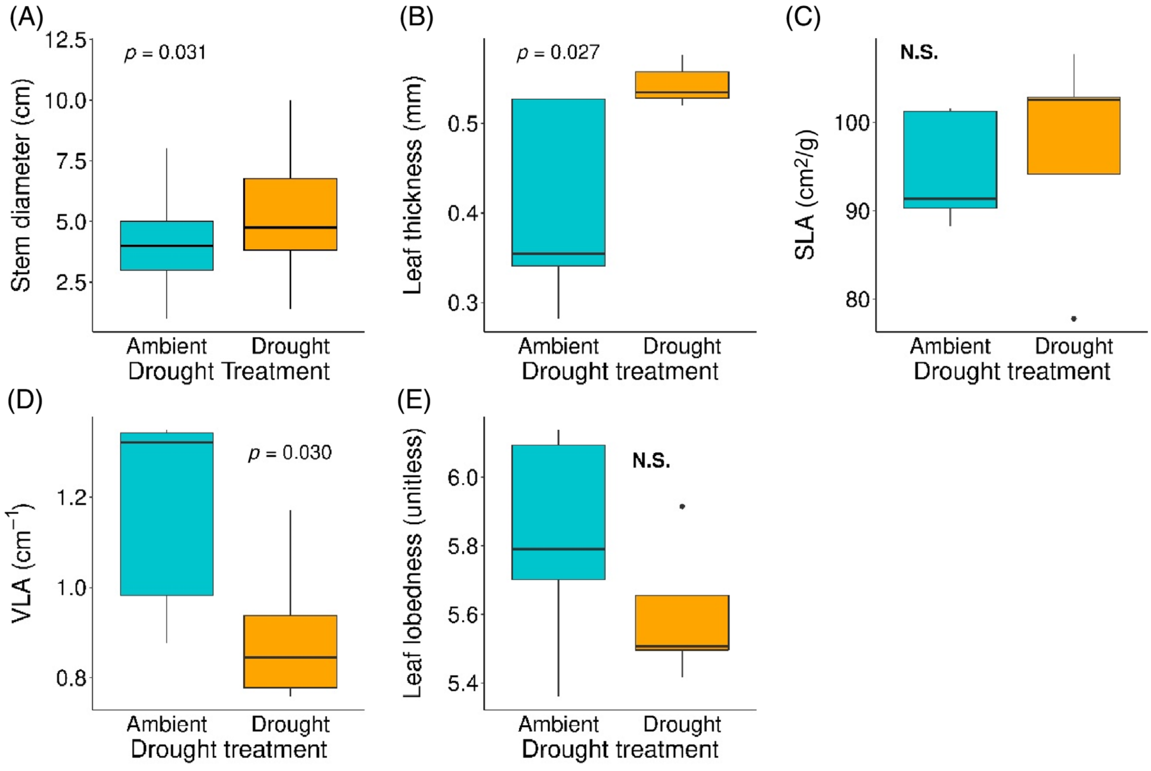

Figure 3. *Baccharis pilularis* (A) stem diameter (cm), (B) leaf thickness (mm), (C) SLA (specific leaf area; cm^2/g), (D) VLA (major vein length per unit area; cm^{-1}), and (E) leaf lobedness (unitless) compared between drought (orange) and ambient (blue) treatments. Leaf traits (B–E) were taken in 2019. Stem diameter was measured in 2020. Boxes represent the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers. N.S., nonsignificant.

($F = 4.30$, $df = 1$, $p = 0.046$), but did not affect cover values ($F = 0.352$, $df = 1$, $p = 0.561$). Abundance did not vary between years ($F = 0.001$, $df = 1$, $p = 0.976$).

B. pilularis exhibited adjustments for stem diameter ($p = 0.031$, $df = 56.48$, $t = -2.21$), major VLA ($p = 0.030$, $df = 7.37$, $t = 2.20$), and leaf thickness ($p = 0.027$, $df = 4.33$, $t = -2.64$), but not SLA ($p = 0.695$, $df = 6.16$, $t = -0.412$) nor lobedness ($p = 0.233$, $df = 6.69$, $t = 1.31$). *B. pilularis* had greater stem diameter and leaf thickness, but lower major VLA on drought plots (Fig. 3).

Bare ground cover increased on drought plots ($F = 7.73$, $df = 1$, $p = 0.013$), but was unaffected by experimental restoration ($F = 0.019$, $df = 1$, $p = 0.891$).

Discussion

Sixyears after initial treatments I found *Baccharis pilularis*growing only in the restored plots, which indicates that restoration activities without ongoing management could facilitate woody shrub encroachment. Although periodic disturbance administered through grazing or prescribed burns can prevent woody species encroachment in grasslands (Smit et al. 2016; Hopkinson et al. 2020; O'Connor et al. 2020), nonperiodic disturbances have been found to positively correlate with *B. pilularis* abundance (Tyler et al. 2007; Laris et al. 2017). When practitioners are performing restoration either through invasive species removal or out-planting, they are creating small nonperiodic disturbances (D'Antonio et al. 2016) which could promote *B. pilularis* recruitment. However, these disturbances are likely supporting recruitment through mechanisms aside from baring ground and clearing open space for germination because the presented data show that drought resulted in decreased *B. pilularis* recruitment (albeit similar cover) despite increased bare ground cover. Soil disturbances often facilitate invasion of seed prolific species like *B. pilularis* because they germinate quickly and have high growth rates (McBride & Heady 1968; Pierce et al. 2017). Planting and invasive species control can also result in reduced soil compaction that facilitates invasion (Kyle et al. 2007).

Because grasslands are historically disturbance-dependent (Ford & Hayes 2007; De Bello et al. 2013; Stevens et al. 2017), especially in California, where grasslands were periodically burned by indigenous tribes as traditional ecological practices (Anderson 2007), the Intermediate Disturbance Hypothesis (IDH) may provide insight on the pattern I observed in this study (Connell 1978; Hobbs & Huenneke 1992). At this study site, the plots were only weeded twice in the first year after a singular planting event, and had no further management actions. The IDH predicts that infrequent or small disturbances are not large enough to maintain extant ecosystem dynamics. Extreme disturbances can push the system toward type conversion (Beisner et al. 2003), whereas moderate or intermediate disturbance is required to maintain the system and maximize diversity (Mayor et al. 2012). Indeed, results support that temporally limited experimental restoration was insufficient disturbance to limit *B. pilularis* recruitment, which may lead to decreased native species richness in later years (Van Auken 2009; Ratajczak et al. 2012). In accordance with IDH, allocating resources to implement a periodic disturbance regime may serve to manage woody species invasion. A review by Hobbs and Huenneke (1992) found that periodic disturbance can maintain and support higher taxonomic diversity, whereas Peterson and Reich (2008) found periodic fire was useful in preventing a gradual conversion of grasslands to forests. Fire employed as a periodic management practice increased native plant and avian diversity in a Brazilian grassland (Beal-Neves et al. 2020). Furthermore, an assessment of the savanna biome found that the occurrence of African savannas was correlated with areas with regular fire return intervals (Lehmann et al. 2011), whereas O'Connor et al. (2020) found fire can reduce the dominance of encroaching shrubs into a native grassland. Moreover, similar to our results, singular prescribed fires (disturbance), were found to promote woody invasion (Abella et al. 2020; Hopkinson et al. 2020).

B. pilularis recruitment was stunted by drought. It is plausible drought could potentially act as an annual or semiregular disturbance event (Derose & Long 2012) preventing type conversion as predicted by the IDH. However, studies from grasslands in both Texas and South Africa suggest that extended droughts may constrain and potentially reverse woody species encroachment (Twidwell et al. 2014; Case et al. 2020). In Australia, woody species encroachment was found to be slowed, but not reversed by extreme drought (Zeeman et al. 2014). Therefore, it is more likely that *B. pilularis* was not able to establish at high rates, in part, due to xeric conditions rather than drought acting as an intermediate disturbance. In fact, it has been observed elsewhere that woody invaders often establish better during wet periods (Williams et al. 1987; Browning et al. 2008).

Observed changes in hydraulic related functional leaf traits may explain, in part, how *B. pilularis* persisted through extreme drought and achieved similar cover as those from control plots at lower abundances. Alternatively, trait differences may be in response to reduced interspecific competition (Bolnick et al. 2011; Welles & Funk 2021). Rain exclusion resulted in *B. pilularis* having thicker leaves but lower major VLA to support reduced leaf water transpiration. Higher leaf thickness can decrease transpiration by increasing mesophyll resistance and reduced major VLA could lead to decreased rates of carbon assimilation and stomatal conductance thereby reducing water transport requirements (Lambers et al. 2008; Sack & Scoffoni 2013; Kröber et al. 2015). It is, however, possible that leaf thickness increased due to nontarget shelter effects (Loik et al. 2019) in response to reduced PAR resulting in compensatory photosynthesis (Lambers et al. 2008). In past work, stem diameter was shown to be negatively related to wood density (Markesteijn et al. 2011), and because increased wood density improves drought and cavitation resistance (Chave et al. 2009), higher stem diameter may promote more drought-related mortality (Twidwell et al. 2014). Stem diameter, similar to cover of *B. pilularis*, likely increased due to reduced intraspecific competition, because it increased as total *B. pilularis* abundance decreased.

These results are novel in documenting woody invasion by a native species following manual hand removal during active grassland restoration. They also support past research that indicates that certain restoration actions can promote woody encroachment into grasslands (Laris et al. 2017; Abella et al. 2020; Hopkinson et al. 2020). Experimental grassland restoration (via planting and nonnative species control) resulted in increased woody shrub invasion compared to nonrestored plots, and *B. pilularis* recruitment, but cover was not diminished, although not reversed by extreme drought. Restoration practitioners that work within coastal grasslands may consider revisiting restored grasslands after planted or an opportunistic targeted weeding event in a subsequent year to ensure their area is not being overtaken by woody species. Practitioners may also consider utilizing periodic prescribed burns which can slow woody species encroachment. In some cases, burns have been shown to reverse encroachment when applied with sufficient periodicity and intensity. Prescribed burns will also clear litter accumulation (Anderson 2007) which can promote species invasions in California grasslands (Stromberg et al. 2007). However, as previously noted, nonperiodic prescribed burns may further promote woody invasion (Abella et al. 2020; Hopkinson et al. 2020). When fire is not feasible, management may consider manual removal with regular return intervals. Spatially and temporally targeted grazing and mowing could also be employed to implement a regular disturbance regime to maintain grasslands. Further research about the rate of woody invasion following grassland restoration using agency implemented projects can indicate if this trend is consistent across larger spatial scales.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. A view from 2021 of each potential factorial treatment combination.
Table S1. The 12 California native planted species that were used in the restoration experiment, their family and life-form.

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