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Impacts and Best Management Practices for Erect Veldtgrass (*Ehrharta erecta*)

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Abstract

Erect veldtgrass (*Ehrharta erecta* Lam.) is an invasive grass actively spreading in California that is capable of invading multiple habitats. Our objective is to contribute to a better understanding of the ecology, impacts, and potential for control of *E. erecta* in order to guide management practices. In a mixed-evergreen forest in Santa Cruz County, we measured impacts of *E. erecta* on native plant species richness and abundance in an observational comparison across 11 sites. Strikingly, we measured nearly four times greater total vegetation cover in plots invaded by *E. erecta*. However, native plants were not significantly less abundant in invaded plots than in reference plots, and native cover was not significantly predicted by *E. erecta* cover within invaded plots. We did, however, find evidence of change in community composition in response to *E. erecta* abundance. Our findings demonstrate that native species can persist in the presence of *E. erecta*, although the long-term impacts on populations of the perennial plants that dominate this forest understory are still unknown.

We also compared the effectiveness of mechanical (hand pulling with volunteers) and chemical (glyphosate) management methods. Twenty-two months following management treatments, we found substantial reductions in *E. erecta* using both mechanical and herbicide treatments, but herbicide application also produced greater reductions in native species cover and species richness. Transplanting native yerba buena [*Clinopodium douglasii* (Benth.) Kuntze] into management plots following treatment did not slow regrowth of *E. erecta*. It did, however, increase total native plant percent cover in herbicide and pull treatments, although largely by increasing *C. douglasii* cover. Effective management is possible using either manual or chemical removal methods; the optimal method may depend on the availability of manual labor and the sensitivity of the habitat to non-target effects on native plants.

Introduction

Invasive plant control can be motivated by a variety of goals, from an aesthetic preference for ecosystems dominated by native species to the mitigation of impacts on biodiversity or economic resources. Management goals usually include reducing the size and spread of the invader population, but may also include increasing native species percent cover or restoring invaded areas to a historical state. To achieve these management goals, potential methods can involve chemical, mechanical, and biological control. Trade-offs among these methods may include implementation time and cost, number of treatments required, non-target effects, and need for follow-up management (Holloran et al. 2004). Selecting the most appropriate method is further complicated by variation in the efficacy of management methods among systems and invader species. Despite the need for strategies to optimize invasion control, studies involving invasive species frequently neglect the applied research questions that are important to stakeholders and would help land managers navigate these decisions (Bayliss et al. 2012; Matzek et al. 2015).

To control an invader, chemical treatments and mechanical removal are among the most common methods employed (Kettenring and Adams 2011). Choosing the right control method without information on its suitability for a system or invader is precarious. Nontested strategies could prove ineffective, exacerbate invasion, or incur additional environmental costs. While chemical treatments require less labor, and are thus less expensive than mechanical treatments, there are potential drawbacks regarding human and environmental health (e.g., Evans et al. 2008; Norgaard 2007). For example, herbicide use can lead to greater reductions in native plant abundance and diversity compared with mechanical methods (Flory and Clay 2009). These impacts in some cases are long-lasting—at least 16 yr in the case

Management Implications

This study measures the invasion impacts of erect veldtgrass (*Ehrharta erecta* Lam.) and compares the efficacy and cost of six management approaches. This is the first extensive management study known to us that focuses on *E. erecta* in its U.S. range. We found that both herbicide and manual removal were effective at reducing *E. erecta* abundance relative to the control and that multiple treatments would be necessary to eradicate the grass at local scales. We also found greater non-target effects with herbicide compared with manual removal. We recommend that this study be referenced for *E. erecta* management and considered an example of an invasion where the effectiveness of multiple management treatments allows for choices based largely on economic and labor resources. Interestingly, while *E. erecta* biomass increased greatly and we found some evidence of community structure change in response, by other measures of invasion impact, we did not find significant changes to the native community (e.g., percent cover native species, species richness). In this community *E. erecta* may not compete strongly with native plants because it is a novel functional group in the system. Alternatively, the effects of *E. erecta* may not have manifested themselves fully yet because the native community is dominantly perennial and the invasion is recent. We recommend that land managers consider community-scale changes and more subtle effects of the invasions, such as reduced pollination or reduced recruitment due to high invader cover.

reported by Rinella et al. (2009). On the other hand, depending on the scale of the invasion and the terrain, mechanical control is often not possible. When it is feasible, it can be disruptive to the soil, potentially causing damage to the roots of non-target species (Holloran et al. 2004) and stimulating germination from the invaders' seedbank.

Knowledge of community interactions and the non-target impacts of management methods on other plants can help managers decide between chemical and mechanical control. Resident plant communities can play an important role in reducing invader numbers (Levine et al. 2004). If invasion by nonnative species is limited by established species, control methods that reduce total plant abundance could leave the treated area vulnerable to reinvasion by the target nonnative or colonization by other invasive species. Both chemical and mechanical control methods can facilitate invasion by reducing the biotic resistance from resident species, and it is important to determine the effects of control methods on resident species to limit undesired outcomes (Flory and Clay 2009).

Because both invasion (Corbin and D'Antonio 2012; Grove et al. 2012) and management treatments (Rinella et al. 2009) can have legacy effects that limit native species success, it is also important to test whether desired species can establish in invaded systems before and following management. Where native plants provide biotic resistance to invasion, supplementing plant cover with competitive native species following management application can serve as an important strategy to limit nonnatives (Funk et al. 2008; Kettenring and Adams 2011). In some systems, native species can reestablish without any further intervention following invader removal. However, in systems where plants are dispersal limited or where desired natives have been extirpated, addition of native seeds or seedlings may be essential (Holloran et al. 2004).

A current challenge facing land managers in California is the spread of the nonnative perennial grass, erect veldtgrass (or panic veldtgrass) (*Ehrharta erecta* Lam.) (Holloran et al. 2004). Native to several countries in eastern and southern Africa (U.S. National Plant Germplasm System n.d.) and Yemen (Wood 1997), *E. erecta* is found in varied habitats in its native range, including shady forest, open areas, disturbed areas, and sand dunes (Launert 1971). *Ehrharta erecta* was first recorded in North America around 1930 in northern California as an adventive species (Stebbins 1985). *Ehrharta erecta* is now present in multiple counties in California (Calflora 2017) and is a common invasive species in several places around the world, including Hawaii, Australia, New Zealand, the Mediterranean, and China (Frey 2005). Despite its extensive nonnative range, little is known about the impacts of *E. erecta* invasion or best management practices (Pickart 2000), though both chemical and mechanical treatment methods have been suggested by practitioners (Holloran et al. 2004).

As an invader, *E. erecta* is especially worrisome, because it can tolerate a wide range of abiotic conditions, which facilitates its spread into diverse habitat types, including sand dunes, closed-canopy forest, riparian areas, and roadsides (Riefner and Boyd 2007; Sigg 1996). *Ehrharta erecta* is able to tolerate drought conditions (Manea et al. 2016) and high shade, but it also thrives in mesic soils (McIntyre and Ladiges 1985). In an experiment comparing nonnative *E. erecta* with Australian native grasses, *E. erecta* showed signs of greater invasion potential under drought conditions due to reduced competition from native plants (Manea et al. 2016).

We studied the ecological impacts and management of *E. erecta* in mixed-evergreen forest in coastal California. We assessed: (1) the impacts of *E. erecta* invasion on native species richness and cover using observational comparisons; (2) the efficacy of chemical and mechanical treatments for managing *E. erecta*, as well as the non-target impacts on native plants; and (3) the effect of native plant addition on species richness and regrowth of *E. erecta* after treatment.

Materials and Methods

Field Site and Focal Species

We conducted this study on the campus of the University of California, Santa Cruz (UCSC) in mixed-evergreen forest. Twelve sites were selected from an area of approximately 2.3 km^2 and included both natural and disturbed areas and different dominant canopies, to capture the diversity of habitats *E. erecta* grows in on campus (Sherman 2012). Canopy species include coast redwood [*Sequoia sempervirens* (D. Don) Endl.], coast live oak (*Quercus agrifolia* Née), Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], and California bay [*Umbellularia californica* (Hook. & Arn.) Nutt.]. The common understory plants are all native species, including California hedgenettle (*Stachys bullata* Benth.), California blackberry (*Rubus ursinus* Cham. & Schltdl.), yerba buena [*Clinopodium douglasii* (Benth.) Kuntze], common snowberry [*Symphoricarpos albus* (L.) S.F. Blake], and western brackenfern [*Pteridium aquilinum* (L.) Kuhn] (Dashe and Hayes 2008). The climate regime of this region is Mediterranean, with characteristic cool wet winters and warm dry summers. *Ehrharta erecta* was deliberately planted on the UCSC campus in three locations on December 16, 1964 (Stebbins 1949–1981). Since its introduction, it has spread considerably on the campus and may also be the source of *E. erecta*

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invasions in urban areas of Santa Cruz and the adjacent Santa Cruz Mountains (Sherman 2012).

Ehrharta erecta can reach heights of 60 cm, has 5- to 15-cm-long leaves, and 6- to 20-cm-long panicle-like inflorescences with sessile to subsessile spikelets that look like beads on a necklace (Holloran et al. 2004; Smith 2012). *Ehrharta erecta* grows in dense mats that can exclude natives (Sigg 1996). In 2006, the California Invasive Plant Council classified *E. erecta* as a moderate invader (Cal-IPC 2017), a ranking that is applied to invasive species with nonsevere ecological impacts that often require specific environmental conditions to invade and are not dispersal limited. Two other *Ehrharta* species are invasive in California, longflowered veldtgrass (*Ehrharta longiflora* Sm.) (annual) and perennial veldtgrass (*Ehrharta calycina* Sm.) (perennial). *Ehrharta erecta*, *E. longiflora*, and *E. calycina* have similar flowering times and relative growth rates, which occur earlier and are faster, respectively, than other species in the genus, which perhaps contributes to their invasiveness (Verboom et al. 2004). In the genus, *E. erecta* is the most widespread globally (Gluesenkamp 2004).

Ehrharta erecta spreads through seed and vegetatively via tillers (Holloran et al. 2004). It is highly fecund (Ogle 1988), and its seeds are easily dispersed by wind, scat (Holloran et al. 2004), water (Frey 2005), and hitchhiking. McIntyre and Ladiges (1985) found that fresh *E. erecta* seeds collected in Australia required a dormancy period before they were able to germinate. However, other studies found that mature *E. erecta* seeds collected directly from the plant could germinate immediately (Gluesenkamp 2004).

To test the effectiveness of native plant revegetation as a technique to reduce *E. erecta* regrowth following removal, we planted *C. douglasii*. A perennial herb in the mint family (Lamiaceae), *C. douglasii* reproduces both sexually and asexually and has a sprawling habit, often forming small mats (Dashe and Hayes 2008). We selected *C. douglasii* because it is easy to propagate, and its low sprawling habit allows it to cover lots of space.

Assessment of *Ehrharta erecta* Invasion Impacts and Management Methods

In 2012, we selected 12 sites from across the invaded area of *E. erecta* on the UCSC campus (Sherman 2012). At each site, we delimited three 4-m^2 treatment plots and randomly assigned them to one of three treatments: herbicide, pull (mechanical removal), or control. In December 2012, we applied the assigned management treatment to all plots. We estimated baseline (pretreatment) percent cover of all herbaceous understory species, but were only able to collect these data on a subsample of 7 out of 12 sites.

Herbicide-treated plots were sprayed until wet with an approximately 2.5% glyphosate solution (Prokoz Glyphosate Pro® 4 [Prokoz, Alpharetta, GA] for all herbicide treatments). While we targeted *E. erecta* patches, the herbicide application method is not specific, and native plants were also sprayed. In mechanical removal plots, researchers and volunteers hand pulled all *E. erecta* vegetation, including roots, being careful to minimize disrupting all other species.

Following the treatment, we assessed the efficacy of the prescribed control methods by estimating percent cover in all plots in January/February 2013. Because some *E. erecta* survived the initial herbicide treatment, a follow-up treatment using a 3% to 4% glyphosate solution was applied soon after this survey, spraying again until wet. At the same time as we resprayed herbicide plots, we also did a follow-up treatment in the mechanical removal plots, removing all new *E. erecta* growth. We surveyed the plots again in October 2014, at 22 mo following the initial treatment. Because one site was destroyed by construction equipment, it was excluded from the final census. To measure plant cover, we subdivided each plot into nine 0.5 by 0.5 m^2 sections leaving a 0.25-m buffer on each side. Randomly selecting three of those nine subplots in each plot, we estimated percent cover of all species using the point intercept method with a 100-point grid. Individual points could have multiple layers of plants, allowing percent cover to exceed 100%.

To measure how *E. erecta* impacts native species richness and cover, in May 2013 we established one 4-m^2 noninvaded reference plot at 11 of 12 sites to compare with the invaded control plot described earlier. We were unable to have a reference plot at all sites, because at one site we could not find a representative noninvaded area nearby. Reference plots were selected by standing in the center of the site and walking in the direction of a randomly selected bearing until reaching a 2 by 2 m^2 area completely free of *E. erecta*. All reference plots were within a few meters of the treatment plots. In October 2014, we estimated percent cover of all species in these plots as described earlier.

Native Species Addition Experiment

To test whether transplanting *C. douglasii* posttreatment had a persistent effect on native species cover and whether it affected the regrowth of *E. erecta*, we set up three additional 1 by 0.5 m^2 plots at five of the sites used in the previous experiments. In March 2013, we randomly assigned three treatments (herbicide, pull, or control) to plots at each site. For herbicide plots, we used a ~2% glyphosate solution that included a blue dye. Plants were sprayed until completely tinted blue. In May 2013, we split these plots into two 0.5- by 0.5-m^2 sections and randomly assigned one side to native plant addition, where we planted nine *C. douglasii* plants in a grid formation with 12.5-cm spacing. Transplanted cuttings were watered for 2 wk, each receiving 0.3 L of water every other day. The *C. douglasii* used in this study were propagated from cuttings of plants collected from the UCSC campus in December 2012. Before their use in this experiment, the cuttings were grown in Cone-tainers™ (Stuewe and Sons, Inc., Tangent, OR; 3.8-cm diameter, 14-cm deep) in the UCSC greenhouses, where they were misted twice daily and kept in mild temperatures (7 to 18 C), then transferred to an outdoor growing space in January 2013. The mean length of transplanted cuttings was 17.9 cm ($\pm$ SE 0.76). Percent cover for all species was estimated in October 2013 and 2014, 7 and 19 mo following initial treatment. As in previous experiments, we used a 0.5- by 0.5-m^2 quadrat with 100 points for all censuses.

Analyses

All described analyses were conducted in R (R Core Team 2016).

Assessment of *Ehrharta erecta* Invasion Impacts and Management Methods

We compared native species percent cover, total percent cover, and species richness in October 2014 in invaded control plots and uninvaded reference plots using generalized linear mixed models (GLMMs) in the 'lme4' package in R (Bates et al. 2015). Unidentified species were included in the total percent cover and species richness. In the GLMMs, treatment was a fixed effect, plot and site were random effects, and the family was a Poisson distribution with a log-link function. Significance ($P \leq 0.05$) was determined using the **summary** function.

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We measured the response of total and native plant cover to *E. erecta* percent cover separately using simple linear regression. We calculated these models with census data from control plots in October 2014, using the average of the three subplots.

Ehrharta erecta percent cover, native species percent cover, and species richness in response to treatment were analyzed for December 2012 (pretreatment), January/February 2013, and October 2014 census data. Again, unidentified species were included in the total percent cover and species richness. Because our *E. erecta* percent cover and native species percent cover were overdispersed when all treatments were considered, we used a GLMM with a negative binomial distribution for each census. Site and plot were random effects. To compare significance across all treatments, we releveled fixed effects once for 2012 and 2013, and twice for 2014, which included a reference treatment. Because species richness was not overdispersed, we were able to use a Poisson distribution with a log-link function. Treatment was a fixed effect, and site and plot were random effects for all analyses.

We compared community composition across the four plot types (control, herbicide, pull, and reference) using the October 2014 census data. Because *E. erecta* is dominant in some of our experimental plots and absent in others by experimental design, we excluded it from our analyses to better perceive differences in the rest of the community. Percent cover was averaged across subplots before analysis, because in some subplots, particularly in herbicide, we recorded zero plant cover. After averaging, some plots still had zero cover, so we measured community distance using Manhattan distances. Manhattan distances are a good choice when the species pool is small and when joint absence of a species should contribute to the similarity between a pair of samples. Using the calculated Manhattan distances, we performed nonmetric multidimensional scaling (NMDS) with the R package 'vegan' (R package v. 2.4-0), comparing among dimension sizes to select a model with low stress. We assessed differences among treatments visually in the NMDS ordination diagram.

To analyze differences in community composition in response to site and treatment (control, pull, herbicide, and reference) we used the model-based, multivariate analysis *manyglm* (package 'mvabund' v. 3.12). Generalized linear models were fit using the sum total percent cover across the three subplots without averaging. To assess significance of the fixed effects, we used the randomization test implemented in the *anova()* function in 'mvabund' with 999 randomizations.

To model the effects of *E. erecta* abundance on community structure, we again used multivariate glm (function *manyglm*) on the abundance of all species (*E. erecta* excluded) in reference and control plots in October 2014. Site and *E. erecta* percent cover were fixed effects. We used the same randomization test as above.

Native Species Addition Experiment Analysis

We tested the effects of transplanting *C. douglasii* on *E. erecta* regeneration, native species cover, and species richness in October 2013 and 2014 (5 and 17 mo postplanting, respectively) using GLMMs. *Ehrharta erecta* cover was modeled with a negative binomial distribution due to overdispersion, while native cover and species richness were modeled with a Poisson distribution (link = log). The management treatment (control, herbicide, and pull), the restoration treatment (with or without *C. douglasii* addition), and the interaction of those treatments were fixed effects. Plot, which encompassed both sides of the split-plot design, and site were random effects. For convergence in the 2014 model of *E. erecta* percent cover, we used an orthogonal set of contrasts and did not use initial optimization (nAGQ = 0) to improve initial estimates of the fixed parameters. Significance was determined in all models using the post hoc test lsmeans (Lenth 2016).

Results and Discussion

The Impacts of Ehrharta erecta Invasion on Native Species Richness and Cover

Comparing noninvaded reference plots with invaded control plots, invasion was not associated with lower native species percent cover (Supplementary Table 1) or lower species richness (Supplementary Table 1). However, total vegetation cover was about 4-fold greater in invaded plots (Figure 1B).

In invaded control plots considered separately, *E. erecta* density varied strongly across sites and strongly predicted total vegetation cover ($y = 13.50 + 1.033x$, $t = 12.99$, $n = 11$, $P < 0.0001$, $R^2 = 0.95$). Despite this, we did not find a relationship between *E. erecta* percent cover and native species percent cover for plots with *E. erecta* present ($y = 13.00 + 0.034x$, $t = 0.42$, $n = 11$, $P = 0.68$, $R^2 = 0.019$; Figure 2).

Chemical versus Mechanical Control: Target and Non-target Effects

Although we randomly assigned treatments to our experimental plots, by chance, pretreatment percent cover of *E. erecta* (December 2012) was significantly greater in the pull plots than the control and herbicide plots. *Ehrharta erecta* percent cover did not significantly differ between control and herbicide plots (Figure 3A; Supplementary Table 2). This higher pretreatment cover in pull plots was driven by extremely high density in three subplots at one site and two subplots at two other sites.

One to two months following treatment (January/February 2013), we found both manual removal in the pull plots and herbicide yielded significantly lower *E. erecta* percent cover than the control. In addition, hand pulling was more effective at removing *E. erecta* compared with herbicide, as assessed at this early stage (Figure 3A; Supplementary Table 2).

Twenty-two months following treatment (October 2014), we still found that *E. erecta* in herbicide and pull plots was significantly lower than the control. However, faster regrowth of *E. erecta* in pull plots compared with herbicide resulted in significantly greater cover in pull versus herbicide plots (Figure 3A; Supplementary Table 2).

Plant communities exhibited a high degree of variation due to treatment. Before implementation of control methods, native species percent cover did not significantly differ across plot types (Figure 3B; Supplementary Table 3). One to two months after treatment, percent cover of native species was significantly lower in plots treated with herbicide than pull or control plots (Figure 3B; Supplementary Table 3). Lower percent cover of native species compared with other treatments persisted in herbicide plots 22 mo following treatment (Figure 3B; Supplementary Table 3).

The response of species richness to management also varied by treatment. Before implementation of management methods, species richness did not significantly vary across plot types (Figure 3C; Supplementary Table 4). One to two months following treatment, richness was significantly lower in herbicide and pull plots compared with the control (Figure 3C; Supplementary Table 4). Twenty-two months following application, species richness recovered in the pull plots and was no longer significantly

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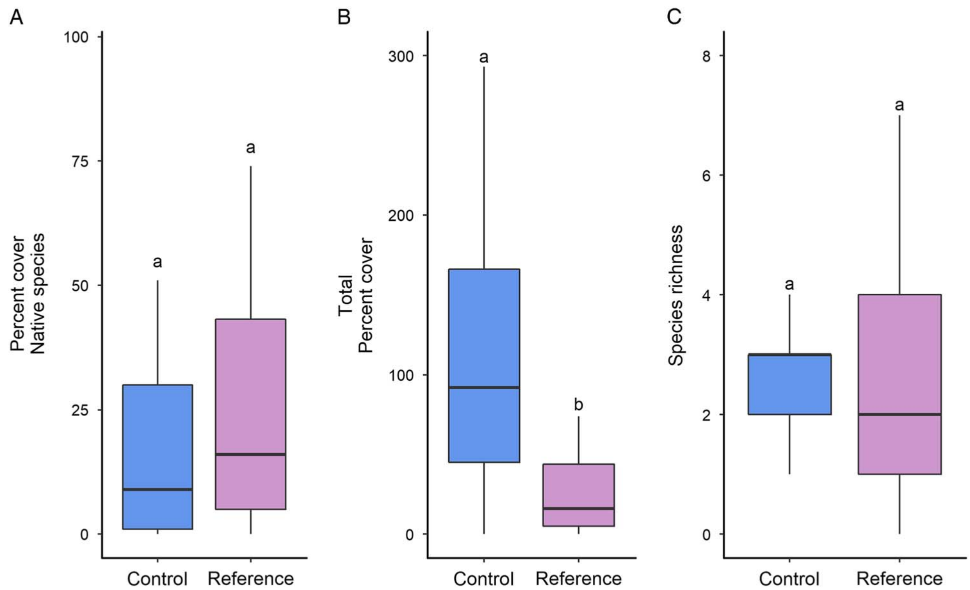

Figure 1. Measure of impact between noninvaded reference plots and invaded plots (==control) from October 2014: (A) native species percent cover, (B) total percent cover, and (C) species richness. Whiskers extend to the outermost points within 1.5*interquartile range; outliers are not shown.

different from control or reference plots. Nearly 2 yr following treatment, species richness in herbicide plots had not recovered to pretreatment levels (Figure 3C; Supplementary Table 4).

Finally, even though native species cover and species richness did not significantly differ across treatments, there were still community-level differences that were detectable in the NMDS plot (Figure 4). Community-level differences were greatest between the herbicide treatment and pull, control, and reference plots. We also found little overlap between control and reference plots (Figure 4). Multivariate analysis revealed significant differences among sites ($n = 11$, $P = 0.001$) and among treatments ($n = 4$, $P = 0.001$). Using only control and reference plot data, we found no evidence of significant differences in community composition among sites ($P = 0.526$), but did find evidence of a response in composition to *E. erecta* abundance ($P = 0.055$). The *anova()* function used to calculate these P-values uses resampling-based hypothesis testing, and in this case we found that stochasticity causes variation in P-values from 0.04 to 0.068.

Native Species Addition Experiment

Within management treatments we did not find that *C. douglasii* addition affected recovery of *E. erecta* (Figure 5A; Supplementary Table 5). Five months after transplanting, native cover was significantly greater in plots where *C. douglasii* was added, though by 17 mo, transplanting only significantly increased native cover

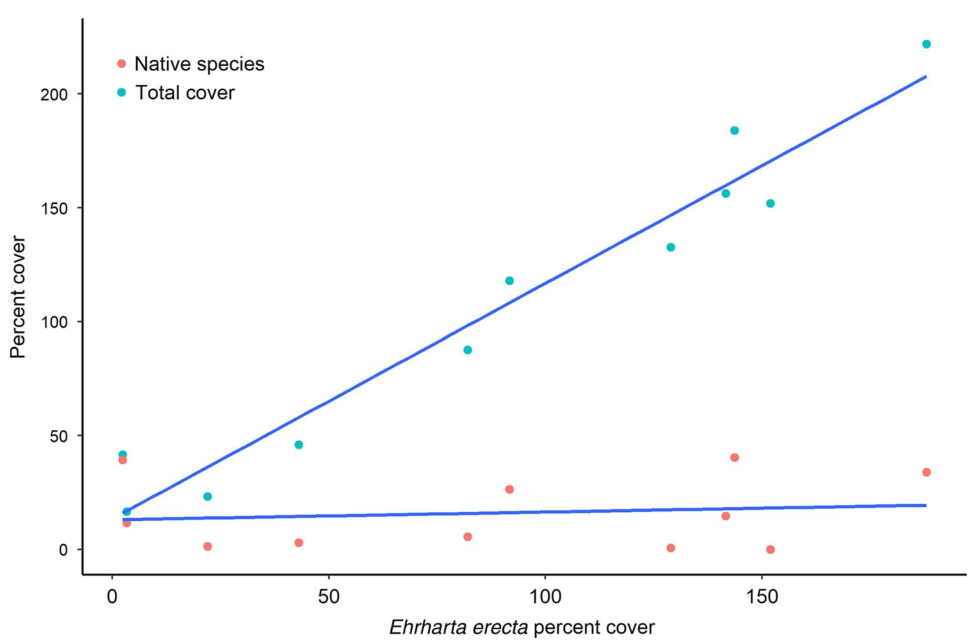

Figure 2. Native and total percent cover versus *Ehrharta erecta* percent cover in control plots (linear regression, $n = 11$), October 2014. Total species percent cover: $y = 13.50 + 1.033x$, $R^2 = 0.95$. Native species cover: $y = 13.00 + 0.034x$, $R^2 = 0.019$. Points are averages across three subplots.

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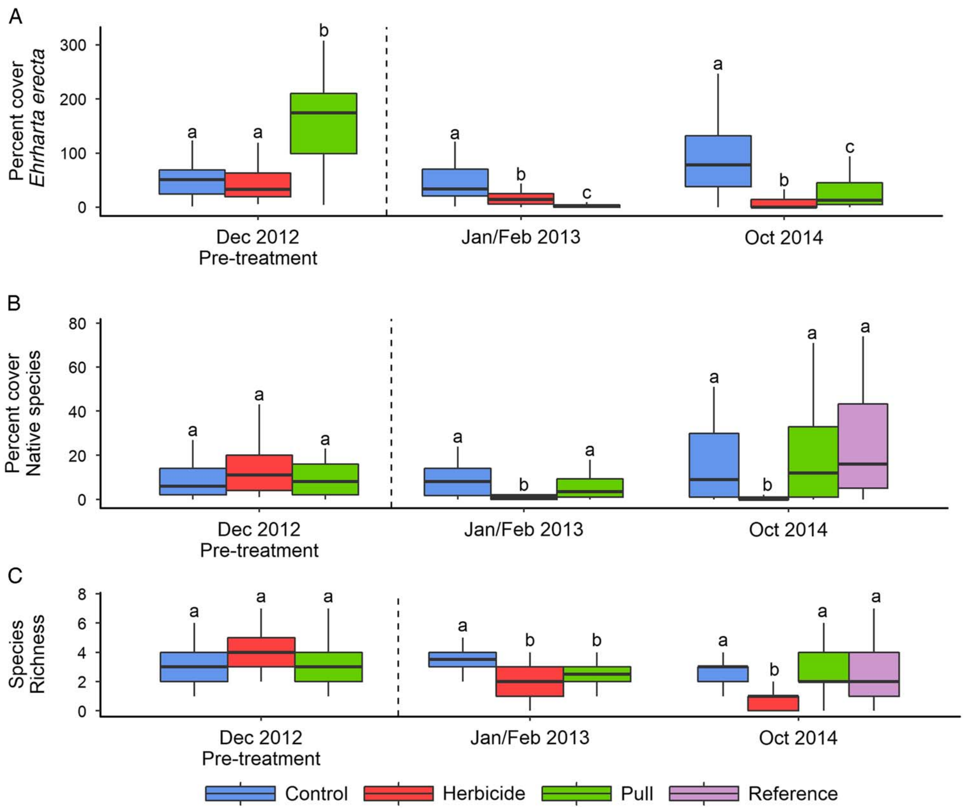

Figure 3. (A) Percent cover of *E. erecta*, (B) percent cover of native species, and (C) species richness per 0.25 m^2 quadrat by census and treatment type. Data were collected before treatment in December 2012, 1 to 2 mo after initial treatment in January/February 2013, and 22 mo following initial treatment in October 2014. Whiskers extend to the outermost points within 1.5*interquartile range; outliers are not shown.

in herbicide and pull plots (Figure 5B; Supplementary Table 6). *Clinopodium douglasii* did not significantly increase species richness 5 or 22 months following transplanting (Figure 5C; Supplementary Table 7).

General Discussion

We found mixed evidence for negative effects of *E. erecta* invasion on native California coastal mixed-evergreen forest communities. We observed almost four times greater total vegetation cover in invaded control plots than in noninvaded reference plots, and we observed an effect of *E. erecta* abundance on community composition. The increase in plant biomass may drive changes in the native plant community through changes to the physical environment, such as soil surface temperatures, moisture availability, and nutrient cycling. Higher plant biomass could also change communities of both soil invertebrates and microbes, such as mycorrhizal fungi. From earlier studies, we have evidence of competitive effects of *E. erecta* on some native species. Hanson (2014) measured significant competitive superiority of *E. erecta* over *R. ursinus*, California figwort (*Scrophularia californica* Cham. & Schltdl.), and *C. douglasii* (but not wood strawberry [*Fragaria vesca* L.]) in a greenhouse experiment, while Godinho (2013) found that removing *E. erecta* from around *S. bullata* in the field increased transpiration rates and chlorophyll content (although the opposite trend was found for *C. douglasii*).

By other measures, however, impacts of *E. erecta* were not evident. In invaded plots, native plant cover was about 11% lower than reference plots, although this difference was not significant. In invaded plots across sites, we did not find a negative relationship between *E. erecta* density and native plant cover. Our assessments of invasion impact (invaded control plots vs. noninvaded reference plots, and analysis of native species cover across invader densities) are observational and therefore may reflect correlated factors, as has been pointed out in other critiques (e.g., MacDougall and Turkington 2005). Of course, the impacts of invasion on native species may also vary by environmental context (Daehler 2003) and depend on scale (Powell et al. 2013). In an extensive meta-analysis, Vila et al. (2011) found that invasions generally cause reductions in plant species abundance and diversity and lead to increased total production. However, in our findings, native plant cover and species richness did not vary significantly between invaded and noninvaded plots. In some systems, invaders may fill open niches in the absence of competitive exclusion (Davies et al. 2011). Total vegetation cover in our noninvaded reference plots was only 27.4 ± 30.25% on average (mean ± SD%, October 2014), suggesting that this plant community may not be saturated. On the other hand, there may be a lag in the ecological impacts of *E. erecta*. The native redwood understory community is dominated by long-lived perennials. For example, in control plots with high *E. erecta* abundance, the most common native plants remaining were *R. ursinus*, *C. douglasii*, and *S. bullata* (October 2014 data).

Because *E. erecta* is a dense, mat-forming species, it may either compete directly with seedlings of other species or obstruct native seeds from reaching the soil (Sigg 1996), which could lead to lower recruitment. Alternatively, impacts on native recruitment in this system may be negligible for some native species due to their ability to propagate vegetatively (e.g., *C. douglasii*, *S. bullata*, *F. vesca*, *R. ursinus*, *S. albus*, and redwood sorrel (*Oxalis oregana* Nutt.). *Ehrharta erecta* was introduced to the UCSC campus in 1964 and was still limited in extent as late as 2000 (IM Parker, personal

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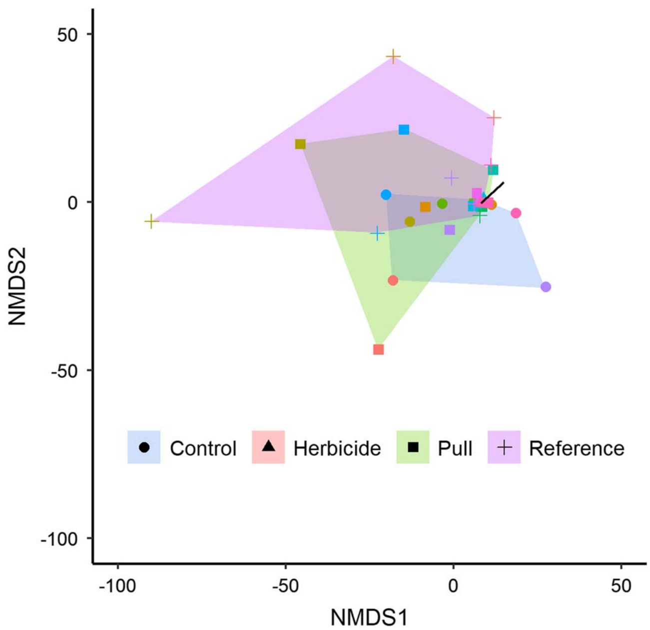

Figure 4. Nonmetric multidimensional scaling (NMDS) using Manhattan distances from the October 2014 census with *Ehrharta erecta* cover excluded. Using Manhattan distances allows us to account for species abundance and shared species absences, while the NMDS allows us to compare community composition using rank order of the distances. Each symbol corresponds to a treatment and the color of the symbol corresponds to a site ($n = 11$). Polygons overlie all sites within a treatment and are distinct by color. Due to its small size at this scale, the approximate location of the herbicide polygon is indicated with a black line. Herbicide plots range from [7.34861, −1.2283] and [6.767844, −0.85864] (lowest NMDS1 and NMDS2 values, respectively) to [8.859624, 0.875689] (highest NMDS1 and NMDS2 values).

observation), so its extensive invasion into local forest understory is new. The long-term impacts on the recruitment of long-lived perennial herbs, shrubs, and trees deserves careful future study.

Apart from its impacts on native species abundance and richness, *E. erecta* invasion changes the character of the coastal mixed-evergreen forest, dramatically increasing herbaceous plant abundance. This increased plant cover may represent an aesthetic and ethical impact for some, as *E. erecta* transforms an iconically sparse and open redwood understory into a savannah-like, grass-filled landscape. On the UCSC campus, grounds services now mow the redwood forest understory where *E. erecta* has invaded as part of their normal maintenance of paths and rights-of-way. This management activity will likely favor the growth of invasive *E. erecta* over the native understory shrubs, reinforcing the change in plant composition.

Our results suggest that substantial reduction of *E. erecta* cover for up to 2 yr is possible through both chemical and mechanical treatment methods. Averaged across all censused plots, in October 2014 compared with December 2012 (pretreatment), *E. erecta* percent cover was 59% lower in herbicide plots, 76% lower in pull plots, and 82% more abundant in control plots. However, one or two control treatments are not sufficient to fully eradicate *E. erecta* at this scale. Although *E. erecta* percent cover was still significantly lower in the pull and herbicide plots relative to the control in October 2014, *E. erecta* abundance was significantly greater in pull plots than in herbicide plots. The greater pretreatment abundance of *E. erecta* in pull plots (by chance) could have contributed to faster regrowth. To explore this possibility, we tested whether the seedbank was larger in pull plots than herbicide and control plots and did not find significant differences among treatments (Ray 2016).

The greater regrowth of *E. erecta* following hand pulling could reflect that soil disturbance promotes *E. erecta* regeneration from the seedbank. *Ehrharta erecta* is a mat-forming species with roots that extend several centimeters deep, so manual removal of *E. erecta* could exhume seeds and stimulate germination. When sites were re-treated in January and February 2013, recently germinated seeds rather than resprouts made up nearly all the new *E. erecta* growth. While manual removal is an effective strategy for removing adult plants, herbicide may be more appropriate for controlling *E. erecta* where there is an established seedbank. Alternatively, a useful strategy for future experiments may be to combine mechanical and chemical treatments to reduce both soil disturbance and herbicide use. For example, mowing *E. erecta* and then spraying the base with herbicide may be effective at controlling *E. erecta*, as well as reducing some non-target effects.

We saw strong variation in *E. erecta* regrowth across sites. It is interesting to note that the site where control methods were least effective at managing *E. erecta* was located at the base of a large storm-water drainpipe that keeps the area wetter than other sites. The timing of this experiment overlapped with some of the driest years on record in California, and the rapid regrowth of *E. erecta* at this site could indicate that the invader benefited from the mesic conditions. In other parts of its invaded range, *E. erecta* has been shown to be an effective competitor with native species under drought conditions (Manea et al. 2016), and our results are another example of the capacity of this plant to thrive under diverse abiotic conditions.

Management Costs

Because both manual removal and chemical control effectively reduce *E. erecta* cover, consideration of trade-offs will help land managers select the option most appropriate for their management goals and resources. Chemical treatment requires the lowest time investment but comes with the additional cost of often having to be applied by someone trained and certified in its use. Each of our herbicide applications was applied by a member of the UCSC grounds services. The labor costs were approximately \$39.00 h^{-1} for a total of \$156.00 for 4 h (2 h per application). Approximately 7.5 L of glyphosate solution were needed to spray twelve 4-m^2 plots. Averaging the percentage of glyphosate used in the two applications to 3%, we used a total of 0.47 L of glyphosate, for a cost of \$23.52. Hand pulling required many more person-hours than herbicide application. Twenty-one volunteers helped pull *E. erecta* from our treatment sites for the first experiment. Before going into the field, volunteers were instructed for approximately 20 min on how to identify *E. erecta* and the importance of removing all vegetative material while avoiding other plant species. During the hand pulling, two leaders familiar with the experimental protocol and species identification were on hand to direct the volunteers and answer any questions. In a period of approximately 2 h, the volunteers manually removed *E. erecta* from eight 4-m^2 treatment plots, for a total of 32 m^2. We estimate that each volunteer pulled at a rate of approximately 0.75 to 1 m^2 h^{-1} (32 m^2/21 people/2 h, including transit time between plots). Remaining plots were pulled by CAR and student volunteers. Assuming all volunteers pulled at the faster rate of 1 m^2 h^{-1}, it took 48 person-hours to manually remove *E. erecta* from our plots, plus the staff time for instruction and guidance of the volunteer team. While this labor was free for us, if land

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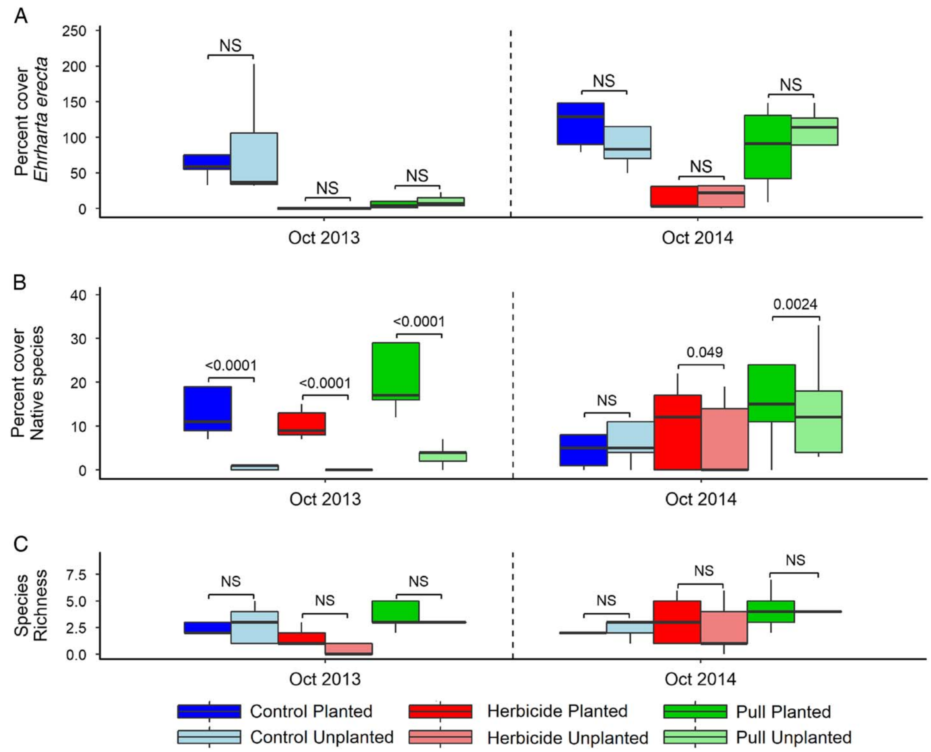

Figure 5. (A) Percent cover of *E. erecta*, (B) percent cover of native species, and (C) species richness for plots subjected to different treatments and with and without *C. douglasii* planted. Plots were censused at 5 and 17 mo following planting in May 2013. Whiskers extend to the outermost points within 1.5*interquartile range; outliers are not shown.

managers had to pay their crews wages, manual removal would be a more expensive treatment than herbicide application.

Non-target effects, however, were greater with herbicide compared with hand pulling. We observed significant reductions in native species richness and cover in herbicide plots even 22 mo following treatment. Such strong non-target effects argue against the use of this approach for some resource management situations, such as in locations with species of special concern. However, in the mixed-evergreen understory systems where we were working, plant species are largely widespread and common, so the non-target effects of chemical treatments might represent an acceptable trade-off. Using a grass-specific herbicide, rather than a broad-spectrum herbicide like glyphosate, could help reduce non-target mortality, but these herbicides are often more expensive and have higher toxicity ratings. Their use is not permitted at UCSC (B Reid, personal communication).

Although competition from restored native species could help slow the regrowth of an invader, transplanted *C. douglasii* did not slow regrowth of *E. erecta* in this case. Transplanting native species may be necessary to meet certain restoration goals, such as increasing native species cover in invaded areas and/or mediating the non-target effects of management. Planting *C. douglasii* did increase native cover (though mostly of that species) in pull and herbicide plots after 22 mo, despite strong drought conditions. We did not find an increase in species richness in any treatment after 5 or 22 mo.

Conclusions

The results of this study highlight the necessity of studying the ecology and management of individual invaders, both to generate general syntheses in invasion biology and to help guide prioritization of invasion problems on the ground. Despite widespread recognition that *E. erecta* is spreading extensively and is a species of management concern (Cal-IPC 2017), surprisingly few studies have been published on its ecology or control in California. Unfortunately, this species is not an outlier; the scope of species that have been studied is narrow. For example, Cal-IPC lists 225 species as invasive in California (Cal-IPC 2017). Across 347 articles on Californian invasive species from 20 journals published from 2007 to 2011, Matzek et al. (2015) found that four nonnative species were the focus of 44% of the Californian invasion literature. This paucity of studies on the impacts and management of the majority of invaders contributes to the challenges land managers face in strategizing which invaders to target and which treatments to apply (Matzek et al. 2015).

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Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/inp.2018.2

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