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INVADING COASTAL CALIFORNIA'S FORESTS: IMPACTS AND BEST MANAGEMENT PRACTICES FOR THE PERENNIAL GRASS, EHRHARTA ERECTA

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ABSTRACT

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INVADING COASTAL CALIFORNIA'S FORESTS: IMPACTS AND BEST MANAGEMENT PRACTICES FOR THE PERENNIAL GRASS, EHRHARTA ERECTA

Ehrharta erecta (panic veldt grass) is an actively spreading invasive grass in California with an uncommon capacity to invade forest understory. Greater understanding of the ecology, impacts, and potential for control of this invader is needed to set priorities and guide management. In a mixed-evergreen forest in Santa Cruz County, we measured impacts of *E. erecta* on native plant species richness and abundance, quantified the effectiveness of mechanical and chemical management methods, and tested whether this species forms a seed bank. We found lower percent cover of native species in plots invaded by *E. erecta* compared to nearby non-invaded plots, but we did not find significant differences in species richness, and we did not find a significant relationship between *E. erecta* cover and native cover in invaded plots. Strikingly, we measured nearly four times greater total vegetation cover in *E. erecta* invaded plots. Twenty-two months following management treatments, we found significant reductions in *E. erecta* using both mechanical and chemical methods. Herbicide application produced greater non-target effects. In a separate experiment, we tested the effects of native plant addition on restoration outcomes and regrowth of *E. erecta.* Transplanting native *Clinopodium douglasii* into management plots did not slow regrowth of *E. erecta*. Transplants did increase the percent cover native plants, but only by increasing *C. douglasii* itself. Finally, in a greenhouse

experiment we compared the number of *E. erecta* germinants from duff and soil collected from two depths. *Ehrharta erecta* germinated from all three substrates, with the greatest number of germinants in the upper soil layer, suggesting that *E. erecta* seeds accumulate in the soil over time. The results of this research demonstrate that *E. erecta* drives ecological change in a mixed-evergreen forest community, effective management is possible using manual and chemical removal methods, and restoration of native species can be promoted through planting. Since we found evidence that *E. erecta* forms a seed bank, we recommend rapid response to *E. erecta* invasion and consideration of management methods that have low soil disturbance in treating established *E. erecta* populations.

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INTRODUCTION

Land managers regularly must decide whether it is worthwhile and feasible to control a given invasive species and then devise a plan to achieve their management goals. Motivations for controlling an invasive can vary from personal or organizational valuing of native ecosystems to concerns about the ecological impacts of the invasion. Goals for management usually include reducing the size and spread of the invader population, but may include restoring invaded areas to a historical state. To achieve these management goals, potential methods can involve chemical, mechanical, and biological control. Trade-offs between these methods often include time and cost to implement, number of applications required, 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 between systems and invader species. Despite the need for effective strategies to appropriately control invasions, 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).

In California, another challenge in deciding to manage an invader and designing management plans is the limited number of species that have been the subject of research. The California Invasive Plant Council (Cal-IPC) lists 208 species as invasive in California (California Invasive Plant Council 2006-2016). Across 347 articles on Californian invasive species from 20 journals published from 2007-2011, (Matzek et al. 2015) found that four non-native species were the focus of 44% of the

Californian invasion literature. The paucity of studies on the impacts and management of the majority of invaders means that it can be harder for land managers to strategize which invaders to target and which treatments to apply (Matzek et al. 2015). Also, in addition to helping land managers forecast how invaders may drive changes in a habitat, broadening the scope of species and systems included in impacts studies is also invaluable for addressing one of the most fundamental questions in invasion biology, whether there are generalizable impacts of invasive species on biodiversity (Powell et al. 2011).

To control an invader, chemical treatments and mechanical removal are the most common methods employed (Kettenring and Adams 2011), but choosing between them without information on their suitability for a particular system or invader is precarious because either strategy could prove ineffective, exacerbate invasion, or incur additional environmental costs. While chemical treatments require less labor and can therefore be cheaper than mechanical treatments, they are controversial due to human health and environmental concerns (Norgaard 2007, Evans et al. 2008). For example, herbicide use can lead to greater reductions in native plant abundance and diversity compared with mechanical methods (Flory and Clay 2009), sometimes with long lasting effects (at least 16 years in the case of Rinella et al. (2009)). On the other hand, mechanical control is often disruptive to the soil, which can damage the roots of non-target species (Holloran et al. 2004) and stimulate germination from the seed bank.

Knowledge of community interactions and the non-target impacts of management methods on other plants can help managers decide between chemical and mechanical control. The resident plant community can play an important role in reducing invader numbers (Levine et al. 2004). If the target non-native is limited from invading by other species, control methods that reduce total plant abundance could leave the treated area vulnerable to reinvasion by the target non-native or colonization by other invasive species. Both chemical and mechanical control methods can facilitate invasion by reducing the biotic resistance from resident species (Puliafico et al. 2011). It is important to test the effects of control methods on resident species in order to limit undesired outcomes (Flory and Clay 2009).

Where native plants provide biotic resistance to invasion, increasing plant cover with desired species following management application can serve as an important strategy to limit non-natives (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). Since 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 if desired species can even establish in invaded systems both before and following management.

If an invader's seeds remain viable in the soil over multiple growing seasons, management efforts must consider the seed bank (Holloran et al. 2004). Strategies for managing invasive species with seed banks can be complicated, often involving multiple treatments over several years. For example, while land managers may want to avoid stimulating the seed bank by using management methods that don't disturb the soil, another management strategy is to stimulate response from the seed bank to exhaust seed reserves (Vivian-Smith and Panetta 2009). Describing the extent and distribution of the invader seedbank and how it responds to management treatments is an important component of evaluating methods.

A current challenge facing land managers in California is the spread of the non-native perennial grass, *Ehrharta erecta* (panic veldt grass), (Tu and Robison 2013). Native to several countries in eastern Africa (USDA-ARS 2013) 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 several counties in California (Calflora 2016) 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 non-native 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 to control the species (Holloran et al. 2004).

As an invader, *E. erecta* is especially worrisome because it can tolerate a wide range of abiotic conditions, which permit its spread into diverse habitat types including sand dunes, closed canopy forest, wetlands, and roadsides (Riefner Jr and Boyd 2007). *Ehrharta erecta* is able to tolerate as little as 2.5% daylight (McIntyre and Ladiges 1985), and unlike most non-native grasses in the area, *E. erecta* is both shade and drought tolerant, while also spreading prolifically in mesic areas (McIntyre and Ladiges 1985). In an experiment comparing non-native *E. erecta* with Australian native grasses, *E. erecta* showed signs of greater invasion potential under drought conditions, taking advantage of reductions in native plant biomass (Manea et al. 2016).

In this study we compared mechanical and chemical control methods for *E. erecta* in mixed-evergreen forest in coastal California. We assess: 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, 3) the effect of out-planting a native species on regrowth of *E. erecta* after treatment, and 4) the extent and vertical distribution of *E. erecta* seeds 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. 12 sites were selected from an area of approximately 2.3 km and include both natural and disturbed areas (Sherman, unpublished thesis 2012). Canopy species in this habitat include *Sequoia sempervirens* (coast redwood), *Quercus agrifolia* (coast live oak), *Pseudotsuga menziesii* (Douglas-fir), and *Umbellularia californica* (California bay). Common understory plants are *Stachys bullata* (California hedgenettle), *Rubus ursinus* (California blackberry), *Clinopodium douglasii* (yerba buena), *Symphoricarpos albus* (white snowberry), and *Pteridium aquilinum* (bracken fern) (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 (George Ledyard Stebbins Papers). Since its introduction it has spread considerably on the campus, and potentially led to *E. erecta* invasions in urban areas of Santa Cruz and into the adjacent Santa Cruz Mountains (Sherman, unpublished thesis 2012).

Ehrharta erecta (Lam.) can reach heights of 60cm, has 5-15cm long leaves, and 6-20cm long panicle-like inflorescences with sessile to subsessile spikelets that appear like beads on a necklace (Holloran et al. 2004). *Ehrharta erecta* grows in dense mats that can exclude natives (Sigg 1996). In 2006, Cal-IPC classified *E. erecta* as a moderate invader (California Invasive Plant Council 2006-2016), a ranking that is applied to invasive species with non-severe ecological impacts that often require specific environmental conditions to invade and are not dispersal limited. Two other *Ehrharta* species are invasive in California, *E. longiflora* (annual) and *E. calycina* (perennial). *Ehrharta erecta*, *E. longiflora*, and *E. calycina*, have comparable relative growth rates and flowering times, which are faster and earlier than other species in the genus, life history traits that have perhaps contributed to their invasiveness (Verboom et al. 2004). In the genus, *E. erecta* is the most globally widespread (Gluesenkamp 2004).

Ehrharta erecta spreads via 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 *E. erecta* seeds collected in Australia required a dormancy period before they were able to germinate. However other studies suggest that mature *E. erecta* seeds collected directly from the plant can germinate immediately (Gluesenkamp 2004). The extent and distribution of the seedbank has not been studied.

To test how *E. erecta* invasion may affect non-target plants, we focused on four understory species that are common in coastal California mixed-evergreen forests: *Clinopodium douglasii* (yerba buena), *Fragaria vesca* (wood strawberry), *Rubus ursinus* (California blackberry), and *Stachys bullata* (California hedgenettle). *Clinopodium douglasii* (Benth.) Kuntze, is a perennial herb in the mint family (Lamiaceae) with sexual and asexual reproduction (Baldwin *et al.* 2012). It has a sprawling habit, often forming small mats (Dashe and Hayes 2008). *Fragaria vesca* L. (Rosaceae) is an erect (3-15cm) perennial herb that can form clones via stolons, as well as reproduce sexually (Baldwin *et al.* 2012). *Rubus ursinus* Cham. and Schltdl. (Rosaceae) is a perennial vine to shrub with sexual and asexual reproduction. *Stachys bullata* Benth. is an erect perennial herb (40-80cm) that can spread vegetatively via rhizomes or sexually (Baldwin *et al.* 2012).

We tested the effectiveness of native plant additions using *C. douglasii*. We selected *C. douglasii* for our study on interactions between biotic resistance and *E. erecta* invasion hypothesizing that its sprawling nature would create a natural barrier to *E. erecta* reestablishment.

The impacts of *E. erecta* invasion on native species richness and cover

In May 2013, we delimited one $4m^2$ uninvaded reference plot at each site to compare to the invaded control plot described below. Locations of reference plots were selected while standing in the center of the site and marking the first patch that was completely free of *E. erecta* in the direction of a randomly selected bearing. All reference plots were within a few meters of the treatment plots. Only at one site, Meyer/Heller, were we unable to find a representative uninvaded area. We estimated percent cover of all species as described above on May/June 2013, February/March 2014, and October 2014.

Chemical vs Mechanical Control: target and non-target effects

In 2012, 12 sites were selected from across the invaded area of *E. erecta* on the UCSC campus (Sherman, unpublished thesis 2012). At each site we delimited three $4m^2$ treatment plots and randomly assigned them to one of three treatments: herbicide, mechanical removal (pull), or control. In December 2012, after estimating percent cover of all species on a subsample of 7 out of 12 sites, we applied the assigned management treatment to all plots.

Herbicide-treated plots were sprayed until wet with an approximate 2.5% Glyphosate Pro 4 solution. While we targeted *E. erecta* patches, the herbicide application method is not specific and native plants were also sprayed. Since some *E. erecta* survived the initial herbicide treatment, a follow-up treatment using a 3-4% Glyphosate Pro 4 solution was applied in January 2013, spraying again until wet. In mechanical removal plots we hand pulled all *E. erecta* vegetation, including roots, careful to minimize disrupting all other species. At the same time as we resprayed herbicide plots in January 2013, we also did a follow-up treatment in the mechanical removal plots, primarily removing new germinants.

Following treatment we assessed the efficacy of the prescribed control methods by estimating percent cover in all plots May-June 2013 and October 2014. One site was destroyed by construction equipment and was excluded from the final two censuses. To census we subdivided each plot into nine $0.5 \times 0.5m^2$ sections leaving a 0.25m buffer on each side. Randomly selecting 3 of those 9 sections 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%.

Native species introduction experiment

To test whether transplanting *Clinopodium douglasii* post-treatment has a persistent effect on native species cover, and whether it affected the regrowth of *E. erecta*, we set up three additional 1 x $0.5m^2$ plots at five of the sites used in the previous experiments. In March 2013, we randomly applied three treatments (mechanical removal, herbicide, or control) to plots at each site. For herbicide plots we used a 2.225% Glyphosate Pro 4 solution that included a blue dye. Plants were sprayed until completely tinted blue. In May 2013, we split these plots into two 0.5 x $0.5m^2$ sections and randomly assigned one side to native plant addition, where we planted nine *C. douglasii* plants in a grid formation with 12.5cm spacing. Transplanted cuttings were watered for two weeks, with each receiving 0.3L every other day. The *C. douglasii* used in this study were propagated from cuttings of plants collected from the UCSC campus in Dec 2012. Prior to their use in this experiment, the cuttings were grown in conetainers (3.8cm diameter, 14cm deep) in the UCSC greenhouses where they were misted twice daily and kept in mild temperatures (7-18°C), then transferred to an outdoor growing space in January 2013. The mean length of transplanted cuttings was 17.9cm (± SE 0.76). Percent cover for all species was estimated in October 2013 and 2014, 7 and 19 months following initial treatment.

Similar to previous experiments, we used a 0.5 x 0.5m^2 quadrat with 100 points for all censuses.

Ehrharta erecta seed bank variation across treatments at three depths

We characterized the vertical distribution of the seed bank and differences in seed density among treatments by censusing the germination from litter and six 10cm soil cores from all plots. Each core was cylindrical with a 1.27cm radius and was divided into two 5cm halves (top and bottom). Each half was combined and homogenized with the other corresponding five cores from each treatment plot. The six cores were collected haphazardly, sampling from various areas across the plot. From one treatment plot were we unable to collect soil cores below 5cm depth due to the extreme rockiness of the area.

To measure the seed bank in the litter layer we collected all litter from within an arbitrarily selected 10cm radius circle near the center of each treatment plot. We extracted seeds from litters by sifting litter samples down to 0.18cm (4.5/64in, round holes, Seedburo, size U) and checking for additional *E. erecta* seeds attached to larger litter particles. All soil and litter samples were air dried at room temperature to avoid inducement of germination until all samples could be collected and the litter sifted. Soil cores and litter samples for all three treatments were generally collected on the same day. Once collected, all soil and litter samples were transferred to garden pots (6.35 x 6.35 cm^2, 5.08cm deep) on February 6 and 7, 2016. For litter samples, 1 cup of potting soil was added to the bottom of each pot to provide substrate. All 98 pots were randomized across six flats (18 pots/flat) and kept moist in the University of California, Santa Cruz greenhouse. To maximize germination and reduce density-dependent effects, we hand pulled germinants from all pots on two occasions (22 February, 2016 and 21 March, 2016). Following removal of germinants we gently raked all pots with a fork to bring new seeds to the surface.

Analyses:

All described analyses were conducted using JMP® Pro Version 12 (SAS Institute Inc. 1989-2007), with the exception of the NMDS, for which we used R (R Core Team 2016).

The impacts of *E. erecta* invasion on native species richness and cover

Using a mixed model ANOVA we compared invaded and paired non-invaded (reference) plots for species richness, percent cover of native species, and total percent cover in October 2014. Site and subplot nested within treatment were random effects.

Chemical vs Mechanical Control: target and non-target effects

We tested the responses of *E. erecta* and four native species, *Clinopodium douglasii, Fragaria vesca, Rubus ursinus,* and *Stachys bullata* to treatment (herbicide, pull, and control) using mixed model ANOVA. Site and subplot nested within treatment were random effects. We used a post-hoc Tukey's test with α=0.05

to determine which treatments were significantly different from each other. We also tested for an effect of treatment on percent cover of native species, combined total percent cover of all vegetation, and native species richness, using mixed model ANOVA and Tukey´s HSD, as above.

Finally, we compared plant community composition across treatments, including the non-invaded reference plots, using a non-metric multidimensional scaling (NMDS) plot. The NMDS was graphed from October 2014 census data using the R package, vegan (Oksanen et al. 2016).

Native species introduction experiment

To test the effects of transplanting *C. douglasii* on *E. erecta* and *C. douglasii* percent cover we used a mixed model ANOVA with treatment (herbicide, pull, and control) and *C. douglasii* transplants as factorial fixed effects. Response variables were the percent cover of *E. erecta* and *C. douglasii*. Site was a random effect. We used a post-hoc Tukey's test with $\alpha=0.05$ to determine which treatments were significantly different from each other.

Similar to the previous experiment, we also tested the effect of management treatment and native species addition on percent cover of native species and native species richness using mixed model ANOVAs. Site was considered to be a random effect. We tested for significant differences between fixed effects using a post-hoc Tukey's test, $\alpha=0.05$.

Ehrharta erecta seed bank variation across treatments at three depths

The number of germinants from all litter samples was scaled to the collected area: soil cores=5.07cm^2 and litter=314.16cm^2. We analyzed the effects of treatment and depth on total number of germinants using a two-factor mixed model, with site as a random effect. We excluded the non-significant interaction term between treatment and depth from our model (F=0.52, DF=4, 79.1, P=0.72).

RESULTS

The impacts of *E. erecta* invasion on native species richness and cover

Comparing un-invaded reference plots to invaded control plots, invasion was associated with lower native species percent cover (F=13.72, DF=1, 6.5, P =0.0087, Figure 1A). Total vegetation cover was about four-fold greater in invaded plots (F=21.80, DF=1, 4.3, P=0.0078, Figure 1B). However, species richness was not significantly different between invaded and non-invaded plots (F=0.61, DF=1, 4.3, P=0.48, Figure 1C).

Ehrharta erecta density in invaded control plots varied strongly across sites and strongly predicted total vegetation cover (Y=13.5 + 1.03X, R^2=0.95, N=11, P<0.0001). Despite this, we did not find a relationship between *E. erecta* percent cover and native species percent cover (Y=12.8 + 0.04X, R^2=0.02, N=11, P=0.68, Figure 2).

Chemical vs Mechanical Control: target and non-target effects

Ehrharta erecta

Although we randomly assigned treatments to our experimental plots, pre-treatment percent cover of *E. erecta* (2012) varied significantly among treatments ($F = 27082.9$, $DF = 2, 60$, $P < 0.001$), and was significantly greater in pull plots ($\alpha=0.05$, Figure 3, fall 2012). This higher pre-treatment cover in pull plots was driven by extremely high density in three subplots at West McHenry (% cover = 388, 308, 300), one subplot at Meyer/Heller (% cover = 277), and one subplot at Health Center (% cover = 264).

Five to six months following application we found significant differences in *E. erecta* percent cover among treatments ($F = 62.17$, $DF = 2, 6$, $P < 0.001$), with both pull and herbicide plots significantly lower than the control ($\alpha=0.05$, Figure 3, spring 2013). Twenty-two months following treatment we still found that both herbicide application and hand pulling were lower than the control ($F = 11.56$, $DF = 2, 6$, $P = 0.0088$) and did not significantly differ from each other ($\alpha=0.05$, Figure 3, fall 2014).

Community level effects

How management affected the plant community varied strongly by treatment. Prior to implementation of control methods, native species percent cover did not significantly differ across treatments ($F = 5.5$, $DF = 2, 4.4$, $P= 0.063$, Figure 4). Five to six months after treatment, percent cover of native species was significantly lower in plots treated with herbicide ($F = 14. 09$, $DF = 2, 6.2$, $P = 0.0048$, Figure 4). Lower percent cover of native species persisted in herbicide plots at least 22 months following treatment ($F = 51.58$, $DF = 2, 6$, $P = 0.002$, Figure 4).

The response of native species richness to management also varied by treatment. Prior to implementation of management methods, native species richness did not significantly vary across plot types ($F = 1.38$, $DF = 2, 5.5$, $P = 0.33$, Figure 5). Five-six months following treatment, richness was significantly lower in herbicide plots compared with pull and control plots ($F = 146.86$, $DF = 2, 5.5$, $P < 0.001$, Figure 5). Twenty-two months following application, there were still significant differences among treatments ($F = 26.92$, $DF = 2, 6$, $P = 0.0010$), with herbicide significantly lower than the other two treatments (Figure 5).

Percent cover of four common native species

Clinopodium douglasii

In response to treatment we saw significant differences in percent cover of *C. douglasii*, both 5-6 and 22 months following treatment ($F = 17.45$, $DF = 2, 6$, $P = 0.0032$, spring 2013; $F = 1.63$, $DF = 2, 6$, $P = 0.27$, Figure 7, fall 2014). The treatments that significantly differed were not consistent between the two censuses. Five to six months after treatment, there was lower *C. douglasii* percent cover in the pull and herbicide plots relative to the control ($\alpha=0.05$, Figure 7, spring 2013). At 22 months, percent cover of *C. douglasii* was still significantly lower in herbicide plots, but pull and control plots did not differ ($\alpha=0.05$, Figure 7, fall 2014).

Fragaria vesca

Five to six months following implementation we did not find significant differences in mean percent cover of *F. vesca* between treatments (F = 1.53, DF = 2, 6, P = 0.29, Figure 7, spring 2013). By 22 months following treatment, *F. vesca* density in pull plots was significantly greater than in control and herbicide plots (F = 8.02, DF = 2, 6, P = 0.02, Figure 7).

Rubus ursinus

We saw a strong negative response to herbicide by *R. ursinus*, both after 5-6 months (F = 10.77, DF = 2, 6, P=0.01, Figure 7, spring 2013) and 22 months after treatment (F = 50.02, DF = 2, 6, P = 0.0002). Percent cover in herbicide plots was significantly lower than in pull and control plots, but these were not significantly different from each other (Figure 7).

Stachys bullata

As with *F. vesca*, we did not detect significant differences between treatments until the last census (F = 3.34, DF = 2, 6, P = 0.11, Figure 7, spring 2013). Twenty-two months after treatment, there was significantly more *S. bullata* in pull plots compared with herbicide and control plots (F = 21.75, DF = 2, 6, 0.0018, Figure 7, fall 2014).

Community level differences

In the NMDS plot (Figure 8) references plots cluster higher on the NMDS2 axis than the control, herbicide, or pull plots, although of these three treatments, the pull plot plant communities appear most similar to the non-invaded reference plots.

Native species introduction experiment

Ehrharta erecta

As in the previous experiment, five months following treatment, *E. erecta* density was lower in both the herbicide and pull plots compared to the control ($F = 12.90$, $DF = 2, 22$, $P = 0.0002$, Figure 9). By 17 months, percent cover still significantly differed among treatments ($F = 5.48$, $DF = 2, 22$, $P = 0.012$, Figure 9), but re-growth of *E. erecta* was evident in both treatments such that only herbicide plots significantly differed from the control ($\alpha=0.05$, Figure 9), though pull plots were trending towards significance ($P = 0.067$). Percent cover in herbicide and pull plots did not significantly differ from each other 5 months or 17 months following treatment ($\alpha=0.05$, Figure 9).

We did not find a significant effect of *C. douglasii* addition on *E. erecta* percent cover after 5 months ($F = 0.18$, $DF = 1, 22$, $P= 0.67$, Figure 9) or after 17 months ($F = 0.15$, $DF = 1, 22$, $P= 0.71$, Figure 9) in any treatment.

Community responses

Five months after transplanting *C. douglasii,* we did not detect significant differences in native species percent cover across *E. erecta* removal treatments ($F = 1.94$, $DF = 2, 22$, $P = 0.17$). There was significantly greater native species cover in subplots where transplanting occurred ($F = 15.28$, $DF = 1, 22$, $P = 0.0008$, Figure 10). Interestingly after 17 months this effect was lost and there was no significant differences in native cover among planted and unplanted subplots ($F = 1.55$, $DF = 1, 22, P = 0.23, Figure 10). Pull plots had significantly greater native cover than herbicide and control plots F = 4.91, DF = 2, 22, P= 0.017, Figure 10).

In response to management, native species richness was significantly greater in pull plots compared with herbicide plots after 5 months (F = 6.05, DF = 2, 22, P = 0.008) and after 17 months (F = 3.98, DF = 2, 22, P=0.034, Figure 11). We observed significantly greater native species richness in planted versus unplanted sites five months after planting (F = 4.95, DF = 1, 22, P = 0.037). However at 17 months, native species richness was similar across subplots (F = 0.35, DF = 1, 22, P = 0.56, Figure 11).

Clinopodium douglasii

Percent cover of *C. douglasii* did not significantly change in response to *E. erecta* management after 5 months: F = 2.29, DF = 2, 22, P = 0.13) or after 17 months: F = 0.92, DF = 2, 22, P = 0.41, Figure 12).

We found that 5 and 17 months after planting, *C. douglasii* addition increased cover of *C. douglasii* relative to unplanted subplots (F=41.48, DF = 1, 22, P < 0.0001, Oct 2013; F = 6.33, DF = 1, 22, P=0.020, fall 2014, Figure 12).

***Ehrharta erecta* seed bank variation across treatments at three depths**

We did not find significant differences among management treatments (F = 0.55, DF = 2, 83.1, P =0.58), but did find significant differences among depths (F = 21.74, DF = 2, 83.1, P = <0.0001, Figure 13). Among depths, “Top”, the upper 5cm of the soil core, had significantly more germinants per cm^2 than the duff layer or the lower 5cm of the soil core. We did not find a significant difference in the number of germinants between Bottom and Duff (α=0.05, Figure 13).

DISCUSSION

We found mixed evidence for negative effects of *Ehrharta erecta* invasion on native California coastal mixed-evergreen forest communities. In invaded plots, native plant cover was about 11.4% lower compared to nearby reference plots. From earlier studies we have evidence of competitive effects of *E. erecta* on some native species. Hanson (unpublished thesis 2014) measured significant competitive superiority of *E. erecta* over *Rubus ursinus*, *Scrophularia californica*, and *Clinopodium douglasii* (but not *Fragaria vesca*) in a greenhouse experiment, while Godinho (unpublished thesis 2013) found that removing *E. erecta* from around *Stachys bullata* in the field increased transpiration rates and chlorophyll content (although the opposite trend was found for *C. douglasii*).

By other measures, however, the impacts of *E. erecta* were not clear. Among invaded plots across sites, we did not find a negative relationship between *E. erecta* density and native plant cover or richness. Both of our datasets on impact (invaded vs. uninvaded reference plots, and comparison 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)). The impacts of invasion on native species may vary by environmental context (Daehler 2003) or appear different at different scales of assessment (Powell et al. 2013), challenging our ability to predict what effect an invasion will have on community diversity. In an extensive meta-analysis, (Vila et al. 2011) found that invasions generally cause reductions in plant species abundance and diversity, as well as lead to increased total production. These findings are consistent with our results, with the exception of species richness, which did not vary significantly between invaded and uninvaded plots. One possible explanation for a lack of competitive exclusion is that the understory community in this forest is not saturated with species. Total vegetation cover in uninvaded reference plots was 27.4 ± SD % on average. In some systems, invaders may fill open niches that might be filled by invaders without competitive exclusion (Davies et al. 2011).

Apart from its impacts on native species abundance and richness, *Ehrharta erecta* invasion changed the character of the coastal mixed-evergreen forest, dramatically increasing herbaceous plant abundance. We observed almost four times more total vegetation cover in invaded control plots than in uninvaded reference plots. This increase in plant biomass can drive changes in the native plant community through physical changes. Since *E. erecta* is a dense mat forming species, native seeds might not be able to reach the soil (Sigg 1996). Or, as seen in other grass invaded systems, increased invasive plant cover can negatively impact native tree success (Flory and Clay 2010). The increased plant cover may also represent an esthetic and ethical impact for some, as *E. erecta* transforms an iconically sparse and open understory into a lush, grass-filled landscape.

Our results suggest that substantial reduction of *E. erecta* cover for up to two years is possible through both chemical and mechanical treatment methods. However, one or two control treatments are not sufficient to fully eradicate *E. erecta.* Averaged across all censused plots, in October 2014, *E. erecta* percent cover was 59% lower in herbicide plots and 76% lower in pull plots, compared with an 82 percent increase in control plots. Two years following treatment, although percent cover of *E. erecta* was still significantly lower in the pull and herbicide plots relative to the control, *E. erecta* abundance had increased on average to 41% of its original cover in herbicide and 24% its original cover in pull plots. In terms of total percent cover, in the Chemical vs Mechanical Control Experiment we observed more rapid reestablishment of *E. erecta* in pull plots than herbicide.

This greater regrowth of *E. erecta* following hand pulling in the first experiment could be the response of the seedbank to soil disturbance. When sites were re-treated in January and February 2013, recently germinated seeds rather than re-sprouts made up nearly all the new *E. erecta* growth. *Ehrharta erecta* is a mat forming species with roots that extend several centimeters deep, so manual removal of *E. erecta* would likely bring seeds in the soil to the surface and stimulate germination. Interestingly, however, in the smaller scale Native Species Addition Experiment we did not observe greater recovery of *E. erecta* in pull plots compared with herbicide plots. One possible explanation for this comes from the manner in which the hand pulling was executed. For the first experiment, teams of approximately 10 volunteers were used. These volunteers mostly pulled from the outside of the plot, but since the plots were large (2 x 2 m^2), they occasionally had to step in the plots to reach all *E. erecta*. In comparison, the pull plots for the NSA experiment were pulled by 1-2 people and were smaller (1 x 2 m^2). Our findings suggest that soil disturbance can be an important mechanism of *E. erecta* recovery, and that while manual removal is an effective strategy for removing adult plants, if minimizing germination is an important goal, then herbicide may be more appropriate for controlling *E. erecta* where there is an established seedbank.

We saw strong variation in *E. erecta* recovery across sites. It is interesting to note that Meyer/Heller, the site where control methods were least effective at managing *E. erecta* (Figure 17), is located at the base of a large storm-water drainage pipe that maintains 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 Meyer/Heller could indicate that the invader may have 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 indication of the versatility of this plant in tolerating a diverse array of abiotic conditions.

Since both management types effectively reduce *E. erecta* percent cover, consideration of tradeoffs will help land managers select the option most appropriate for their management goals and resources. Chemical treatment required the lowest time investment, but it was monetarily more expensive. Herbicide also comes with the additional cost that it often must 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 per hour were approximately $39.00/hr. for a total of $156.00 for four hours (two hours per treatment). Approximately 2 gallons of glyphosate solution were needed to spray 12 4m^2 plots. Averaging the percentage of glyphosate used in the two applications to 3%, we used a total of 16oz of glyphosate, for a cost of $23.52.

Hand pulling required many more person-hours than herbicide application. Twenty-one volunteers helped us hand-pull the *E. erecta* from our treatment sites for the first experiment. Prior to going into the field, volunteers were instructed in how to identify *E. erecta*, as well as the importance of removing all vegetative material and 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 hours, the volunteers manually removed *E. erecta* from eight 4m^2 treatment plots, for a total of 32m^2. We estimate that each volunteer pulled at a rate of approximately 0.75-1 m^2/hr (32m^2/21 people/2 hrs, including transit time between plots).

Non-target effects were greater with herbicide compared to hand pulling. We observed significant reductions in native species richness and cover in herbicide plots even 22 months following treatment. Such strong non-target effects argue against the use of this approach for some resource management situations, such as 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 tradeoff. 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, June 17, 2016).

Biological resistance from restored native species could help slow the regrowth of an invader. However, we did not find that planting in native *C. douglasii* slowed re-growth of *E. erecta*. Planting in native species may be necessary to meet certain restoration goals, such as increasing native species cover in invaded areas or mediating the non-target effects of management. From that perspective, planting *C. douglasii* was somewhat successful, increasing percent cover of the species over the 22-month time frame despite strong drought conditions. However, the transplants drove changes in that species alone. By 22 months, there was no detectable effect on overall native cover or richness.

Whether *E. erecta* is a recent arrival or a long established invader may also influence the choice management method. *Ehrharta erecta* is a seed bank forming species. In our seed bank study, we observed germination from the litter, from the top 5cm of soil, and from 5-10 cm depth, with 73% of germinants (scaled to area) coming from the top soil layer and 24% from lower depths, suggesting accumulation of seeds over time in the soil. Interestingly, we did not detect a significant reduction in the seed bank in terms of numbers of germinants in the hand pull treatment, suggesting that despite the flush of new seedlings, the seedbank was not exhausted by that treatment. In areas where *E. erecta* is a very recent invader, manual removal is possible with less risk of response from the seed bank and would allow managers to avoid the non-target effects that come with herbicide use. Where *E. erecta is* established, managers should anticipate that the seed bank could be an important source of regrowth, and the cost/benefit ratio may favor herbicide.

Forest ecosystems are considered relatively resistant to invasion due to low light availability (Aguilera et al. 2015) and the California redwood forest in particular has experienced few aggressive invasive plants until recently. The invasion of *E. erecta* is a good example of how it is the combination of the traits of an invader and the characteristics of the ecosystem that determine invasion outcomes (Daehler 2003). Fortunately in this case, we have found that multiple management tools can be used to control the invader.

FIGURES

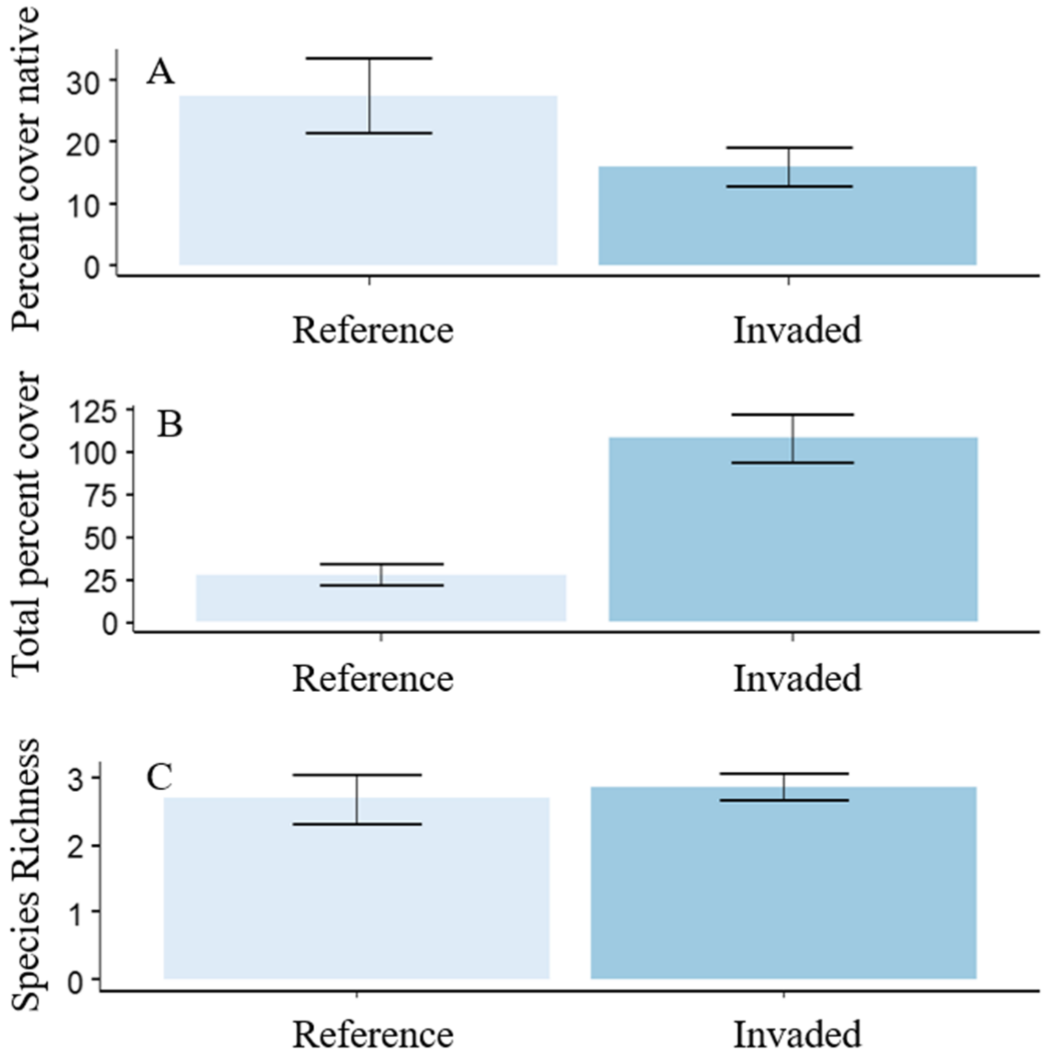

Figure 1: Measure of impact between non-invaded reference plots and invaded plots from October 2014. A: Percent cover of native species; B: Percent cover of all species; C: Species richness. Error bars represent 1±SE.

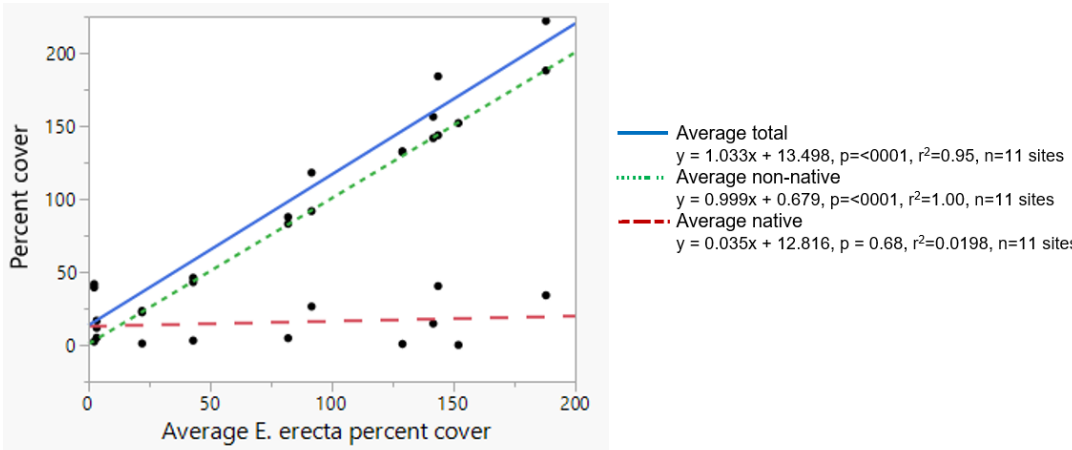

Figure 2: Average native and total species percent cover versus average *Ehrharta erecta* percent cover. Native species percent cover: Y=12.8 + 0.04X, R^2=0.02, N=11, P=0.68. Total species percent cover: (Y=13.5 + 1.03X, R^2=0.95, N=11, P<0.0001).

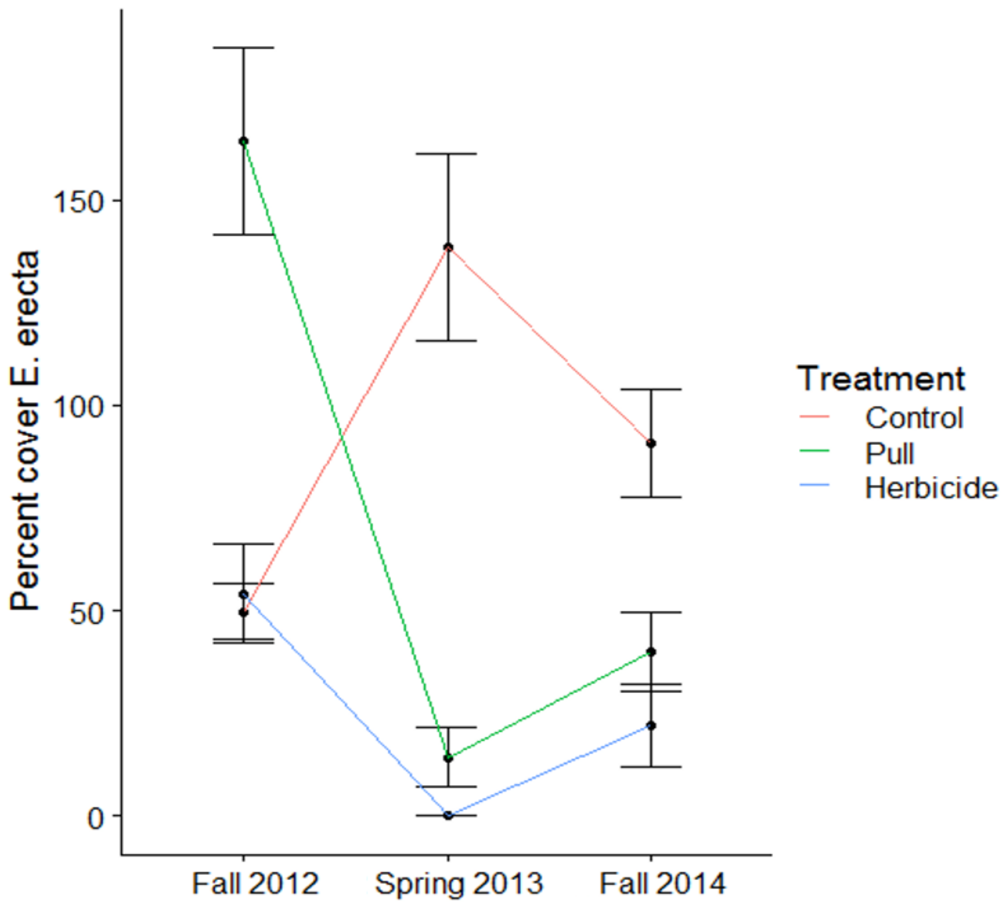

Figure 3: Percent cover of *E. erecta* per 0.25m^2 quadrat by census and treatment type for Chemical vs Mechanical Control Experiment. Data was collected prior to treatment in fall 2012, 5-6 months after treatment in spring 2013 and 22 months following treatment in fall 2014. Error bars represent 1±SE.

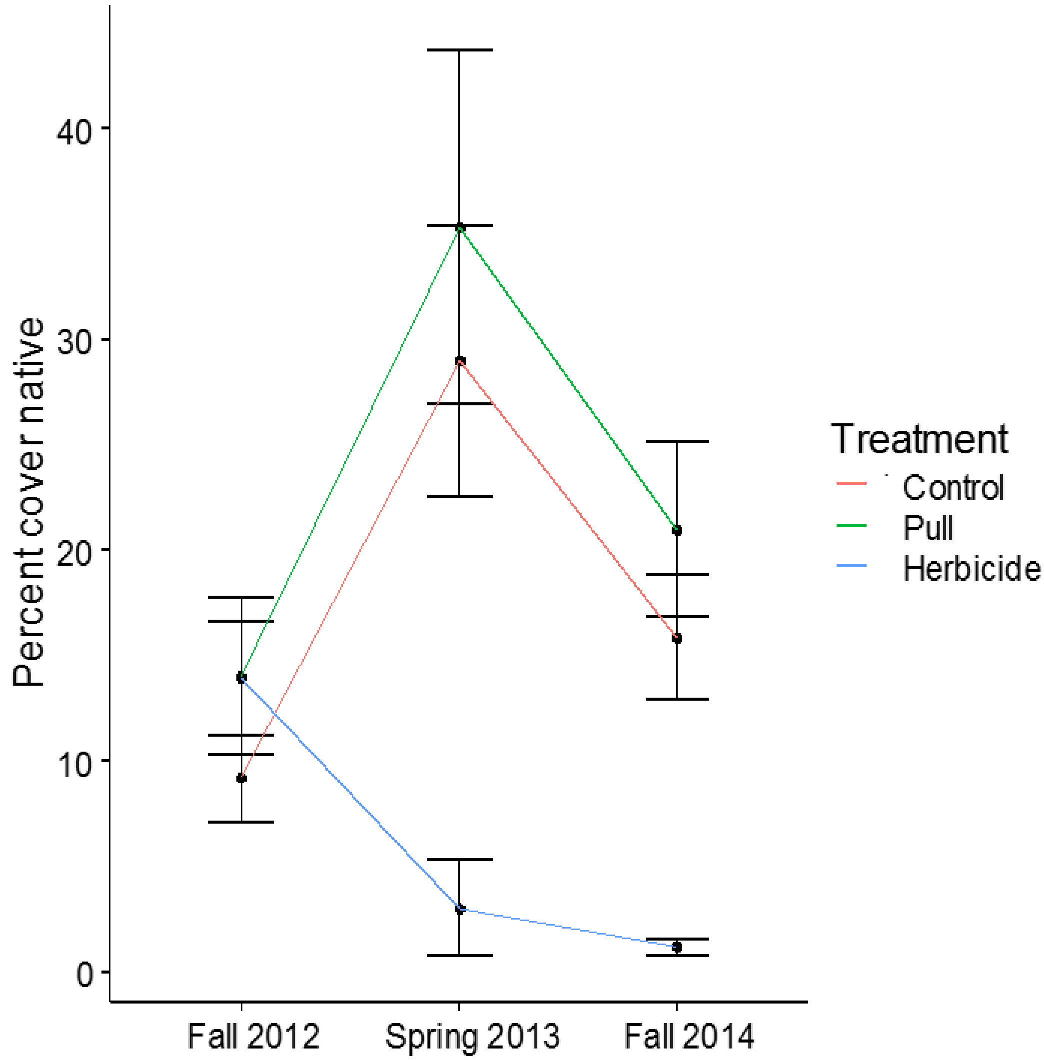

Figure 4: Percent cover of native species by census and treatment type for chemical removal (herbicide), mechanical removal, and control. Data was collected prior to treatment in fall 2012, 5-6 months after treatment in spring 2013 and 22 months following treatment in fall 2014. Error bars represent 1±SE.

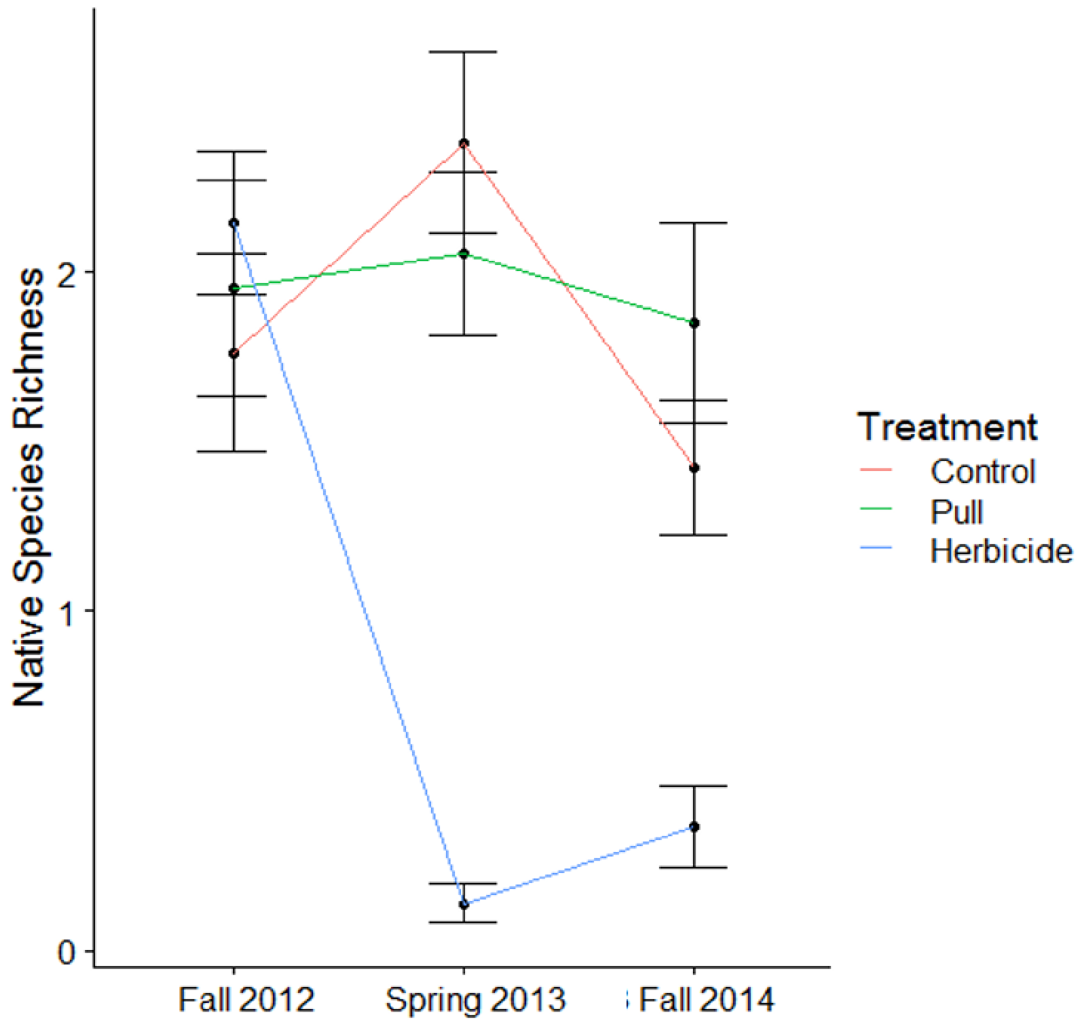

Figure 5: Native species richness per 0.25m^2 quadrat by census and treatment type for chemical removal (herbicide), mechanical removal, and control. Data was collected prior to treatment in fall 2012, 5-6 months after treatment in spring 2013 and 22 months following treatment in fall 2014. Error bars represent 1±SE.

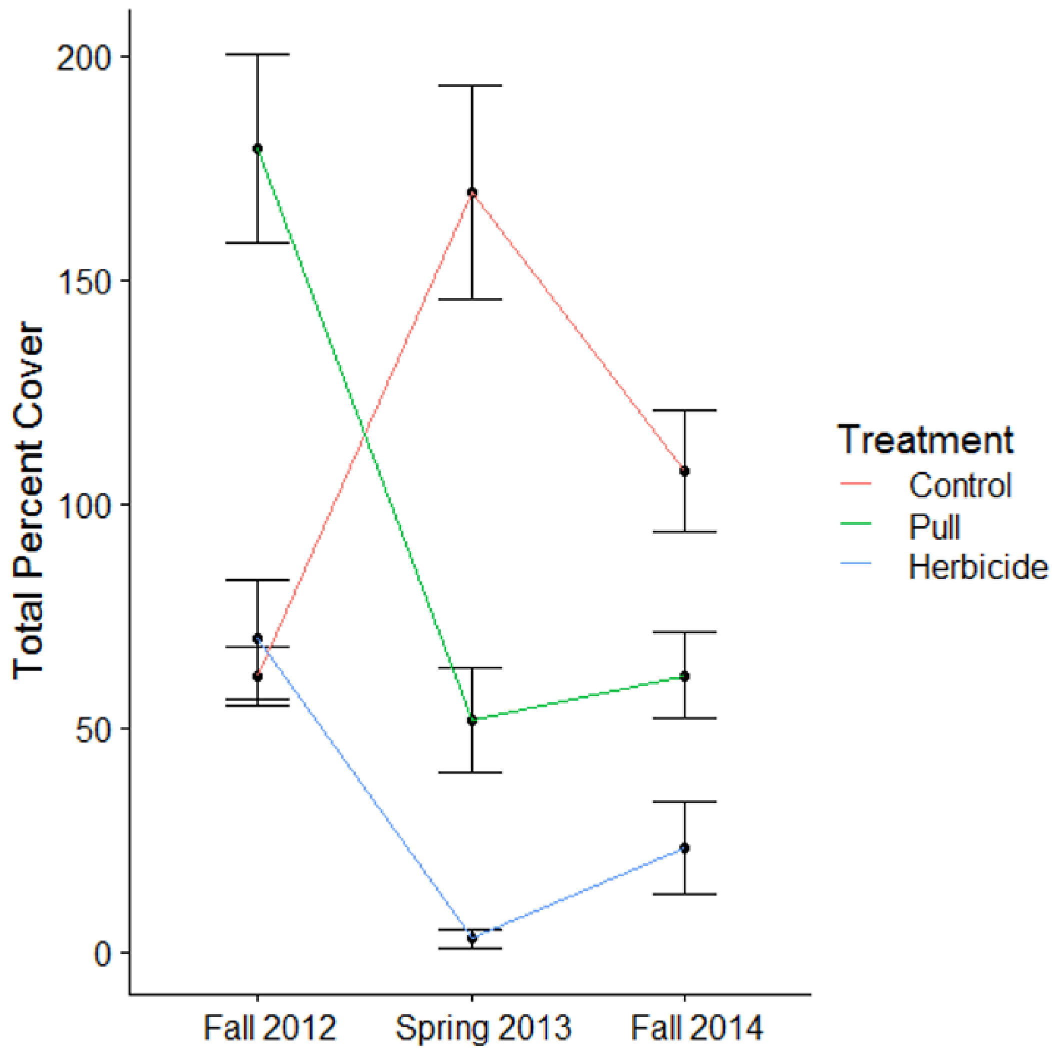

Figure 6: Percent cover of all vegetation for chemical removal (herbicide), mechanical removal, and control. Data was collected prior to treatment in fall 2012, 5-6 months after treatment in spring 2013 and 22 months following treatment in fall 2014. Error bars represent 1±SE.

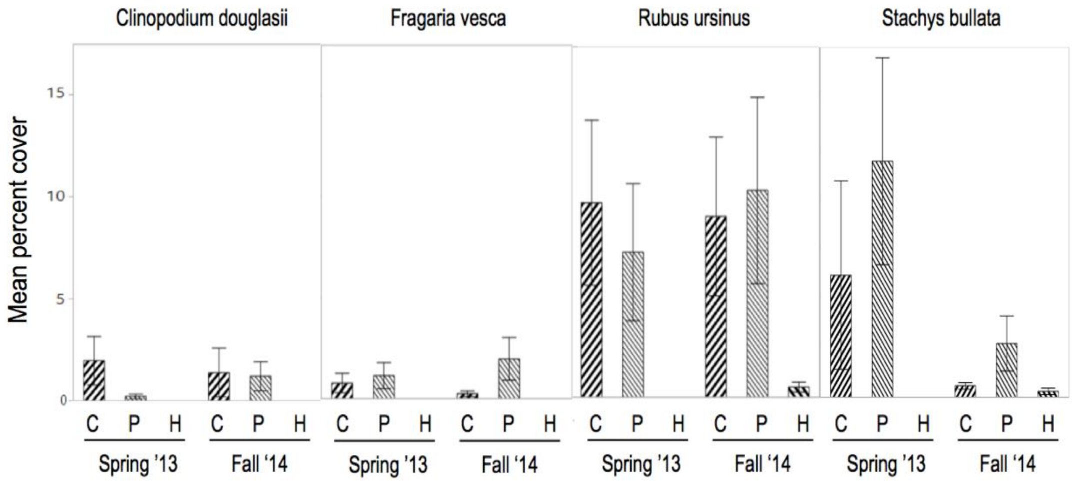

Figure 7: Percent cover of *C. douglasii*, *F. vesca*, *R. ursinus*, and *S. bullata* by treatment and census. Data was collected prior to treatment in fall 2012, 5-6 month following after treatment in spring 2013 and 22 months following treatment in fall 2014. “C” = Control, “P” = Pull, “H” = Herbicide. Error bars 1±SE.

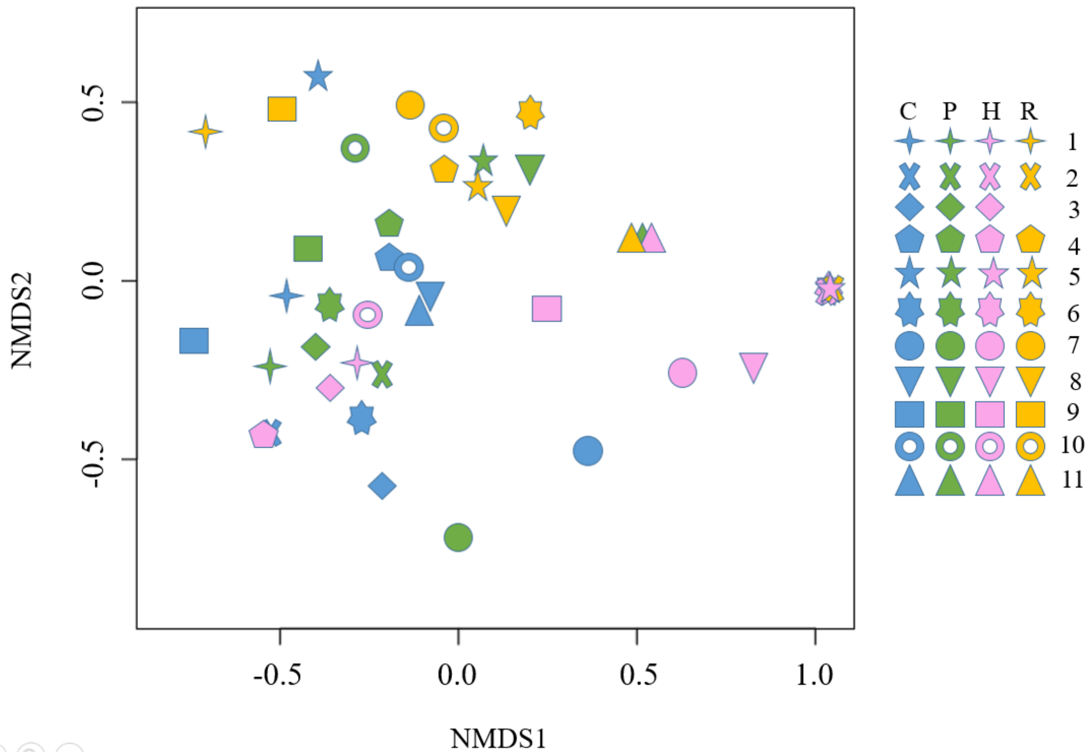

Figure 8: Non-metric multidimensional scaling (NMDS) with Bray Curtis Dissimilarity for the October 2014 census. Each shape corresponds to a site (1-11) and each color corresponds to a treatment “C” = Control, “P” = Pull, “H” = Herbicide, “R”=Reference. Site 3 did not have a reference plot due to lack of nearby non-invaded habitat.

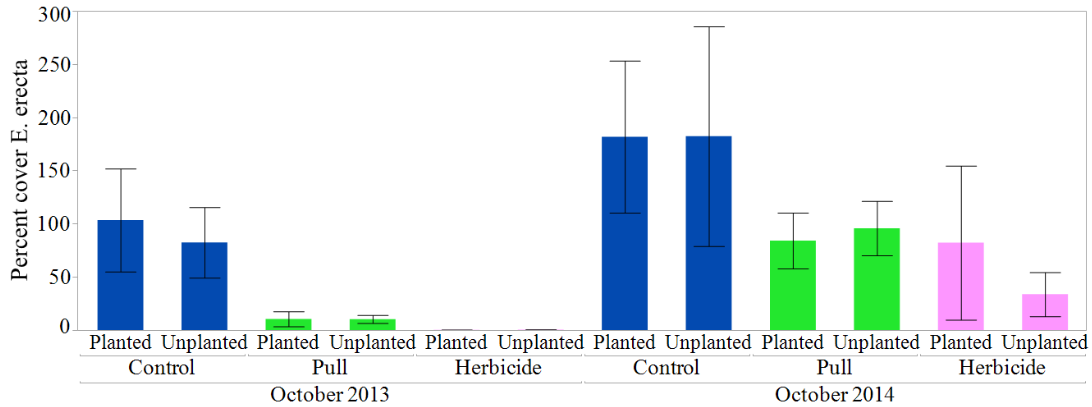

Figure 9: Percent cover of *E. erecta* for plots subjected to different treatment (herbicide, pull and control) and with and without *C. douglasii* planted. Plots censused at 5 and 17 months following planting in May 2013. Error bars 1±SE.

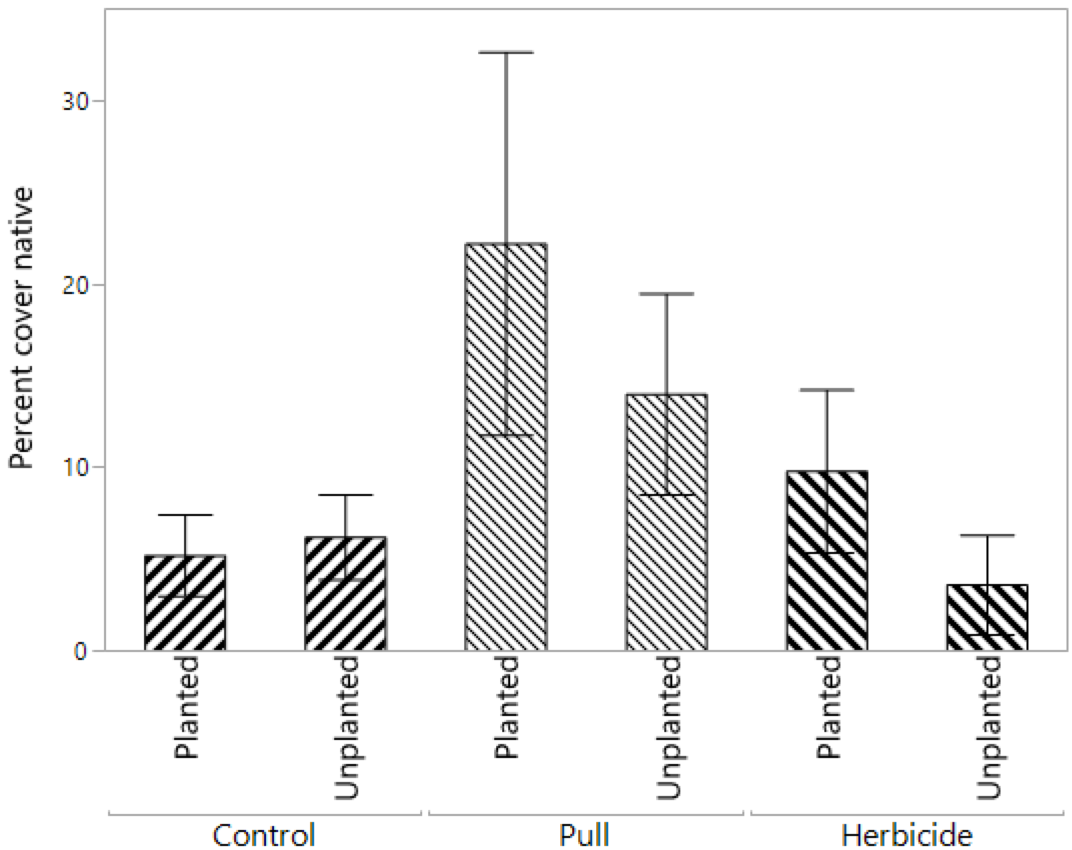

Figure 10: Percent cover of native species for plots subjected to different treatment (herbicide, pull and control) and with and without *C. douglasii* planted. Plots censused at 5 and 17 months following planting in May 2013. Error bars 1±SE.

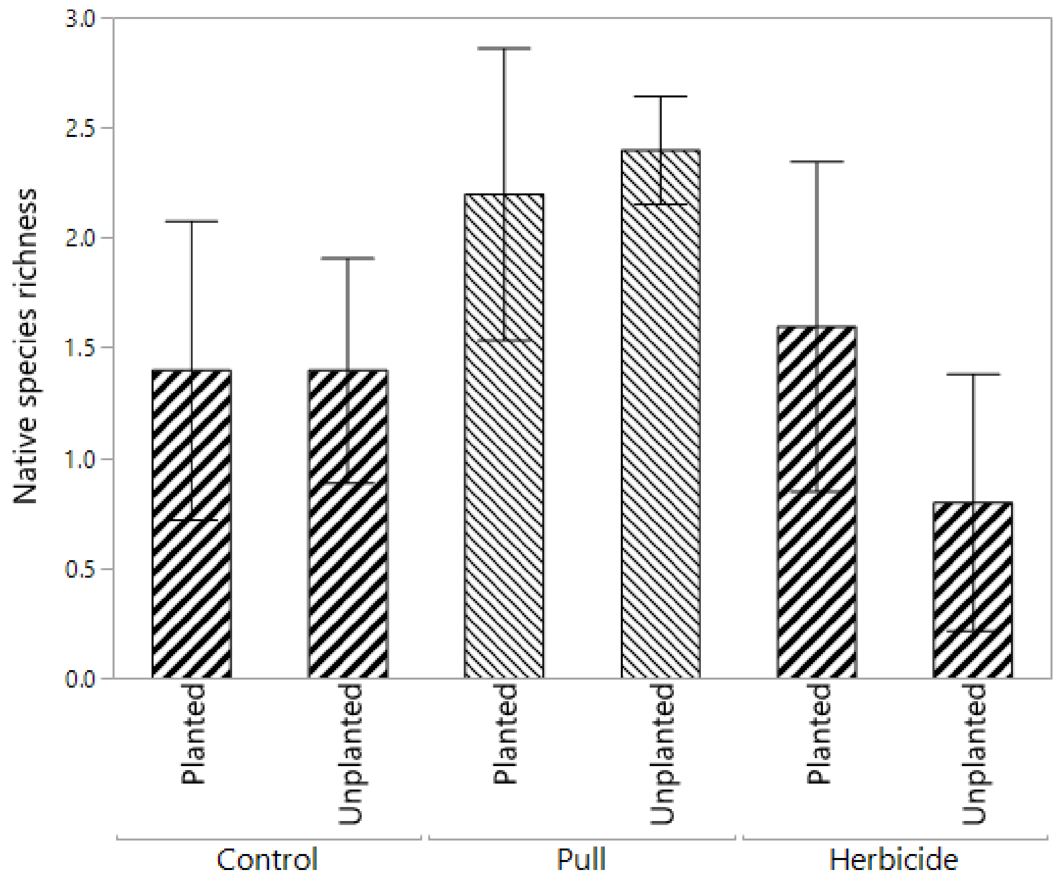

Figure 11: Species richness of natives in $0.25m^2$ for plots subjected to different treatment (herbicide, pull and control) and with and without *C. douglasii* planted. Plots censused at 5 and 17 months following planting in May 2013. Error bars 1±SE.

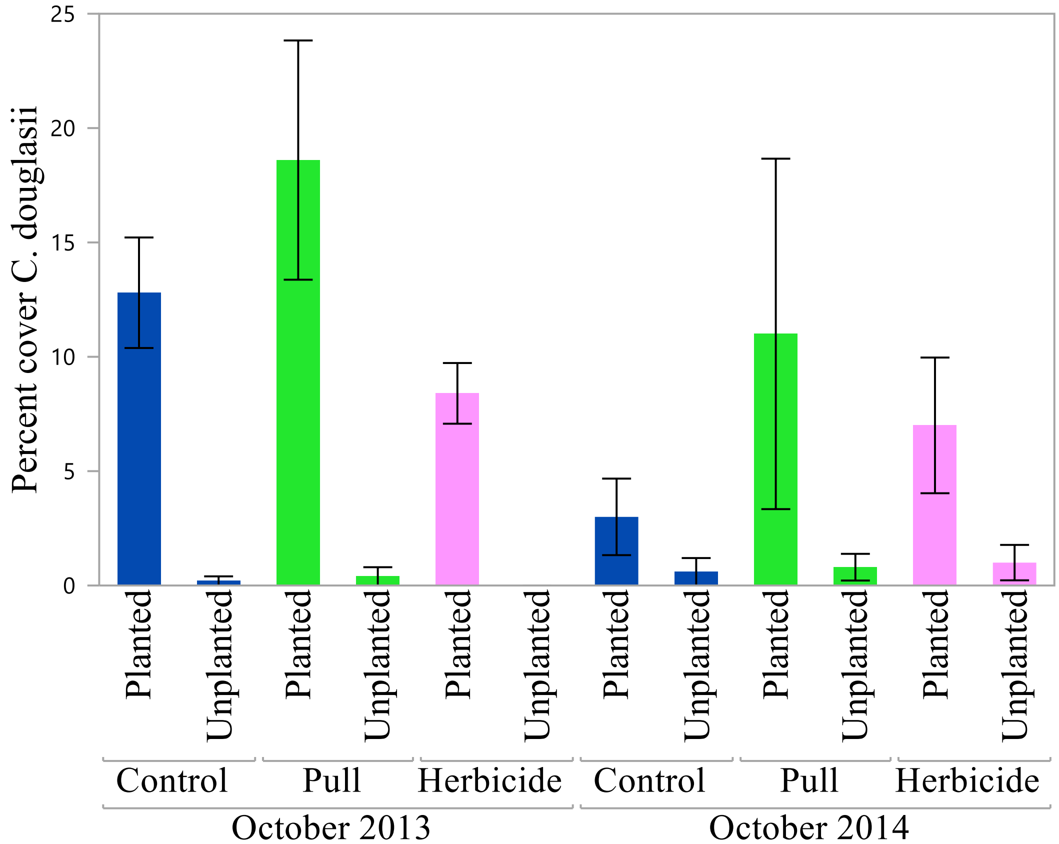

Figure 12: *Clinopodium douglasii* percent cover for plots subjected to different treatment (herbicide, pull and control) and with and without *C. douglasii* planted, censused at 5 and 17 months following planting in May 2013. Error bars 1±SE.

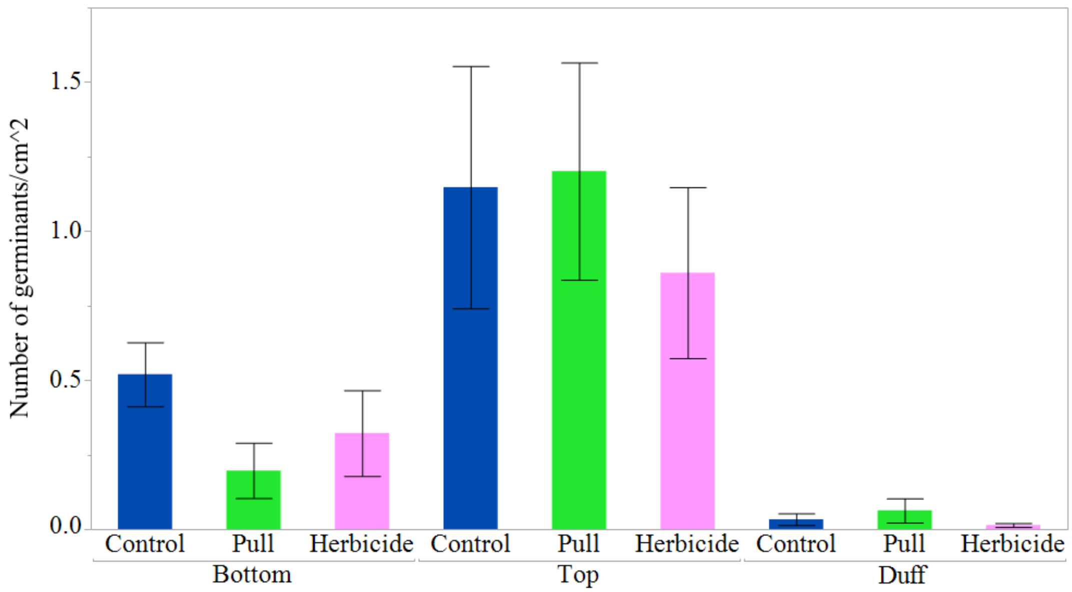

Figure 13: Number of *E. erecta* germinants per cm^2 by treatment and source depth. Soil and duff samples were collected in Jan-Feb 2016, 49-50 months following treatment. Bottom=lower 5 cm of 10 cm soil core, Top=upper 5cm of 10 cm soil core, Duff=leaf litter. Error bars represent 1±SE.

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