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To cite this article: Sheherezade N Adams , Scott Jennings & Nils Warnock (2020): Plant invasion depresses native species richness, but control of invasive species does little to restore it, Plant Ecology & Diversity, DOI: [10.1080/17550874.2020.1817998](https://doi.org/10.1080/17550874.2020.1817998)

To link to this article: <https://doi.org/10.1080/17550874.2020.1817998>



Published online: 20 Oct 2020.



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Plant invasion depresses native species richness, but control of invasive species does little to restore it

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ABSTRACT

Background: Invasive plants are associated with the decline of native plant richness, but the impact of removal of invasives on native plant richness is often unknown.

Aims: We investigated whether the presence of the introduced plant *Centaurea solstitialis* (Asteraceae) was correlated with reduced native plant richness; whether rain in late spring, when *C. solstitialis* is virtually the only plant actively growing, increased its cover; and whether native species richness increased following the control of *C. solstitialis*.

Methods: From 2011 to 2017 in a grassland in Sonoma County, California, USA, we treated 20 1-m² plots in *C. solstitialis*-invaded patches with chemical and mechanical removal. We monitored cover of all plants in those plots, plus 20 invaded untreated and 20 uninvaded plots, for a total of 60 plots in two blocks.

Results: Native plant richness was lower in invaded than in non-invaded plots. More late spring rainfall resulted in greater *C. solstitialis* cover in the following year. Native species richness in the six years after initial removal was slightly higher in removal plots than in untreated control plots.

Conclusions: *Centaurea solstitialis* removal alone results in modest benefits for native plant species richness. Managing this invasive requires more resources in years with more late spring rainfall.

ARTICLE HISTORY

Received 31 January 2020
Accepted 28 August 2020

KEYWORDS

Centaurea solstitialis;
diversity impacts; invasive
removal; species traits;
yellow starthistle

Introduction

The impacts of invasive plant species can be significant and are on the rise (Pyšek et al. 2012, 2020). They can have significant negative impacts on native ecosystems, agricultural production and other commercial and recreational activities (National Invasive Species Council 2008; USDA Forest Service 2013). Invasive plants are associated with declines in abundance and diversity of native species (Gaertner et al. 2009; Hejda et al. 2009; Vilà et al. 2011). They can impact native species through direct competition for resources as well as by altering the physical or chemical environment (Skurski et al. 2014). The control of invasive introduced species has received considerable attention at regional, national and international levels, yet the effectiveness of control efforts for restoring native communities is often dependent on specific factors working at local scales (National Invasive Species Council 2016).

Many projects to control invasive species track only the species targeted for removal, and not the species found filling the newly available niches after the removal of invasive species (Reid et al. 2009; Hazelton et al. 2014; Pearson et al. 2016). Some

studies have reported an increase in richness or abundance of introduced species other than the one being targeted by removal (Hulme and Bremner 2006; Story et al. 2006; Nsikani et al. 2020). While some studies have found a positive response from native species when invasives were removed (D'Antonio et al. 1998; Andreu & Vilà 2011), one meta-analysis has found that native species gains were frequently modest or none were found (Kettenring and Adams 2011). In addition, while the impact of an invasion may take many years to become evident (Crooks 2005), many studies of invasive species control have only looked at a single growing season (Kettenring and Adams 2011).

In communities dominated by annual plants, the interaction between variation in weather (within and among years) and invasive species traits strongly influences the outcome of the management of invasive species (Pitt and Heady 1978; Germino et al. 2016; Fahey et al. 2018; Moffet et al. 2019) and may either overshadow or interact with the impact of control actions (Ogden and Rejmànek 2005). For example, when rainfall conditions after the control of an invasive species are favourable to the invasive,

the invasive population may rebound, whereas rain conditions unfavourable to the invasive species may result in more effective removal (Davy et al. 2015).

Most California grasslands are dominated by grasses of Eurasian origin from a guild (annuals) not well represented in the native flora (D'Antonio et al. 2007). The annual forb *Centaurea solstitialis* L. (Asteraceae), native to Eurasia, was introduced to California in the 1800s and is now found on over 7 million ha in the western United States (Randall et al. 2017). It is easily spread and establishes where human activities disturb the soil (DiTomaso et al. 2006) and has greater growth rates in California than in its native Spain (Montesinos and Callaway 2018). It is toxic to horses (Wang et al. 1991) and reduces the carrying capacity of rangeland (Connor 2003). The species is predicted to continue spreading in the western United States in response to global environmental change (Dukes et al. 2011).

Centaurea solstitialis has characteristics expected to negatively impact native plants. This includes competing for native pollinators (Barthell et al. 2005). The species depletes soil moisture deeper in the soil profile and later in the growing season than either native perennial bunchgrass communities or the more common communities of introduced annual grasses (Enloe et al. 2004).

Large *C. solstitialis* plants can produce over 100,000 seeds (DiTomaso et al. 2006). Under experimental conditions seeds can remain viable in the seedbank for at least a decade (Callihan et al. 1993). However, in California, it appears that typical conditions (i.e. Mediterranean climate) degrade most seeds in the seedbank within a few years (Benefield et al. 2001). *Centaurea solstitialis* flowers and sets seed late in the growing season when rains have typically ceased for the year and most other annual plants have died (DiTomaso et al. 2006), a reproductive phenology uncommon in parts of its introduced range. In years with late-season moisture, late-germinating plants may successfully flower and set seed as they are not sensitive to photoperiod (Roché et al. 1997). Successful management of *C. solstitialis* depends in part on carefully timing control efforts. Because of the short time required to develop viable seeds, post-emergence management techniques must be implemented before most flowers are open (DiTomaso et al. 2006). However, some individuals may be missed at that time because they are small, germinate late, or are hard to see before flowering; and these individuals may develop viable seeds, particularly if there is late-season moisture.

Many herbicides can be used to control *C. solstitialis* (USDA Forest Service 2014), and those that provide both pre- and post-emergence control are the most widely used (DiTomaso et al. 2006). Glyphosate is a post-emergent herbicide available in a variety of concentrations which can be very effective in controlling *C. solstitialis* if application is timed correctly (DiTomaso et al. 1999), and will have minimal impacts on non-target plants in locations where other plants have senesced or died for the year at the time of use.

We were interested to quantify if *C. solstitialis* was associated with reduced richness of native species and if sustained removal of *C. solstitialis* over 6 years resulted in an increase in native species richness. We hypothesised that competition for space and resources would result in negative impacts on native plant species richness where *C. solstitialis* had invaded. We also hypothesised that our removal treatment would lead to reduced *C. solstitialis* cover and that late spring rainfall in one year can be used to guide *C. solstitialis* management efforts the following year. Finally, we predicted that the release from competition resulting from *C. solstitialis* removal would lead to a positive response in native species richness and that this positive response would be stronger where there was higher pre-treatment native richness.

Materials and methods

Study site

We conducted the experiment at the Modini Preserve of Audubon Canyon Ranch (hereafter called Modini), a 1200-ha protected area in north-eastern Sonoma County, California, USA. Modini is in a region with a Mediterranean-type climate of dry, hot summers and cool, wet winters. Prior to 2009, when the Modini Preserve was established, the grassland was grazed by cattle. Grazing pressure was low and patchy, though specific stocking levels at that time are unknown. We conducted our experiment in an area of the ranch that had not been grazed for at least five years to avoid the additional variable of grazing pressure in our study.

We selected two areas of vegetation invaded by *C. solstitialis* for our experiment. The areas were located 375 m apart, at an elevation of 300 m, with a south-west aspect, and with soils classified as Suther-Laughlin loams or Hugo very gravelly loam (USDA Natural Resource Conservation Service 2016). The western patch covered 2.39 ha and the

eastern patch 0.24 ha. Adjacent to each patch with *C. solstitialis* there was an uninvaded area of grassland with the same aspect (e.g. also facing south-west). We placed 1-m² experimental plots in a randomised block design, treating each invaded patch plus the neighbouring uninvaded area as a block. We used GIS (ArcGIS, version 10.5) to place a grid of 25-m² squares over each block. In each block, we randomly selected 20 squares in the invaded area and 10 squares in the adjacent uninvaded area, excluding any squares along the invaded-uninvaded boundary. We located a 1-m² plot at the centre of each of these squares. We randomly selected half of the invaded plots in each block to receive removal treatment. This yielded 20 plots for each of 3 treatments ('invaded-treated', 'invaded-untreated', 'uninvaded'), split between the two blocks; for a total of 60 plots.

Field methods

Between 2011 and 2017, we visited all plots in early May and identified all plants to species. Cover for each species within each plot was visually estimated within the following cover classes: <1%, 1–5%, >5–15%, >15–25%, >25–50%, >50–75%, and >75%. Because we recorded absolute cover for each species, total cover could exceed 100% if plants overlapped. We also estimated cover for all annual grasses as a group, and per cent cover of bare soil, litter and rock.

In early June 2011 we spot-applied Glyphosate, a non-selective post-emergent herbicide, at label rates (19.5 cc of a 40% solution per litre of water) to *C. solstitialis* in each invaded-treated plot, plus a 1-m buffer around that plot, using a backpack sprayer. Even when neighbouring squares were selected to have survey plots, plot edges were separated by at least 4 m, and thus the effect of treatment did not overlap between plots. In early June of all subsequent years, the *C. solstitialis* in invaded-treated plots and their surrounding buffer zones was either hand-pulled (when abundance was very low), or sprayed with Glyphosate, after conducting the plant survey. We measured rainfall from a manual rain gauge each morning of the study at the same elevation as the study site, approximately 3 km away.

Data preparation and analysis

We classified each plant species as native or introduced based on Baldwin et al. (2012). We assigned

the binned *C. solstitialis* per cent cover the median value for the bin (e.g. >0.5–5% bin assigned value of 3) and treated it as a continuous variable. We defined previous year late spring rainfall as the cumulative rainfall from 15 May – 30 June of the previous year. For the third set of predictions, we used total current-year annual rainfall (1 October of the previous year through 30 September of current year).

We tested each prediction in Table 1 by constructing a Generalised Linear Model (GLM) containing the primary predictor variable for inference plus variables that we thought might account for additional variation in response variables, including spatial and temporal autocorrelation resulting from our repeated measures of plots within the same invaded patches (full model structure shown in Table 2). We included block or the interaction of block and relative east/west position (expressed in metres as the UTM easting value) to account for spatial autocorrelation. We included the additive effect of year to account for temporal autocorrelation. However, because intra-annual growing conditions in our study system often vary much more than underlying annual trends (Goldstein and Suding 2014), particularly over the relatively short period of this study, we were not primarily interested in interpreting

Table 1. Predictions and analysis design testing the response of native plant species to removal of the invasive plant *C. solstitialis* at Modini Preserve, Sonoma Co., CA, USA, 2011–2017. The removal treatment was initiated after data collection in 2011, so where 2011 data are included this represents pre-treatment conditions.

Prediction	Data subset (years and treatment)
1.1 Native species richness will be lower in plots invaded by <i>C. solstitialis</i> than in not invaded plots.	2011, all treatments
1.2 In <i>C. solstitialis</i> -invaded plots, native species richness will be higher where <i>C. solstitialis</i> cover is lower.	2011, invaded plots only
2.1 In invaded plots once treatment has begun, <i>C. solstitialis</i> cover will be lower in treated than untreated plots.	2012–2017, all invaded plots
2.2 In invaded-untreated plots <i>C. solstitialis</i> cover will be higher when late spring rain the previous year is higher than when previous year late spring rain is lower.	2011–2017, invaded-untreated plots
3.1 In invaded plots once treatment has begun, native species richness will be higher in treated than in untreated plots.	2012–2017, all invaded plots
3.2 In invaded-treated plots, the positive response of native species richness to treatment will be stronger in plots that had higher pre-treatment native richness.	2012–2017, invaded-treated plots
3.3 In invaded-treated plots, native species richness will be higher after treatment than before.	2011–2017, invaded-treated plots

these year coefficients as measures of annual trends. Rather, we evaluated the overall effects of treatment across a set of years with the expected range of growing conditions. The exception to this is prediction 3.2 (Table 2) where we explicitly compared annual trends in post-treatment native richness among plots with high vs. low pre-treatment richness.

We fitted GLMs with a Poisson error distribution and the log link for count response variables. For per cent cover responses we converted per cent cover to a proportion and used zero-inflated beta regression and the logit link. We validated the full models (containing all explanatory variables) by checking for evidence of any remaining spatial autocorrelation in the residuals, for correlation between predictor variables and for overdispersion (Zuur et al. 2009).

To test each prediction, we used the Likelihood Ratio Test (LRT) to compare the full models to corresponding nested models with the same variables except the primary predictor variable for inference. We used the P-value from the χ^2 test of the LRT as evidence to reject the nested model. Instead of selecting an *a priori* alpha-level for significance, we interpreted and reported P-values as providing a range of evidence (from convincing evidence to no evidence) against the nested null model (Murtaugh 2014). Where there was evidence to reject the nested model, we evaluated goodness of fit of the full model by calculating deviance explained (1 - (residual deviance/null deviance)) for Poisson regression or pseudo- R^2 for beta regression (Nagelkerke 1991; Stasinopoulos and Rigby 2007). We evaluated and

visualised the effect size and biological importance of the predictor variable in question by plotting the estimated coefficient and 95% confidence intervals (CI; estimate \pm SE * 1.96) from the full model.

We used R version 3.6.1 (R Core Team 2019) for all data preparation and analyses. Generalised Linear Models with Poisson distribution were fitted with the R package stats (included in base R). Zero-inflated beta regression models were fitted with the package GAMLSS (Stasinopoulos and Rigby 2007).

Results

Six plots were excluded from analysis because an invaded plot selected *a priori* fell into an uninvaded area of the 3.2 ha area we mapped as invaded, the plot markers were damaged by feral pigs, or uninvaded plots were invaded during the study. We analysed the remaining 54 plots including 10 invaded-treated plots, 10 invaded-untreated plots and 9 uninvaded plots in the east block; and 8 invaded-treated plots, 9 invaded-untreated plots and 8 uninvaded plots in the west block. During the study, mean annual rainfall at the Preserve was 1210 (\pm 193 SE) mm, and late spring rainfall (May 15-June 30) was highly variable with a mean of 45 (\pm 22 SE) mm.

Before treatment, mean *C. solstitialis* cover did not differ between invaded-treated plots (15.0%, \pm 3.1 SE) and invaded-untreated plots (12.8%, \pm 2.9 SE) (t-test, $n = 37$, $P = 0.6$). Across all post-treatment years, average *C. solstitialis* cover was 20.2% (\pm 2.1 SE) in invaded-untreated plots. The cover of plots was dominated by non-native plants both before and after treatment. In invaded-untreated plots, *C. solstitialis* had the

Table 2. Analysis result for testing predictions regarding native plant species and removal of the invasive plant *C. solstitialis* at Modini Preserve, Sonoma Co., CA, USA, 2011–2017. Likelihood Ratio Test was used to test the fit of a full model (shown) versus a nested model that was identical to the full model except that it lacked the primary predictor variable for inference. The variable for inference is listed first, except for prediction 3.2 where the pre-treatment * year interaction is the variable for inference. P-value is from the χ^2 test with $df = 1$. Estimated coefficients and 95% CI (back-transformed to the scale of the response variable inverse link function) represent the multiplicative change in the response variable for the 1-unit change in the predictor variable (i.e. coefficient = 1 represents no effect). Explained variation represents goodness of fit and is either 1- (residual deviance/null deviance) (predictions 1.x and 3.x) or pseudo- R^2 (2.x). See Table 1 for predictions.

Prediction	Full model	χ^2 P-value	Estimated coefficient (95% CI) for inference variable	Deviance explained
Response: pre-treatment native species richness				
1.1	<i>C. solstitialis</i> invaded/uninvaded + Block * Easting	0.035	0.598 (0.37, 0.96)	0.46
1.2	<i>C. solstitialis</i> % cover + Block * Easting	0.61	1.01 (0.98, 1.04)	-
Response: post-treatment <i>C. solstitialis</i> cover (%)				
2.1	Treatment + Pre-treatment <i>C. solstitialis</i> cover + Year + Block	<0.001	0.28 (0.21, 0.37)	0.27
2.2	Late spring rain prev. year + Pre-treatment <i>C. solstitialis</i> cover + Year + Block	<0.001	1.12 (1.07, 1.16)	0.24
Response: post-treatment native richness				
3.1	Treatment + Year + Total rain + Block	<0.001	1.30 (1.04, 1.62)	0.34
3.2	Pre-treatment native richness * Year + Total rain + Block	0.53	1.01 (0.98, 1.05)	-
3.3	Pre- vs Post-treatment + Year + Total rain + Block	0.64	1.21 (0.62, 2.37)	-

highest cover of any single species, followed by four species of introduced annual grasses. In invaded-treated plots, four introduced annual grasses had the highest cover, with native bunchgrass *Stipa pulchra* (3%) and introduced forb *Carduus pycnocephalus* (5%) having fifth greatest cover in the west and east blocks, respectively. In uninvaded plots, introduced annual grasses made up the majority of the cover, however the native perennial bunchgrass *Stipa pulchra* had the second highest cover in the west block (10%) and the introduced forb *Erodium botrys* had fifth highest cover in the east block (2%). The most common species of introduced annual grasses were *Briza maxima*, *Avena barbata*, *Bromus diandrus*, *Festuca perennis*, and *Brachypodium distachyon*.

Testing predictions regarding native plant species and the removal of *C. solstitialis*, we found a negative relationship between *C. solstitialis* presence and native plant species richness before removal, although the full model only explained a moderate amount of deviance in the data (prediction 1.1; Table 2). Native species richness was lower in invaded plots than in uninvaded plots by a factor of ca. 0.6 (Table 2, Figure 1). Our data provided no support for the prediction of a negative relationship between native plant richness and *C. solstitialis* cover (prediction 1.2; Table 2, Figure 1).

We found strong evidence that the cover of *C. solstitialis* following treatment was lower for treated than untreated plots (prediction 2.1; Table 2). *Centaurea solstitialis* cover was lower in treated plots than untreated plots by a factor of ca. 0.3 throughout the study (Table 2, Figure 2). We also found that the cover of *C. solstitialis* was greater following years with more late spring rain (prediction 2.2; Table 1). Each additional mm of rain was associated with an increase of about 10% in *C. solstitialis* cover (Table 2, Figure 2).

Our data provided support of our prediction that native richness would be higher in treated plots than in untreated plots (prediction 3.1; Table 2). However, the size of the effect was modest in both absolute value and relative to the estimated 95% CI (Figure 3). Native species richness was higher in treated than untreated plots by a factor of 1.3 (Table 2, Figure 3). We failed to show that the response of post-treatment native species richness to treatment was greater in plots with higher pre-treatment native species richness (prediction 3.2, Table 2, Figure 3). We also did not find evidence that native species richness was greater in treated plots after treatment than before (prediction 3.3, Table 2, Figure 3).

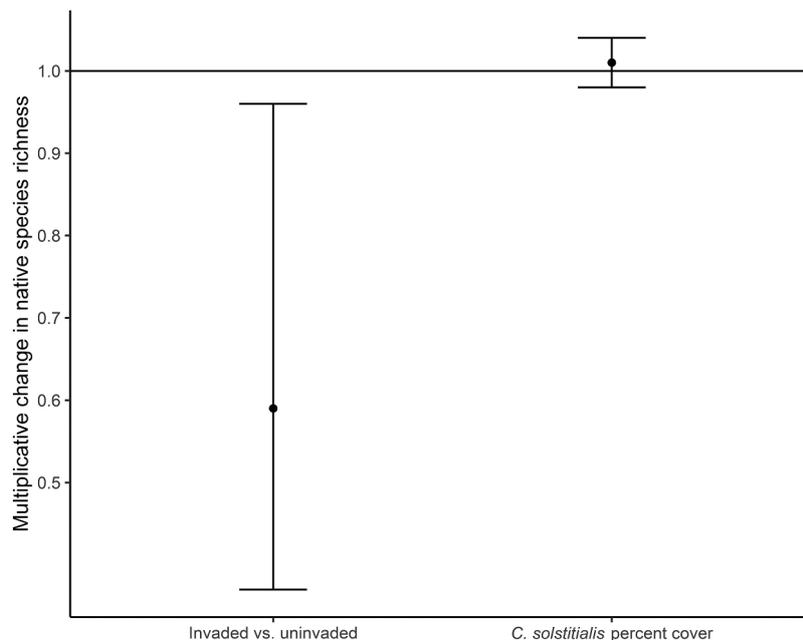


Figure 1. Estimated effect and 95% CI of *C. solstitialis* invasion status and per cent cover on native plant species richness at Modini Preserve, Sonoma Co., CA, USA, 2012–2017. Y-axis represents the multiplicative change in native richness associated with study plots being invaded vs not invaded or a 1% increase in *C. solstitialis* cover. Estimates close to 1 and/or 95% CI overlapping 1 indicate no change.

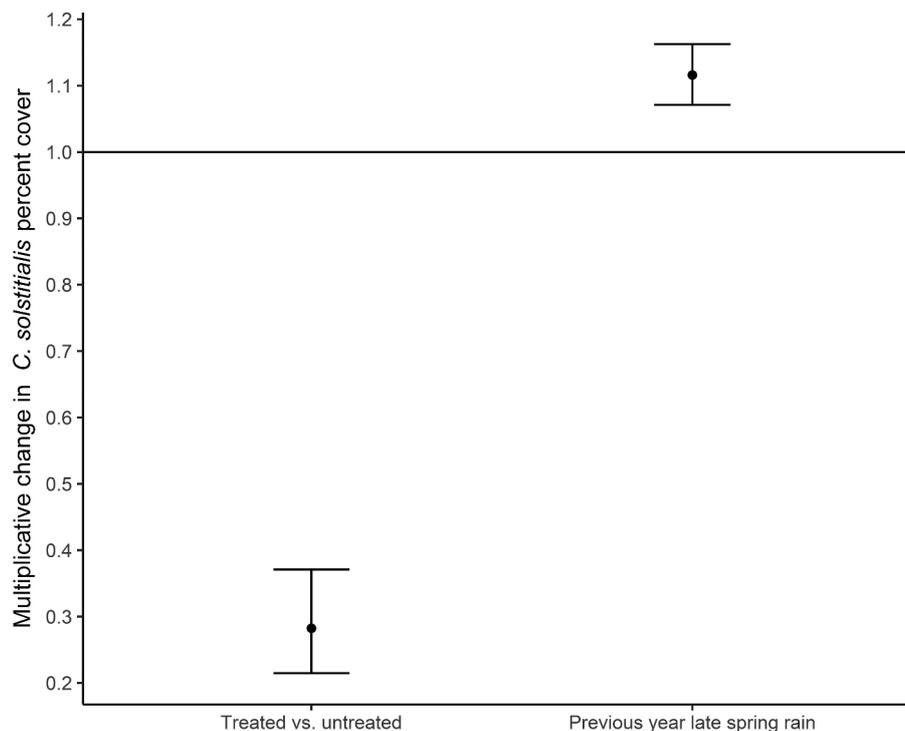


Figure 2. Estimated effect and 95% CI of previous year late spring rain and removal treatment *C. solstitialis* per cent cover at Modini Preserve, Sonoma Co., CA, USA, 2012–2017. Y-axis represents the multiplicative change in *C. solstitialis* per cent cover in treated vs untreated plots or associated with a 1 mm increase in late spring rainfall the previous year. Estimates close to 1 and/or 95% CI overlapping 1 indicate no change.

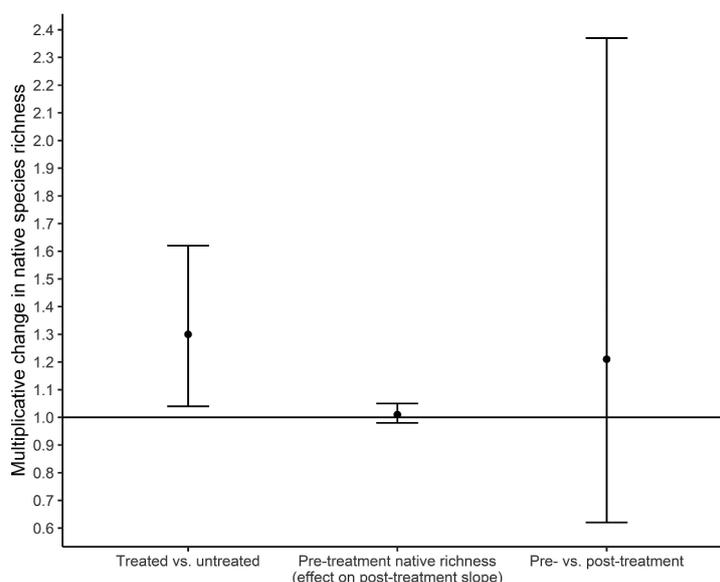


Figure 3. Estimated relationship and 95% CI between *C. solstitialis* removal treatment and native plant species richness at Modini Preserve, Sonoma Co., CA, USA, 2012–2017. Y-axis represents the multiplicative change in native richness in treated vs. untreated plots; the multiplicative change in post-treatment trend associated with each additional native species present before treatment; and before and after treatment. Estimates close to 1 and/or 95% CI overlapping 1 indicate no change.

Discussion

As in other studies (Gaertner et al. 2009; Davies 2011; Vilà et al. 2011), we found that the presence of an invasive plant, *C. solstitialis*, was associated with reduced richness of native plant species. However, we did not find evidence for our predicted

negative relationship between *C. solstitialis* per cent cover and native richness. Our ability to detect such a difference may have been limited by the overall low values and low variability in both the response (native species richness) and the predictor used for inference (*C. solstitialis* cover).

We also demonstrated that removing *C. solstitialis* annually was effective in mostly eliminating it. Our treatment methods reduced *C. solstitialis* to few plants the year following treatment, substantially lower than untreated plots, throughout the duration of the study. Recurring *C. solstitialis* may have come from three possible sources: *in situ* seedbank from before the study began; seeds dispersed by wind or animals from outside of plot and the buffer zone; and/or from plants that were missed in removal, either because they were very small (e.g. cotyledon leaves only) or because they germinated after removal was completed. Other researchers have found that 4 years after removal efforts ceased, *C. solstitialis* had rebounded (Kyser and DiTomaso 2002).

We confirmed our prediction that *C. solstitialis* responded positively to late spring rainfall in the previous year. For managers who constantly balance time and expense spent on control of invasive species (e.g. Leung et al. 2005; Januchowski-Hartley et al. 2011), this is important information. Rainfall data are readily available and control resources for *C. solstitialis* can be allocated based on them. Effective control of *C. solstitialis* will take greater resources following years with high late spring rainfall. While our study focused on one specific invader, our hypothesis about late spring rainfall was based on comparing the phenology of the invader to that of other plant species in the study plots: knowing how an invader's traits compare to those of the extant vegetation can help achieve management objectives (Moles et al. 2008).

We found slightly higher (1.3 times) native species richness in treated plots than untreated plots; however, the estimated 95% CI for this effect nearly overlapped 1. Native richness was very low in all our plots so this result may not be particularly important to the ecological function of our study system. If the lack of the propagules of native species limits the response of native species richness to invasive removal and higher above-ground native species richness indicates locations with higher native species propagules present, a pre-treatment survey would identify the most efficient locations for control projects. However, we did not find evidence to support our prediction that native species richness would respond stronger to treatment where pre-treatment richness was higher. We also did not find evidence that native species richness would increase in treated plots following treatment. However, there was substantial variability in post-treatment native richness in treated plots, leading to

broad 95% CI for the estimated effect of treatment and possibly obscuring our ability to detect a significant difference. In an annual-dominated system such as at Modini, inter-annual fluctuations due to weather are expected to be greater than differences due to long-term trends in any given year (Reis et al. 2006).

The response of native species to the removal of invasive species can be influenced by which other invasive species are present, time since the invasion started, and what native species propagules are extant (Zavaleta et al. 2001). We think the lack of extant native species at our study site that are functional equivalents (i.e. late-season forbs) to *C. solstitialis* helps explain why native plants did not benefit more from the removal of *C. solstitialis*, as such species are best suited to utilise resources made available by effective control (Zavaleta and Hulvey 2007; Cadotte et al. 2011). Therefore, focusing removal projects in locations that have such species present, or adding such species after removal, may give better results.

The modest response of native species in our study may also be due to poor native plant representation in the seedbank (Cione et al. 2002), or by the overall low abundance and richness of native plants in our invaded plots. Eurasian annual grasses have become dominant in many locations in California, precipitated by historic overgrazing and other land use decisions, along with a relative dearth of annual grasses in the native flora. Invasive plants are broadly known to reduce native species richness (e.g. Orrock et al. 2015; Fahey et al. 2018; Bernard-Verdier and Hulme 2019), and it may be that non-native grasses in our system continued to suppress native plant richness even after *C. solstitialis* removal.

It is possible that our treatment negatively impacted native species. Due to the natural history of these native species and the mechanism by which Glyphosate operates we do not think this is a direct result of the herbicide. The removal treatment coincided with the beginning of the dry season, after most other annual plants had died for the year and perennials had senesced for the year. Glyphosate is a post-emergent, broad-spectrum, non-selective herbicide: it acts on all plants that are actively growing (Baylis 2000). However, any plants not actively growing at the time of application, such as most of those in our system, are unaffected. In addition, we applied herbicide using a backpack sprayer and all species other than *C. solstitialis* were avoided. While the herbicide is diluted with

water for application, we do not think this addition of moisture had an impact since most landed on leaves of target plants.

Conclusions

Our results provide important new guidance for managers seeking to control populations of *C. solstitialis*. Elimination of *C. solstitialis* following above average late spring rain is critical to reducing the spread of this plant. The recovery of native plant richness in ecosystems invaded by *C. solstitialis*, even after many years of removal, will be quite modest if removal is the only restoration action taken.

Acknowledgements

The authors thank Jim and Shirley Modini for their foresight in protecting the Modini Preserve, Tomás Ruiz for rainfall observation and recording, John Kelly and T. Emiko Condeso for experimental design feedback, and two anonymous reviewers for feedback on an earlier draft.

Data availability statement

The data that support the findings of this study are available from the corresponding author, SNA, upon reasonable request.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This project was funded by numerous generous donors to Audubon Canyon Ranch.

Notes on contributors

Sheherezade N Adams was the Modini Preserve Biologist and Manager from 2009 until 2017.

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Nils Warnock is director of conservation science.

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