

Removing an invader: evidence for forces reassembling a Chihuahuan Desert ecosystem

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Abstract. Community reassembly is an important concept in community ecology, but in most circumstances cannot be observed and is hypothetical. Reassembly of communities is an observable process that can be examined effectively following species invasions. Our study system in southeastern Arizona has declined in diversity and abundance of native winter annual plants coincident with a sustained irruption of a nonnative invasive Eurasian species, *Erodium cicutarium*, and a major reassembly of the winter annual plant community. To understand the role of *E. cicutarium* in the reassembly process, we initiated a multiyear *E. cicutarium* removal experiment that varied the timing of removal. Species richness was higher as a result of removal, although this effect was variable over time. Surprisingly, the abundance of native species collectively was decreased by *E. cicutarium* removal. However, previously rare *Astragalus nuttallianus* appears to be facilitated by *E. cicutarium*, as demonstrated by higher density and relative abundance in the presence of *E. cicutarium*, and is now codominant. Excluding *A. nuttallianus* abundance, the remaining native species are collectively increased by removal of *E. cicutarium*. Although our results showed strong effects of removal, the timing of removal never significantly affected any plant variables. Our experiment implicates a major role for *E. cicutarium* in the reassembly of the native plant community. Our work suggests a broadening of perspective on processes structuring annual plant communities in arid regions, and calls for an integrated approach beyond the recent popular focus on the interaction between competition and the physical environment.

Key words: *Astragalus nuttallianus*; Chihuahuan Desert; community reassembly; *Erodium cicutarium*; plant invasions; winter annuals.

INTRODUCTION

The concept of community assembly guides thinking about the ways in which natural communities are structured (HilleRisLambers et al. 2012), and much work has focused on how the properties of organisms and the relationships of their niches affect the outcome of the process (HilleRisLambers et al. 2012). Despite its conceptual importance, community assembly has been a largely hypothetical concept because no community has a defined beginning, except in the particular instances of primary succession or experimental communities (Drake 1991, Chase 2003). Thus, no meaning can be given to the preassembly situation in the structuring of communities. Communities may be viewed as continually reassembling after various perturbations occur; for instance, disturbance initiating secondary succession, a change in climate, or the invasion of a new species previously absent from the regional species pool. Species interactions are regarded as having major roles in community assembly processes, but strong evidence for these roles is uncommon.

Invasive species can provide an opportunity to study the role of species interactions in community assembly, especially when the course of the invasion has been well studied. An alien species that has become invasive can be used to probe two aspects of assembly. First, studies can examine how a new arrival (the alien species) interacts with locally established species. Second, if the alien species becomes abundant, it may strongly perturb the local biological and physical environment, driving further evident community reassembly. For instance, it has often been argued that nonnative species invasions have numerous impacts beyond altering community structure. These include alterations in ecosystem processes (D'Antonio and Vitousek 1992, Mack et al. 2000), patterns of nutrient cycling (Vitousek and Walker 1989, D'Antonio and Vitousek 1992), and energy fluxes through ecosystems (Walker and Smith 1997, Mooney and Hobbs 2000, Huxman et al. 2004). These outcomes may be observed if an invasive species displaces nonnative species that play major functional roles (D'Antonio and Vitousek 1992) not matched by the invasive species. Such changes in ecosystem functioning may be an integral part of the reassembly process as early changes in functioning may drive subsequent reassembly. An alien species that merely becomes naturalized, but not invasive (i.e., does not achieve high

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abundance and only displaces native species locally), would only be a weak probe of the reassembly process. A strong probe can be provided by a species that becomes invasive, or essentially becomes an invader of large effect (Shea and Chesson 2002).

We have documented changes that have occurred as an invasive species increased in abundance and came to dominate a Chihuahuan Desert ecosystem of southeastern Arizona, USA (San Simon Valley; Ignace et al., *unpublished manuscript*). This ecosystem previously supported a rich community of native winter annual plant species. Prior to 1997, the nonnative Eurasian species *Erodium cicutarium* had a minor presence in the area, except near roads. The year 1997 marked the beginning of a sustained irruption of *E. cicutarium* over a broad area coincident with the decline of the native annual plant species, the alteration of community composition, and the loss of species richness (Ignace et al., *unpublished manuscript*). *Erodium cicutarium* is most common in the desert and semiarid grasslands of the Southwest (Kearney 1964, Mensing and Byrne 1999). It first established in the southwest United States 250 years ago (Mensing and Byrne 1998), and was widespread in southern Arizona by at least 100 years ago (Burgess 1991). Commonly found as a weedy species across many areas of North America, *E. cicutarium* is often associated with disturbed areas or roadsides (Gelbard and Belnap 2003, Brooks et al. 2006). *Erodium cicutarium* is currently abundant over many areas of the San Simon Valley, with relative abundance ranging from 80% to 96% of the total annual plant community in recent years. It is important to note that the dominance of *E. cicutarium* represents a sustained irruption of an alien species. It has been present in the seed bank at our study site since our first observations in 1986, but until the recent irruption, had not been abundant away from road verges.

Modern discussions of community assembly often make a distinction between neutral assembly and niche-based assembly (Adler et al. 2007). Although species have common needs, which might lead to the expectation of neutral assembly, they also have individualistic responses to the environment, which suggest niche-based assembly (Grubb 1977, Chesson et al. 2001, Stewart 2009) or reassembly processes. For example, desert annual plants commonly have species-specific germination responses to temperature and soil moisture (Adonakis and Venable 2004, Facelli et al. 2005). Indeed, there is much evidence for species differences in the nature of this sensitivity in the San Simon Valley, with different species favored in different years (Baskin et al. 1993, Chesson et al. 2013). Such differences in germination response to precipitation patterns are believed to be a major factor in diversity maintenance of annual plants in arid environments (Chesson et al. 2004, Angert et al. 2009, Chesson et al. 2013), and therefore should be of major significance in community reassembly.

Erodium cicutarium appears less specialized than native species in germination requirements. Preliminary studies of *E. cicutarium* from the San Simon Valley show that *E. cicutarium* germinates under a broad range of temperature conditions (P. Chesson, *unpublished data*), perhaps allowing it to germinate under conditions unfavorable to the native species. Vigorous growth of *E. cicutarium* throughout the season has the potential to reduce resources for natives, demonstrating strong competitive effects (Sears and Chesson 2007). Several factors suggest that changes in the environment have caused the sustained irruption of *E. cicutarium* at the study site. First, *E. cicutarium* has long been present in the seed bank, but failed to grow away from road verges until the mid-1990s. Second, *E. cicutarium* irrupted broadly in the San Simon Valley without the evident invasion front that would be expected if a genetic change were responsible. It now grows vigorously over a broad area, in contrast to the frequent poor performance of native species, suggesting that it is now better adapted, on average, than the native species. An explanation has been given in recent work implying that a change in the rodent community is a major factor in the sustained irruption of *E. cicutarium* (Allington et al. 2013). This change led to rarity of the large kangaroo rats in the genus *Dipodomys*, which prefer the relatively large seeds of *E. cicutarium*, hence likely decreasing seed predation on *E. cicutarium* relative to native species. This change occurred coincident with the irruption of *E. cicutarium*.

Elsewhere, we have documented environmental changes in the form of shifts in weather patterns and associated plant responses (Ignace et al., *unpublished manuscript*). Regardless of whether these changes contributed to rise of *E. cicutarium*, it appears that *E. cicutarium*, and some newly abundant native species, may have positive responses to the current climate regime, while the previously abundant species find it less favorable. In particular, *E. cicutarium* appears to be extremely plastic with regard to growth, allowing prodigious seed production in El Niño years. Experimental studies suggest that *E. cicutarium* has a strong competitive effect on native species (Schutzenhofer and Valone 2006, Sears and Chesson 2007), which is consistent with the decline of native annuals coincident with the increase in *E. cicutarium*. Generalist germination requirements favor the consistent presence of *E. cicutarium* whenever sufficient rain falls to support an annual plant community.

Various methods might be used to understand the role of an invasive species in subsequent community changes. Direct experimental manipulation, however, is the only sure way to establish causation. Properly designed removal experiments can reveal the role of the invasive species in the reassembly process. Thus, to test for a causative role for *E. cicutarium* in the observed changes in the native plant community, we implemented a removal experiment with four removal start months (November, December, January, and February) from

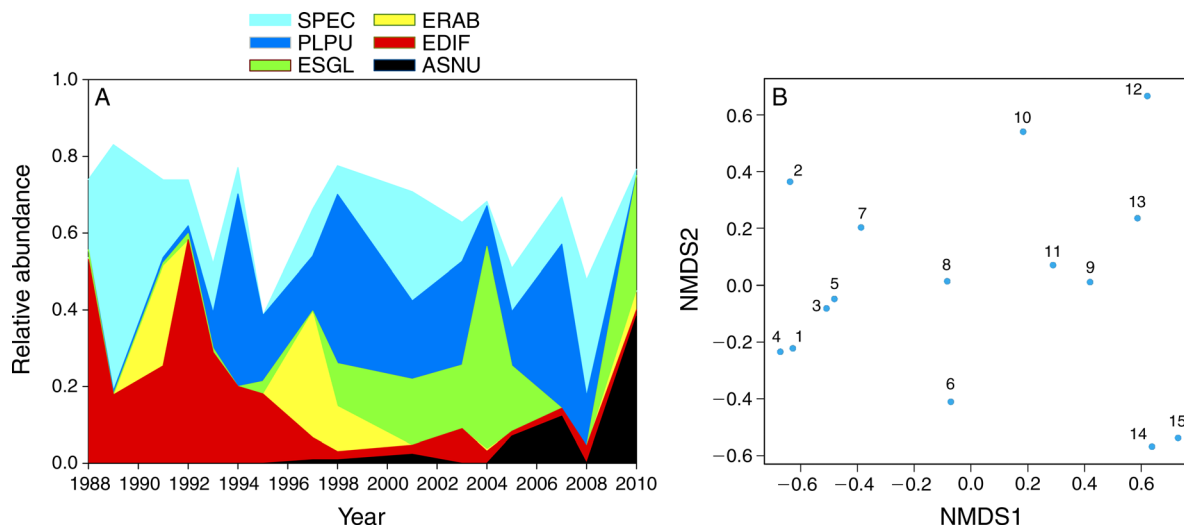


FIG. 1. Relative abundance of the six most abundant native species from 1988 to 2010. (A) Proportions of total native abundance. (B) The same data represented in nonmetric multidimensional scaling (NMDS) space (R metaMDS [Oksanen et al. 2013], with $k = 3$ [where k is dimension], and Bray-Curtis dissimilarity on the proportions in panel A). Numbers in panel (B) are the temporal order of the samples. Drought years when no plants (or extremely few) were recorded are omitted in panel (B), but in panel (A), values for drought years are interpolated values and can be identified by the absence of kinks in the lines at a given date. These data are derived from total abundances in each year of flowering individuals on 12.50×80 cm permanent plots 300–500 m east of the *Erodium cicutarium* removal experiment in the same plant community. Species are *Spergularia echinata* (SPEC), *Plantago purshii* (PLPU), *Eschscholzia glyptosperma* (ESGL), *Eriogonum abertianum* (ERAB), *Eriastrum diffusum* (EDIF), and *Astragalus nuttallianus* (ASNU).

2007 to 2010. If the early establishment of *E. cicutarium* has an important role in its effects on native species, earlier removal of *E. cicutarium* should lead to a greater response from the native community. As different species tend to germinate and grow most vigorously at different times during the growing season, differences in timing of removal would also be expected to differentially affect native species, and so test the idea that such niche differences should feature importantly in the reassembly process.

METHODS

Study system and climate

Our study site (31.93° N, 109.08° W) is a Chihuahuan Desert ecosystem located in the San Simon Valley, approximately 6 km east of Portal, Arizona, USA. The study site is at an elevation of 1644 m on the gently sloping bajada region of the Chiricahua Mountains that flank the eastern side of the valley. Open-range cattle grazing has occurred at this site since the late 1800s (Schutzenhofer and Valone 2006), but a 20-ha area was fenced to exclude livestock in 1977, within which permanent plots were established by P. Chesson and N. Huntly in 1987, and censused at flowering yearly since that time. A further 2.73 ha were fenced in 1994, and our experimental plots are located in this area. Common shrub genera include *Acacia*, *Ephedra*, *Flourensia*, and *Prosopis* (Guo et al. 2002), and the soil at the site is characterized as clay- and gravel-rich with much

spatial variation in particle size (Sears and Chesson 2007).

The winter annual plant community at the site has undergone profound changes in the last 15 years (Ignace et al., *unpublished manuscript*). These changes are illustrated by the permanent plot data from the field site (Fig. 1A). The same data are presented as a nonmetric multidimensional scaling (NMDS) analysis (Fig. 1B) showing a trend on the first axis aligned with time, and the second axis orthogonal to time showing stochastic fluctuations relative to time. A regression of the first axis on time is highly significant ($P < 1 \times 10^{-6}$). These are attributes to be expected from a system that is strongly affected by weather fluctuations, but is also undergoing directional change. Not evident from Fig. 1 is the rise of *E. cicutarium*, which began increasing in the mid-1990s, and is now the major part of the winter annual plant biomass at the site (Ignace et al., *unpublished manuscript*). *Erodium cicutarium* is currently abundant over many areas of the San Simon Valley, with relative abundance ranging from 80% to 96% of the total annual plant community in recent years. There are no evident effects of the livestock fences on *E. cicutarium* abundance or native species composition (D. Ignace and P. Chesson, *unpublished data*).

Meteorological data came from a station inside the 20-ha fenced area, and all data have been generously provided by S. K. Morgan Ernest (Utah State University, Logan, Utah, USA). Gaps in the meteorological record were filled by data from the San Simon weather

station accessed at the National Climate Data Center (*available online*).⁴ The meteorological station collected daily precipitation (mm) and temperature (°C). We obtained monthly precipitation by summing daily precipitation amounts through the entire winter season (October–April). Daily temperature was averaged for each month. The regional climate has a bimodal precipitation regime that is primarily concentrated in the summer and winter. Summer rains (May–September) average 156 mm and winter rains (October–April) average 115 mm.

Experimental design

In the 2007 season (fall 2006, winter and spring 2007), we set up a split-plot randomized complete block design on 20 (240 × 120 cm) plots inside the cattle-excluding fence. Each plot contained two 120 × 120 cm subplots. The perimeter of each plot had metal flashing buried to a 10 cm depth to restrict water runoff. An eighth-inch (1 inch = 2.54 cm) nylon cord marked a buffer zone 20 cm in width around each subplot, leaving an 80 × 80 cm interior sampling area. *Erodium cicutarium* removal (split-plot factor) was randomly assigned to one subplot of each plot, while the other subplot served as the control. We implemented four timings of *E. cicutarium* removal. The 20 plots were divided into five blocks, and each of the four plots was assigned a different removal time: November, December, January, or February. Removal and non-removal subplots were maintained consistently over the four years of the study, allowing the effects of removal to accumulate. The implementation of the removal timing varied slightly from year to year, however. In 2007, all plots were subject to a November removal in addition to their designated removal timing. In 2008, due to an error, blocks were ignored and completely randomized removal timing was implemented. In 2009, implementation of the split-plot randomized complete block design was restored and maintained through 2010. As the design variation was randomized with respect to previous and subsequent treatment assignments, it does not invalidate any of our statistical tests, but has possibly reduced their power.

Once a designated removal month arrived for a plot, *E. cicutarium* was removed in that month and in all subsequent months through February, after which further germination is unlikely. Due to the lack of early season precipitation, there was no germination of any winter annuals by the November removal start date over the course of the experiment, with the exception of 2007. Therefore, we began the *E. cicutarium* removal in December, which included the group of plots that were assigned the November removal start date. During the 2007 season, *E. cicutarium* individuals were removed from the entire removal subplot (including sampling area and buffer region) with forceps, carefully eliminat-

ing the root and the potential for new growth, while minimizing disturbance to the soil surface. Sears (2004) found no effect of this degree of disturbance on native plant performance in this system. However, we were not always able to obtain the root. Thus each subsequent year of the experiment, *E. cicutarium* was removed by clipping at the base of the plant just above the soil. Both methods ensured no regrowth of any of the *E. cicutarium* plants while minimizing disturbance to the soil.

Plant measurements

During each removal date, the number of *E. cicutarium* individuals present in each subplot was counted during the removal process. All harvested individuals were brought back to the laboratory at the University of Arizona (Tucson, Arizona, USA), where they were dried to constant mass at 60°C to give aboveground dry biomass of *E. cicutarium* on control subplots.

A census of flowering and fruiting plants was completed at the end of each growing season (April–May), when most of the winter annual plants were maturing seeds. Each growing season (October–April) is labeled with the year of the final census; for example, the 2006–2007 growing season is referred to as the 2007 season. We completed a final census of the winter annual plant community in April 2007, 2008, and 2010. The 2009 season had little rain, leaving no plants surviving at the end of season plant census. We counted all individuals per species within the sampling area of the removal and control subplots, giving a total of 40 (80 × 80 cm) sampled subplots. We measured height (*H*), maximum diameter (*MD*), and perpendicular diameter (*PD*) of each individual plant. We used individual plant canopy volume (*H* × *MD* × *PD*) and summed the individual canopy volumes to obtain subplot-level cumulative canopy volume.

Statistical analysis

All statistical analyses were performed with JMP statistical software (JMP 8; SAS Institute, Cary, North Carolina, USA). To maximize robustness while remaining quantitative, we used a matched pairs analysis to test for the effects of *E. cicutarium* removal on species richness, plant densities, and canopy volume in 2007, 2008, and 2010. To analyze the effects of timing of removal (a plot-level factor), we used analysis of variance on the paired difference between *E. cicutarium* removal and control subplot treatments. This was a simple analysis of variance for 2008 and a randomized block analysis for 2007 and 2010, respecting the designs in these years. These analyses test for an interaction between the removal and the time of removal. Due to the design differences in different years, we did not perform a repeated measures analysis. All plant variables were ln-transformed at the scale of the subplot for analysis.

⁴ <http://www.ncdc.noaa.gov/cdo-web/datatools/findstation>

TABLE 1. Summary of matched pairs analyses (*P* values) testing for the effects of *Erodium cicutarium* removal.

Year	Species richness	Natives	ASNU	ASNU relative abundance	Natives without ASNU
2007	n.s.	0.008	0.0002	0.01	n.s.
2008	0.001	n.s.	0.02	<0.0001	0.002
2010	n.s.	0.002	0.003	0.05	n.s.

Notes: ANOVAs testing the difference in *E. cicutarium* removal and control treatments across removal start months (November, December, January, and February) were not significant for any response variable in any year, and thus are not included in the table. Response variables are species richness excluding *E. cicutarium* (species richness), native plant density (natives), *Astragalus nuttallianus* density (ASNU), *A. nuttallianus* relative abundance (ASNU relative abundance), and natives without *A. nuttallianus* density (natives without ASNU). All variables were ln-transformed and results are shown for 2007, 2008, and 2010 separately. Nonsignificant results are shown with "n.s."

RESULTS

We tested for the effect of the timing (removal start month) of *E. cicutarium* removal on species richness and plant abundances, but this was not significant for any variable in any year. Removal, however, did have strong main effects on all variables, even though its timing within the year did not stand out (Table 1). Results showed a strong significant increase in species richness with removal for 2008, a nonsignificant increase in 2007, and a slight, nonsignificant decrease in 2010 (Table 1, Fig. 2). Native plant density was significantly affected by removal, but in an unexpected way. Native plant density was significantly reduced by removals in 2007 and 2010, but was not significantly affected by the removal in 2008 (Table 1, Fig. 3).

We observed significant changes in the plant community during the experiment, which led us to suspect that these unexpected reductions with removal were driven by the presence of one species, *Astragalus nuttallianus*. To investigate this further, we tested for the effect of removal on *A. nuttallianus* density. We found a significant reduction in all years of the experiment (Table 1, Fig. 4A), suggesting a facilitative

relationship between *A. nuttallianus* and *E. cicutarium*. To further explore this effect, we analyzed *A. nuttallianus* relative abundance (Table 1, Fig. 4B). In all years, *A. nuttallianus* relative abundance was significantly higher in control subplots than in removal subplots. In 2010, *A. nuttallianus* was a dominant species in the native plant community, demonstrating mean relative abundances ranging from 0.87 to 0.94 in control subplots and 0.79 to 0.97 in removal subplots (Fig. 4B).

These results showed that the native plant density was strongly influenced by the presence of one species, *A. nuttallianus*, especially in 2007 and 2010. To see if other native species were affected in the same way as *A. nuttallianus* by removal, we analyzed the combined abundance of all native species except *A. nuttallianus*. There was a significant increase in the density of natives without *A. nuttallianus* in 2008 (Table 1, Fig. 4C), which was consistent with the strong increase in species richness with removal (Fig. 2). A nonsignificant increase in this variable was evident in 2007.

The results so far were based on counts of individuals without taking account of their size. However, there were enormous overall differences between years in canopy volumes. Thus, analyses on canopy volume

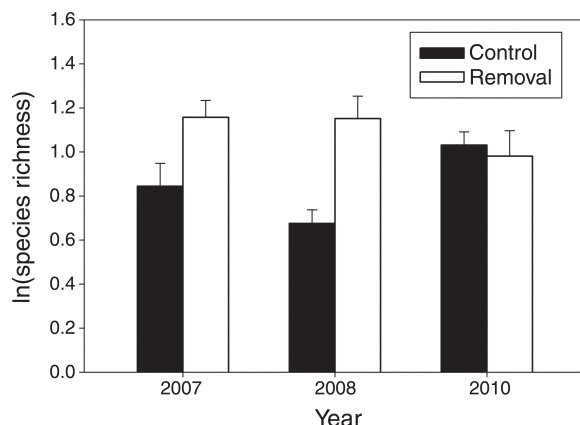


FIG. 2. Average species richness response to *E. cicutarium* removal. Each year (2007, 2008, and 2010) is the average ln(species richness) from all removal treatments. Black bars indicate plant response to no *E. cicutarium* removal (control), and white bars indicate plant response to *E. cicutarium* removal (removal). Error bars show standard error.

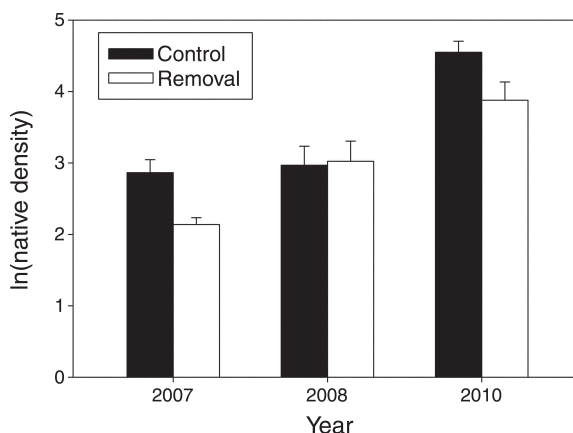


FIG. 3. Average native plant density response to *E. cicutarium* removal. Each year (2007, 2008, and 2010) is the average ln(native density) from all removal treatments. Error bars show standard error.

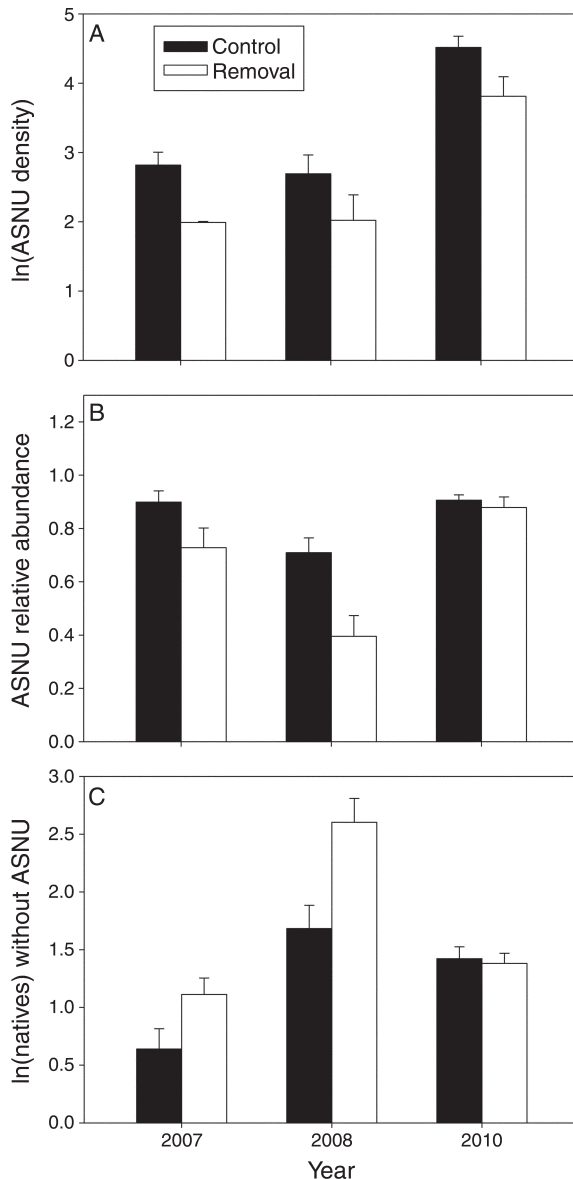


FIG. 4. (A) Average $\ln(\text{ASNU})$ response to *E. cicutarium* removal. (B) Average ASNU relative abundance response to *E. cicutarium* removal. (C) Average $\ln(\text{native density})$ with ASNU excluded from the data in response to removal. Each year (2007, 2008, and 2010) is the average taken from all removal treatments. Error bars show standard error.

might be expected to differ from those based on counts alone. To examine this issue, the same analyses were done on canopy volume as for the other variables, segregated in the same categories: natives, *A. nuttallianus*, and natives without *A. nuttallianus* (Table 2). Again, there was no significant effect of the time of removal on the effect of removal. The overall volume of native plants was only significantly affected by removal in the low productivity year, 2008, when it was significantly increased by removal. In 2007, canopy volume of *A. nuttallianus* was significantly reduced by

removal, but not significantly affected in other years. Native canopy volume without *A. nuttallianus* was significantly increased by removal in 2007 and 2008, but not 2010.

DISCUSSION

We experimentally removed an alien invader with a goal of understanding an observed community reassembly process. If the alien invader has had an important role, then direct and indirect interactions with other species should be revealed by removal. Spatially localized competitive and facilitative interactions might be evident on short spatial and temporal scales following a removal. Some effects might take longer to emerge if they involve soil properties, or require time for the seed bank of native species to recover. Other effects might require manipulation over a large area if natural enemies are the mediators of the interactions between species. It might be argued that the ideal study would involve replicated controlled introductions of an alien species to places where it is not found. Apart from the dangers and ethical considerations of such a manipulation, the evident strong spatial heterogeneity in alien and native associations in nature (Davies et al. 2005) means that replicating the particular reassembly process of some locality elsewhere is unlikely. Even more fraught is the idea of a correlative study that compares community structure in invaded and uninvaded localities. In our study, the alien species *E. cicutarium* has irrupted over a wide area. Localities where it is absent are sufficiently distant to have distinctly different environmental conditions, and so communities there reflect much other than the presence or absence of *E. cicutarium*.

Our experimental removal shows that *E. cicutarium* has profound effects on the native plant community. Our results varied between years, which is hardly surprising given the highly variable environment. Nevertheless, strong effects emerged. Removal of *E. cicutarium* had a positive effect on native species richness in 2007 and 2008 (strongly significant in 2008, but nonsignificant in 2007). Our experiment was conducted over four years with the expectation that the effects of

TABLE 2. Summary of matched pairs analyses (*P* values) testing for the effects of *E. cicutarium* removal on canopy volume.

Year	Natives	ASNU	Natives without ASNU
2007	n.s.	0.02	0.02
2008	0.02	n.s.	<0.0001
2010	n.s.	n.s.	n.s.

Notes: ANOVA testing the difference in *E. cicutarium* removal and control treatments across removal start months (November, December, January, and February) were not significant for any response variable in any year, and thus are not included in the table. Response variables are native plants (natives), *A. nuttallianus* (ASNU), and natives without ASNU. All variables were \ln -transformed and results are shown for 2007, 2008, and 2010 separately. Nonsignificant results are shown with "n.s."

the removal of *E. cicutarium* would be cumulative over time as the seed bank of previously depressed species built up. However, strong year-to-year temporal variation in the physical environment (see Appendix) may have largely masked such effects. This outcome is consistent with our NMDS analysis of the unmanipulated system, which shows clear long-term direction change parallel to the rise of *E. cicutarium*, but also strong fluctuations about that trend. Surprisingly, strong effects of *E. cicutarium* seemed to be evident in the first year of the removal study. Stronger effects appeared in the second year (2008) for native species richness as well as native abundance excluding *A. nuttallianus*, and *A. nuttallianus* relative abundance. The second year had relatively low rainfall and low plant abundances, seemingly too sparse for strong interactions to be expected. The observed strong effects might in fact be a reflection of strong interactions in the previous year leading to changes in plant abundances in the seed bank. Alternatively, differences in the timing of rainfall between the 2007 and 2008 seasons might be the explanation, given the concentration of rain during December in 2008, an ideal time for many native species to germinate (see Appendix). The 2009 season produced no winter annual plant community, while the 2010 season was characterized by late-occurring rain (January), with strong effects seen for *A. nuttallianus* but not for other species. However, that year differed from others in having exceptionally high *A. nuttallianus* abundance, potentially strongly influencing the outcome.

Unexpectedly, the removal of *E. cicutarium* decreased native plant abundance. However, this decrease in native plant abundance was due to what appears to be a facilitative effect that *E. cicutarium* had on a single species, *A. nuttallianus*. Although long recorded at our study site, this species has only become abundant in recent years (Fig. 1), and it seems likely that the strong facilitative effect of *E. cicutarium* on *A. nuttallianus* was responsible for its rise. In the last year of the study, these two species were codominant at the study site. Although a positive effect of *E. cicutarium* on total annual plant abundance was observed in a previous study on an adjacent site (Schutzenhofer and Valone 2006), that study mainly showed competitive effects of *E. cicutarium* as it suppressed the diversity and abundance of native plants. That study also found that *E. cicutarium* removal significantly lowered plot-level biomass. However, given the short duration of that study, it is not surprising that total plant biomass, including *E. cicutarium*, was higher on the controls, and so it is not clear whether the presence of *E. cicutarium* had increased community productivity over pre-irruption conditions. We found an increase in the total canopy of native plants other than *A. nuttallianus* with *E. cicutarium* removal in 2007 and 2008, implying that those members of the community were indeed more productive without *E. cicutarium*.

Removing *A. nuttallianus* from the analysis showed mostly positive effects of *E. cicutarium* removal on the rest of native plant community. In 2010, when *A. nuttallianus* abundance was extremely high, there was no net effect of removal on species richness. As we did not remove *A. nuttallianus*, it remained in high abundance even on *E. cicutarium* removal subplots despite the negative effect of removing *E. cicutarium* on *A. nuttallianus*. This continued high abundance of *A. nuttallianus* on removal subplots might have prevented significant recovery of other natives. Experimental removal of *A. nuttallianus* would be required to settle this issue. A previous study at our field site found intraspecific facilitation in *E. cicutarium* under harsh local environments, but not under more favorable conditions where the net intraspecific interaction was competition (Sears and Chesson 2007). This outcome is consistent with the conventional wisdom that the balance between competitive and facilitative interactions depends on the harshness of the environment (Bertness and Callaway 1994). Moreover, facilitation has been found to be most influential in periods of high environmental harshness (Bertness and Callaway 1994, Callaway 2002). Facilitation commonly stabilizes community dynamics in moderately severe environments, due to a buffering effect of increased facilitation during severe environmental periods, and enhances competitive effects in mild conditions (Butterfield 2009).

An enduring puzzle is why *E. cicutarium* appeared to facilitate *A. nuttallianus* among the winter annuals at our field site, while it appeared to have competitive effects on others. Interspecific facilitation by an *Erodium* species, *E. laciniatum*, has been seen previously to have a nurse plant effect on smaller desert annuals generally, with early facilitation by *E. laciniatum* changing to competition later in the season (Lortie and Turkington 2008). In our study, however, we found that the facilitative effect was unique to *A. nuttallianus* and thus species-specific for the affected species, while Lortie and Turkington (2008) emphasize species specificity from *E. laciniatum* being the only large annual species demonstrating facilitative effects.

Several traits distinguish *A. nuttallianus* from other reasonably abundant winter annuals at our field site. First, *A. nuttallianus* is the only legume and is a nitrogen fixer due to its symbiotic relationship with rhizobia found in root nodules. We have observed it to have well-developed root nodules (D. Ignace, *personal observation*) at our site, and this feature has been reported elsewhere in the Chihuahuan Desert (Whitford and Gutierrez 1989). Second, we have observed *A. nuttallianus* to display very deep roots compared to the other natives. *Erodium cicutarium* forms rosettes, often with a substantial three-dimensional structure, and typically achieves high biomass and leaf area compared to most natives. These traits may permit *A. nuttallianus* to benefit from shading and reduction of soil evaporation by *E. cicutarium*, without suffering simultaneously from

strong competition for nitrogen and water. Finally, *A. nuttallianus* and *E. cicutarium* tend to germinate earlier than the other members of the winter annual community and to co-occur in space. Although such temporal and spatial association would be disadvantageous were their net interactions competitive, it ought to be advantageous for *A. nuttallianus* given that it has a positive association with *E. cicutarium*.

These potential advantages are not the only possibilities that might explain the appearance of a facilitative relationship between *A. nuttallianus* and *E. cicutarium*. For example, it is possible that *A. nuttallianus* is benefiting from indirect facilitation due to *E. cicutarium* suppressing a competitor of *A. nuttallianus*. Previous work used a three-species model to show indirect facilitation through suppression of a shared competitor (Levine 1976) and was supported by more recent experimental work that showed evidence for indirect facilitation in a riparian community (Levine 1999). Furthermore, there is the possibility that other native species suppress *A. nuttallianus* more than *E. cicutarium*, which has been demonstrated in other studies that incorporate additive and nonadditive effects of competing species (Weigelt et al. 2007). The presence of *E. cicutarium* reduces native plant abundance (with *A. nuttallianus* excluded from the analysis), thus possibly having an indirect positive effect on *A. nuttallianus* and only appearing like direct facilitation.

It is likely that the strong negative effect that *E. cicutarium* had on native species, other than *A. nuttallianus*, resulted from a strong ability to reduce water and nutrient availability as seen in the Chihuahuan and Mojave Deserts (Brooks et al. 2006). Because *E. cicutarium* germinates earlier than most native species, it potentially preempts them in resource acquisition. Moreover, *E. cicutarium* appears to be extremely plastic in growth, with high seed production in favorable years. Sears and Chesson (2007) showed that *E. cicutarium* had a strong competitive effect at our site on at least one native species that was formerly abundant. In essence, *E. cicutarium* could be shaping the changes in this community through both direct and indirect interactions, an idea which is gaining consideration in the invasion literature (White et al. 2006).

We had expected that further details of the interaction between *E. cicutarium* and the native species might emerge from varying the time of removal because of differences between the germination requirements of *E. cicutarium* and native species, and the general sensitivity of the germination of annual plant species to the timing of rainfall (Baskin et al. 1993, Adonakis and Venable 2004, Facelli et al. 2005, Chesson et al. 2013). However, all effects of removal timing appeared minor and none were significant. Weather in 2008 and 2010 (see Appendix) concentrated the time of germination late in the year, rendering few opportunities for timing differences to emerge. For instance, suitable weather (see Appendix) concentrated germination in December in

2008 and in January in 2010, leaving limited opportunities for timing effects to emerge. In 2007, the design difference, where all plots had a removal in November, eliminated any potential timing effect from October germination in that year. Overall, it seems that this question would be more effectively answered by controlled watering treatments, varying the timing of sufficient water for germination, given the highly unpredictable natural rainfall.

Conclusions

Perturbed systems provide the opportunity for the hypothetical process of community assembly to become an empirically observable phenomenon in community reassembly. The modern world provides numerous opportunities to observe reassembly as a consequence of various human-wrought changes in the environment and the increased rate of alien introductions. Frameworks for understanding invasion ecology using concepts from community ecology have been proposed (Shea and Chesson 2002, MacDougall et al. 2009). Study of invasions conversely has the potential to advance community ecology. In our study system, we provide evidence for a role for an alien species in a profound community reassembly process. There are often questions about the role of competition in community assembly, even though the presence of competition is broadly expected. The idea of the ghost of competition past, sometimes disparaged (Connell 1980), is that observed community structure has been greatly influenced by the effects of past competition on community assembly and coevolution. The introduction of alien species, however, provides credence to this idea. Alien species sometimes have strong enough competitive effects to produce profound changes in a community (Schlesinger et al. 1990, D'Antonio and Vitousek 1992, Davis et al. 2000, Mack et al. 2000), as we have seen here. Many years hence, these strong competitive effects may just persist as ghosts replaced by much smaller effects in the reassembled and coevolved persisting community.

In addition to strong competitive effects of the alien species on the majority of native species, we see a possible role of facilitation by the alien species on the now codominant species, *A. nuttallianus*, with potentially major consequences for the rest of the community. Facilitation was originally considered an essential process in succession (Clements 1916), but then relegated to just one hypothesis in the case of secondary succession (Connell and Slatyer 1977). In recent decades, it has been suggested as a critical structuring force in some habitats (Brooker et al. 2008). Its role seems far more general than the common nurse plant effects often discussed for arid ecosystems, facilitation of annual plants under the canopy of shrubs (Schlesinger et al. 1996, Tielborger and Kadmon 2000) or larger annual species (Lortie and Turkington 2008), and interspecific facilitation during establishment of some perennials by

others (Tielborger and Kadmon 2000, Maestre et al. 2005, Butterfield et al. 2010). Although there has been recent discussion of how competition and environmental variation shapes community structuring processes in these systems (Angert et al. 2009, Chesson et al. 2013), our results suggest a substantial broadening of the perspective to include a major role for facilitation. There is a need for an integrated understanding of these different forces in structuring annual plant communities. Studying community reassembly following invasions has the potential to greatly advance understanding.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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