2017

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Ghost of invasion past: legacy effects on community disassembly following eradication of an invasive ecosystem engineer

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Abstract. By changing ecosystem processes and altering the physical landscape, invasive ecosystem engineers can have substantial impacts on ecosystem functions and human economies and may facilitate other non-native species. Eradication programs in terrestrial and aquatic systems aim to reverse the impacts of invasive species and return the system to its pre-invasion conditions. Despite an extensive focus on the impacts of both native and non-native ecosystem engineers, the consequences of removing invasive ecosystem engineers, particularly in coastal ecosystems, are largely unknown. In this study, we quantified changes in a benthic community following the eradication of the invasive ecosystem engineer, hybrid cordgrass *Spartina*, in San Francisco Bay, California. We used field experimental manipulations to test for persistent effects of both aboveground and belowground structural modifications of the invasive plant on the benthic community. We found significant effects of the invasive plant more than four years following eradication. Experimental modification of the above- vs. belowground structure of this ecosystem engineer revealed taxonomic specific effects resulting in hysteresis in the recovery of the benthic food webs. We found that these "legacy effects" resulted from two specific mechanisms: (1) delayed breakdown of belowground structures (stems, roots) and (2) persistence of other invasive species whose invasion was facilitated by the ecosystem engineer. Both of these mechanisms are likely to occur in similar systems where belowground structures breakdown more slowly or where other associated long-lived invaders persist. Our work is among the first to quantify the slow rate of change in food web and community processes and the persistent legacy effects of an invasive ecosystem engineer in a coastal ecosystem. We suggest that this delayed transition to pre-invasion conditions could resemble an alternate state that would be misidentified without a sufficient monitoring interval or recovery duration, with consequences for future management and restoration activity planning.

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Introduction

The impacts of biological invasions on ecosystem functions and human economies are increasingly well documented (Simberloff et al. 2013). Ecologists now recognize that the invaders of greatest concern include "ecosystem engineers," which can alter fundamental ecosystem processes through their impact on the abiotic environment and consequently influence the distribution and functioning of entire communities (Wright and Jones 2006). By altering the physio-chemical landscape, invasive ecosystem engineers may in some cases facilitate the invasion of other non-native species (Simberloff and Von Holle 1999, Grosholz 2005, Mendez et al. 2015, Gallardo et al. 2016). These invasion impacts may be reversed by management actions that attempt to completely eradicate, or substantially reduce, non-native invasive ecosystem engineers. By reversing the invasion impacts, this could potentially allow the system to return to pre-invasion conditions. However, unintended consequences can accompany invader removal, and successful restoration is not a certainty (Zavaleta et al. 2001).

Despite a substantial body of work on the changes produced by ecosystem engineers both native and non-native (Crooks 2002, Wright and Jones 2006), we know considerably less about what happens when these engineers are removed (Coleman and Williams 2002, Hacker and Dethier 2009, Corbin and D'Antonio 2012), although there are some compelling examples from terrestrial systems. Studies of invasive grasses showed that increased nutrient and light availability following local eradication increased seedling recruitment and growth of native shrubs (D'Antonio et al. 1998). Other studies quantifying the effects of non-native grasses as secondary invaders following the removal of non-native grazers found that invasive grasses altered light and soil conditions and slowed the recovery of native shrubs (Yelenik and Levine 2011). Additionally, some invasive plant ecosystem engineers modify the mineralization and retention of nitrogen in ways that may influence soil nitrogen for several years after they have been experimentally removed (Maron and Jefferies 2001, Grove et al. 2015). Other engineering invaders may change the chemical composition of soils, either via changes in salinity and pH (D'Antonio et al. 1998) or as a function of the addition of allelopathic chemicals (Ridenour and Callaway 2001, Grove et al. 2012), with consequences for the subsequent colonization by native or non-native species many years after the engineer is removed (Von Holle et al. 2013). For example, co-occurring non-native plants persisted for more than six years after the experimental removal of the invasive tree *Acacia longifolia*, which reduced native species via accumulation of leaf litter and light reduction (Marchante et al. 2011). A common feature of many of these studies is that there are often persistent effects of the invasive ecosystem engineer long after its removal, referred to as "legacy effects" (Corbin and D'Antonio 2012).

These primarily terrestrial studies highlight several mechanisms by which legacy effects of invasive ecosystem engineers may have a persistent, long-term influence on community assembly and ecosystem recovery processes and pose significant challenges for restoring ecosystem functions and services. However, in contrast to terrestrial ecosystems, we know far less about the consequences of removing non-native ecosystem engineers in coastal communities due in large part to the small number of successful removals in these systems (Hacker and Dethier 2009). Some of the consequences of losses of native marine ecosystem engineers through over-exploitation are known (Coleman and Williams 2002), but whether these apply to eradications of invasive engineers is unclear.

We predict that invasive ecosystem engineers in coastal systems may have substantial legacy effects. Wetland soils are frequently water-logged and anoxic and rates of decomposition may be slow, allowing for an extended legacy of below-ground effects of invasive plants. Also, many benthic invertebrates have easily dispersed planktonic life stages as well as gregarious recruitment and, in some cases, long life spans. Thus, species that may be facilitated by invasive plants can potentially persist long after the ecosystem engineer has been removed, further delaying the recovery of the community to the pre-invasion condition.

Studies to date documenting the removal of invasive salt marsh plants have provided unique opportunities to investigate the consequences of eradicating invasive marine engineers, although they have typically focused on the responses of single taxa or specific sets of associated non-native species (Patten and O'Casey 2007, Holsman et al.

2010). These studies have also provided insights into the effects of partial removal of the invasive engineer (Reeder and Hacker 2004) and potential long-term impacts of invader removal on erosional processes and geomorphology (Sheehan and Ellison 2015). However, studies on the magnitude and the duration of legacy impacts of ecosystem engineers on entire benthic communities are needed if we hope to understand the direction and speed of ecosystem recovery and, ultimately, how to manage the restoration of invaded ecosystems (Suding et al. 2004, Norton 2009). A few studies have made progress in this direction in salt marshes (Reeder and Hacker 2004) and macroalgal beds (Piazzi and Ceccherelli 2006), but they have not experimentally investigated the mechanisms underlying legacy impacts on the restoration process. Thus, mechanistic experiments are critical to determine whether processes producing hysteresis and thwarting recovery after eradication of an invasive ecosystem engineer are similar in coastal ecosystems as well as in other, more well studied systems.

We undertook this challenge by experimentally exploring the consequences of the eradication of invasive hybrid cordgrass *Spartina* (*S. alterniflora* × *S. foliosa*) from San Francisco Bay, California, United States, and the prospects for recovery of the benthic community to pre-invasion conditions. At the height of its invasion (prior to 2006), this ecosystem engineer had transformed previously unvegetated mudflats into thick meadows of dense emergent vegetation that produced large quantities of detritus aboveground and created thick, impenetrable rhizome mats belowground. This invasion had profound impacts on the system resulting in greatly altered invertebrate biomass and diversity, food web shifts, changes in sediment geochemistry, dramatically reduced light and water flow at the sediment surface, increased accretion of fine sediments, and increased tidal elevation (Levin et al. 2006, Neira et al. 2006, Rosso et al. 2006, Tyler et al. 2007). Experimental manipulations of sediments and benthic communities inside and outside the invaded zone (Neira et al. 2006) showed that these physical effects of hybrid *Spartina* produced lower levels of sediment chlorophyll-*a* (i.e., epibenthic microalgae), which is the main primary producer on unvegetated mudflats in this region (Kwak and Zedler

1997), and increased levels of sediment organic matter, porewater sulfide, and anoxia (Neira et al. 2006). Additionally, infaunal abundance was generally lower within invaded zones compared to uninvaded mudflats (Levin et al. 2006).

These changes to the physio-chemical environment were strongly associated with dramatic changes in the benthic food webs, as supported by stable isotope tracer studies (Levin et al. 2006). The benthic communities shifted from one dominated by surface-feeding species (including bivalves, amphipods, and cirratulid polychaetes) to a community dominated by subsurface detritivores, including capitellid polychaetes and tubificid oligochaetes (Levin et al. 2006, Neira et al. 2006). This shift in the community from surface to subsurface invertebrates has potentially important implications for higher trophic levels as well.

These invasion-driven changes began to shift beginning in 2006, when California state agencies conducted an extensive eradication program to eliminate hybrid *Spartina* throughout San Francisco Bay using aerial application of herbicide (imazapyr). By 2010, hybrid *Spartina* was eradicated (or nearly eradicated) at most sites within the Bay and this program continues to date. The eradication efforts left dense mats of decaying belowground plant material, elevated sediment topography, and standing dead aboveground stems.

We used this large-scale eradication to examine the possibility of legacy effects of above- and belowground effects of hybrid *Spartina*. We hypothesized that aboveground legacy effects might include the persistence of long-lived species initially supported by refugia and other engineering modifications by the invasive plant. Also, the potential for persistent effects on the sediment surface, including sediment characteristics such as elevation, may also result in legacy effects on the abundance and composition of infauna. We further hypothesized that belowground legacy effects of hybrid *Spartina* may include delayed breakdown of belowground biomass consisting of roots and rhizomes, which would continue to influence benthic communities and food web structure via persistent effects on sediment characteristics including detritus and porewater chemistry.

In order to experimentally quantify the legacy effects of hybrid *Spartina* on benthic communities

and potential constraints on the recovery process, we experimentally added structural elements that mimicked the structure and biomass of invasive hybrid *Spartina*. We added aboveground structural mimics to reproduce the physical effects on water flow and light on the sediment, and measured changes in sediment composition and porewater chemistry, as well as the abundance and diversity of the species-rich benthic infaunal and epifaunal communities. We also added hybrid *Spartina* litter in belowground treatments to support detritivores, thus affecting community assembly and altering trophic interactions. We reasoned that these manipulations, by recreating much of the physio-chemical environment of the recently removed hybrid *Spartina*, would delay the transition of the recovering invertebrate community and/or potentially shift the community back toward the invaded state. We compared these results with appropriate controls to understand how quickly, or even if, the community would return to pre-invasion state. We explored the possibility that this system, like many others, might respond much more slowly to the removal of invasive ecosystem engineers than expected, following a slower-than-expected trajectory toward recovery of the pre-invasion food web.

METHODS

Field site and invasion history

We conducted our experimental study of recovery following the eradication of an invasive ecosystem engineer at a long-term study site, the Elsie Roemer Bird Sanctuary in Alameda, CA (37.752589 N, −122.248755 W; Appendix S1: Fig. S1), where the impacts of the hybrid *Spartina* invasion were experimentally quantified over a five-year period from 2001 to 2005 (Neira et al. 2005, 2007, Levin et al. 2006, Tyler et al. 2007). This site (described in Neira et al. 2006) was first invaded by hybrid *Spartina* nearly 40 yr ago, and the invasion continued to spread through 2007. Beginning in 2008, an extensive eradication program was undertaken using herbicide, with nearly complete eradication of the hybrid at this location by 2011 and no observable hybrid by 2013 (Invasive Spartina Project Report 2013), making it an ideal location for testing for legacy effects on habitat recovery to the pre-invasion

mudflat state. While eradication is complete at this site, recovery can only be considered in progress. Our experimental manipulations were intended to quantify the degree to which eradication sites are actually on their way to recovery.

Structural manipulations

Six field plots (1 m^2) were established in each of eight blocks parallel to the shoreline at approximately +1.5 ft mean lower low water (MLLW) within the eradicated hybrid *Spartina* zone (hereafter "hybrid zone") adjacent to the Elsie Roemer Bird Sanctuary on 28 June 2013. Plots within each block in the hybrid zone were randomly assigned to one of six structural manipulation treatments to mimic different types of legacy effects (Appendix S1: Fig. S1) including three aboveground manipulations, two belowground manipulations, and an unmanipulated control (UC). The purpose of these manipulations was to determine to what degree the system has remained in the invaded state vs. transitioning toward the pre-invasion state.

The three aboveground manipulations included additions of either dowels (D) or shade screens (S) to mimic the physical effects on water flow and light availability at the substratum surface, respectively. Because *Spartina* stems remain partially intact following eradication, their engineering effects may persist for a year or more post-eradication. The dowel (D) addition plots contained 500 evenly placed wooden stakes emerging 50 cm above the sediment with a 900-cm^2 opening in the center for access for faunal and sediment sampling. The dowels were intended to mimic both the reduction in water flow and the shading effects of hybrid *Spartina* and were based on observed stem densities and light attenuation (Neira et al. 2005, 2006). The shade screens (S) were constructed with a PVC frame covered in Vexar mesh (0.25 cm^2 openings) wrapped in burlap. These were placed approximately 0.3 m above and parallel to the sediment surface and were intended to create similar shading effects as the dowels but with minimal effects on flow. Shade screen controls (Vexar without burlap) were included as the third aboveground treatment, but the results from those plots are not included in this analysis as the screens experienced periodic fouling.

The two belowground manipulations entailed either the addition of dead hybrid *Spartina* litter (L) to mimic the effects of *Spartina* on the detrital pool, or aeration (A) of sediments using a hand trowel to assess whether modest hastening of the breakdown of the belowground *Spartina* root mat accelerated the transition of the benthic communities toward the pre-invasion state. The litter addition (L) plots received six bags of 20 g dried hybrid *Spartina* roots and stems buried 5 cm in a standardized array within the center of the plot. This treatment was intended to mimic the significant amounts of hybrid *Spartina* litter typical of invaded sites, which provides additional trophic support for benthic detritivores. The quantity of experimentally added litter is within the normal range of belowground biomass typical for this site (Tyler et al. 2007). The aeration (A) treatment, despite efforts to regularly maintain this manipulation, showed no changes from the UCs, indicating that modest aeration is insufficient to influence sediment nor food web characteristics, and is thus not presented here.

The above- and belowground manipulations were intended to provide the physical structure needed to mimic the conditions present during the *Spartina* invasion. If species that had been originally facilitated by the *Spartina* invasion were still present in the system, we predicted that they would potentially increase in abundance in response to these re-created conditions. We hypothesized that *Spartina*-facilitated infaunal species would still be present if there were legacy effects of the invasion, such as decomposing roots and rhizomes that maintained belowground conditions similar to the invaded state. We also predicted that adding structure and recreating the conditions typical of the invasion would reduce the abundance of surface-feeding species that were more common prior to the invasion on uninvaded mudflats.

Two additional plots were set up in each of eight neighboring blocks at no lower than +1.0 MLLW elevation within the mudflat on 22 July 2013 (hereafter "mudflat"). Although these mudflat plots are approximately 5–10 m from the hybrid zone plots, they had no prior history of hybrid *Spartina* invasion and thus provide a pre-invasion community control. The slight elevational difference between the mudflat and hybrid zones was another legacy effect caused by modest sediment accretion by the hybrid *Spartina* prior to its eradication. These two zones were of equivalent tidal height prior to the *Spartina* invasion (Rosso et al. 2006). Furthermore, intact mudflat can be found elsewhere at this site at both of our experimental elevations. Plots within each block in the mudflat zone were randomly assigned to one of two treatments, either UCs or dowel additions (D). Because this zone was never invaded, it provided an area to test whether any observed aboveground structural effects could arise without the persistence of any belowground structure. We did not construct belowground manipulations in the mudflat due to technical difficulties observed in prior transplant experiments and because it was never invaded and consequently never had any belowground plant biomass.

Blocks were sampled prior to experimental manipulation. All plots were sampled during daytime low tides at 90 d (17 September 2013) and 270 d (23 March 2014) after treatment establishment. All structural manipulations were then removed and the plots re-sampled after 30 d to assess recovery. Experimental structures were maintained as necessary throughout the experiment and drift algae removed where it accumulated around plot marking poles. We assessed the effects of these experimental manipulations on the following features of the benthic habitat.

Responses

Infauna.—To assess the effects of experimental manipulations on infaunal abundance and community structure, one core (5 cm diameter × 5 cm deep) was collected in the center of each plot on each sampling date. Cores were fixed in 8% formalin for at least two days, then rinsed for 24 h in deionized water before transferring for storage in 70% ethanol. Rose bengal was added to increase invertebrate detectability. Samples were sieved to 300 μm and all retained invertebrate infauna counted, identified to species, and classified to surface or subsurface deposit feeders or predator/omnivore feeding mode (sensu Levin et al. 2006). Infauna were quantified from within half of the plots on day 90 ($n = 4$ for 24 total plots), whereas all plots were surveyed on day 270 and again after 30 d of recovery ($n = 8$ for 48 total plots).

Epifauna.—We assessed epifaunal communities in the UC plots and the dowel aboveground

structure plots using pit fall traps and visual censuses during each sampling event. Pit fall traps (10 cm dia. × 15 cm depth) were opened at low tide and all captured invertebrates were censused after 24 h. Visual counts of all mobile epifauna were made in three quadrats (0.0625 m^2) within fixed locations in the plot. Due to large *Ilyanassa obsoleta* accumulations, total epifaunal abundance (summed across the three quadrats per plot) was quantified on day 270 and 30 d post-manipulation removal.

As a follow-up experiment, to assess the potential refuge of the aboveground structure for the invasive Eastern mudsnail *I. obsoleta*, we conducted a tethering experiment in summer 2014. Five adult *Ilyanassa* were marked and tethered within each of newly constructed dowel and UC plots within the first five original blocks. An additional five marked untethered (free) snails were added to each plot to test the snails' dispersal. Plots were checked after 48 h and scored for the number of recovered live and dead snails. This assay was conducted twice (June and July) and, as responses were consistent, results were pooled for ease of presentation. Individual snails were excluded if there was evidence that the tether broke or there was a failure of glue adhesion (22 out of 800 snails).

Belowground biomass.—To assess changes in belowground biomass of the decaying hybrid *Spartina* root mat during the experiment, one core (25 cm deep, 5 cm diameter) was collected from the center of each plot during the structure removal. Cores were sieved to 500 μm and all root materials dried and weighed. Cores were not collected from the mudflat as personal observations and historical data indicated that there was no belowground biomass and *Spartina* has never been present in this zone.

Sediment organic content.—Organic content was quantified by assessing the total organic matter and the ratio of silt to sand in the sediment. Two sediment cores (10 cm deep) were collected from the center of each plot, frozen, and then dried at 60°C for 24 h prior to sieving through 500-μm mesh to remove debris. To assess the organic matter in the sediment, cores were combusted at 500°C for 6 h to quantify loss on ignition. To assess silt content within the sediment, sediment from the combusted cores was shaken through a 63-μm sieve on an oscillator (KJ-201BD) at

210 rpm for 5 min. We then weighed the resulting two size fractions (silt vs. sand).

Chlorophyll-a.—Responses of benthic microalgae were assessed by collecting small (0.5 cm deep) surface sediment cores in the center of each plot, which were frozen and analyzed within 30 d on a 1700 Shimadzu spectrophotometer for chlorophyll-*a* concentration as proxy for microalgae accumulation following Neira et al. (2006). We extracted each core with 6 mL of 90% acetone and then sonicated in a cold water bath for three one-minute intervals with a one-minute break between each interval. Samples were then refrozen, shaken to ensure complete extraction, and 24 h later centrifuged for 5 min at 4 rpm before placement in the spectrophotometer, where they were read at 665 and 750 nm. Samples were acidified with HCL to assess phaeophyton. Samples were calibrated according to overall sediment dry mass.

Porewater sulfide.—We measured sulfides from porewater samplers installed at 10–12 cm depth. Porewater was sampled 48 h after sampler installation and stored in an antioxidant buffer (NaOH + disodium ethylenediaminetetraacetic acid) on ice. Back in the laboratory, the mV for each standard and sample were recorded using a silver sulfide ion-selective electrode and compared to standards prepared with the buffer, deoxygenated water, and disodium sulfide (see Zhang et al. 1997).

Statistical analyses

Data were analyzed in R (v3.1.1) (R Core Team 2015) using a generalized linear model with habitat by structural manipulation as fixed factors along with spatial block. Because this was not a fully crossed model, we conducted a priori planned contrasts to test among habitats (e.g., eradicated hybrid vs. mudflat) and structural manipulations (e.g., UC vs. dowel across habitats, control vs. dowel and shade or all manipulations in eradicated hybrid, and control vs. dowel in mudflat only). We used a quasi-poisson distribution as needed for count data. Plots from which infauna were not preserved adequately for identification and/or in which significant maintenance was necessary within one month of the sampling were excluded from the analyses (day 90: one mudflat dowel and one hybrid shade out of 24 total sampled plots; day 270 and recovery day 30: two hybrid dowels, one mudflat dowel, and one

Table 1. A priori planned contrasts of structural manipulations across habitats on the infauna for 90 and 270 d after experimental initiation, and 30 d after experimental removal.

Response	Estimate	SE	t-Value	Pr(>|t|)
Total infauna abundance				
Habitat (mudflat vs. hybrid)	1.790; −1.277; −0.373	2.546; 0.317; 0.222	0.707; −4.030; −1.683	0.490; **<0.001**; 0.101
Habitat ctrl vs. dowel	5.100; 1.557; 0.324	3.764; 0.384; 0.316	1.355; 4.075; 1.023	0.194; **<0.001**; 0.313
Hybrid ctrl vs. aboveground	1.294; 2.476; 0.897	4.411; 0.609; 0.404	0.293; 4.062; 2.222	0.773; **<0.001**; **0.033**
Mudflat ctrl vs. aboveground	6.045; 0.408; −0.150	2.772; 0.193; 0.217	2.180; 2.111; −0.691	**0.044**; **0.042**; 0.494
Hybrid ctrl vs. belowground	0.244; 1.059; 0.319	4.103; 0.612; 0.385	0.060; 1.731; 0.827	0.953; 0.092; 0.414
Annelids				
Habitat (mudflat vs. hybrid)	19.250; −1.062; −0.246	28.468; 0.312; 0.236	0.676; −3.401; −1.043	0.509; **0.002**; 0.304
Habitat ctrl vs. dowel	−92.574; 0.531; 0.213	42.083; 0.420; 0.341	−2.200; 1.263; 0.623	**0.043**; 0.215; 0.537
Hybrid ctrl vs. aboveground	−90.750; 1.753; 0.703	49.308; 0.604; 0.425	−1.840; 2.900; 1.656	0.084; **0.006**; 0.106
Hybrid ctrl vs. belowground	−67.153; −0.198; −0.073	45.865; 0.244; 0.402	−1.464; −0.811; −0.311	0.163; 0.423; 0.758
Mudflat ctrl vs. aboveground	−46.074; 0.779; 0.230	30.992; 0.591; 0.234	−1.487; 1.317; 0.572	0.157; 0.423; 0.571
Polychaetes				
Habitat (mudflat vs. hybrid)	−0.100; −1.361; −0.613	1.490; 0.273; 0.304	−0.067; −4.980; −2.016	0.947; **<0.001**; 0.051
Habitat ctrl vs. dowel	−5.904; 0.699; 0.277	2.203; 0.355; 0.431	−2.680; 1.968; 0.643	**0.016**; 0.057; 0.525
Hybrid ctrl vs. aboveground	−6.328; 1.895; 0.815	2.581; 0.541; 0.580	−2.451; 3.503; 1.405	**0.026**; **0.001**; 0.169
Hybrid ctrl vs. belowground	−4.507; −0.264; −0.071	2.401; 0.194 0.269	−1.877; −1.359; −0.265	0.079; 0.182; 0.792
Mudflat ctrl vs. aboveground	−3.457; 0.919; 0.234	1.623; 0.532 0.560	−2.131; 1.729; 0.418	**0.049**; 0.093; 0.678
Oligochaetes				
Habitat (mudflat vs. hybrid)	1.981; −0.545; 1.386	1.359; 0.678; 0.747	1.458; −0.804; 1.855	0.164; 0.426; 0.071
Habitat ctrl vs. dowel	0.233; 0.313; 0.098	1.809; 0.959; 1.138	0.129; 0.326; 0.086	0.899; 0.746; 0.932
Hybrid ctrl vs. aboveground	−0.109; 1.480; 0.488	1.182; 1.249; 0.836	−0.092; 1.186; 0.584	0.928; 0.243; 0.563
Hybrid ctrl vs. belowground	−0.286; −0.052; −0.066	1.074; 0.610; 1.025	−0.266; −0.086; −0.064	0.794; 0.932; 0.949
Mudflat ctrl vs. aboveground	0.639; 0.553; −0.074	1.647; 1.204; 0.774	0.388; 0.460; −0.056	0.703; 0.648; 0.924
Crustaceans				
Habitat (mudflat vs. hybrid)	1.800; −0.890; −0.050	2.546; 1.014; 0.502	0.707; −0.878; −0.099	0.490; 0.386; 0.922
Habitat ctrl vs. dowel	5.100; 5.162; 1.233	3.764; 1.060; 0.719	1.355; 4.870; 1.716	0.194; **<0.001**; 0.095
Hybrid ctrl vs. aboveground	1.294; 5.133; 2.400	4.411; 1.769; 0.797	0.293; 2.902; 3.040	0.773; **0.006**; **0.005**
Hybrid ctrl vs. belowground	0.245; 2.554; −0.437	4.103; 0.552; 0.592	0.060; 4.624; −0.738	0.953; **<0.001**; 0.465
Mudflat ctrl vs. aboveground	6.045; 2.149; 0.026	2.772; 1.789; 0.853	2.180; 1.201; 0.031	**0.045**; 0.237; 0.976
Species richness				
Habitat (mudflat vs. hybrid)	0.026; −4.762; −1.373	0.144; 0.813; 1.381	0.180; −5.861; −0.994	0.859; **<0.001**; 0.327
Habitat ctrl vs. dowel	0.173; 4.998; 1.008	0.209; 1.216; 2.068	0.826; 4.110; 0.487	0.421; **<0.001**; 0.629
Hybrid ctrl vs. aboveground	0.263; 11.746; 2.947	0.243; 1.460; 2.482	1.080; 8.046; 1.187	0.296; **<0.001**; 0.243
Hybrid ctrl vs. belowground	0.095; 0.264; 0.310	0.229; 0.848; 1.441	0.417; 0.311; 0.215	0.682; 0.757; 0.831
Mudflat ctrl vs. aboveground	0.008; 5.020; 0.856	0.157; 1.324; 2.252	0.048; 3.791; 0.380	0.962; **<0.001**; 0.706

Note: Bold numbers are significant ($P < 0.05$).

hybrid UC out of 48 total sampled plots). The infaunal community was further explored using non-metric multidimensional scaling (NMDS) with the vegan package in R.

RESULTS

Infauna

We detected significant effects of experimental manipulations on infauna after 90 and 270 d (Tables 1 and 2; Appendix S2: Tables S1, S2). After 90 d, total abundance of infauna increased in the aboveground (dowel) plots in the mudflat (Fig. 1A). This pattern occurred across mudflat and hybrid habitats for total annelid abundance (Fig. 1B) and within the mudflat for small non-decapod crustaceans (i.e., amphipods and tanaids, Fig. 1C, Table 1). After 270 d, total infaunal abundance was greater in the mudflat where no invasive *Spartina* was ever present (i.e., our pre-hybrid *Spartina* invasion reference habitat), compared to the hybrid zone where eradication had been conducted (Fig. 1E). The presence of aboveground (dowels, shade screen), but not belowground (litter) manipulations promoted total infaunal abundance in the hybrid zone (Table 1). Aboveground

Fig. 1. Generally, after 90 d of treatment application, neither habitat nor aboveground *Spartina*-mimicking structures influenced infaunal species abundance or species richness per core (A–D). After 270 d, habitat type (mudflat, eradicated hybrid zone) and/or structural manipulations influenced the abundance of some infauna (E–H). These responses generally disappeared within 30 d of manipulation removal (I–L), while habitat effects generally persisted. UC, unmanipulated control plots; and D, dowel; S, shade; L, litter addition.

the dowel addition plots (Fig. 3). Other epifauna including *Urosalpinx cinerea*, *Carcinus maenas*, and *Haminoea japonica* were present but not abundant enough for analysis.

All epifauna began disappearing from the aboveground structure plots within 48 h of dowel removal (direct observation); after 30 d, only two *Ilyanassa* were found across all plots
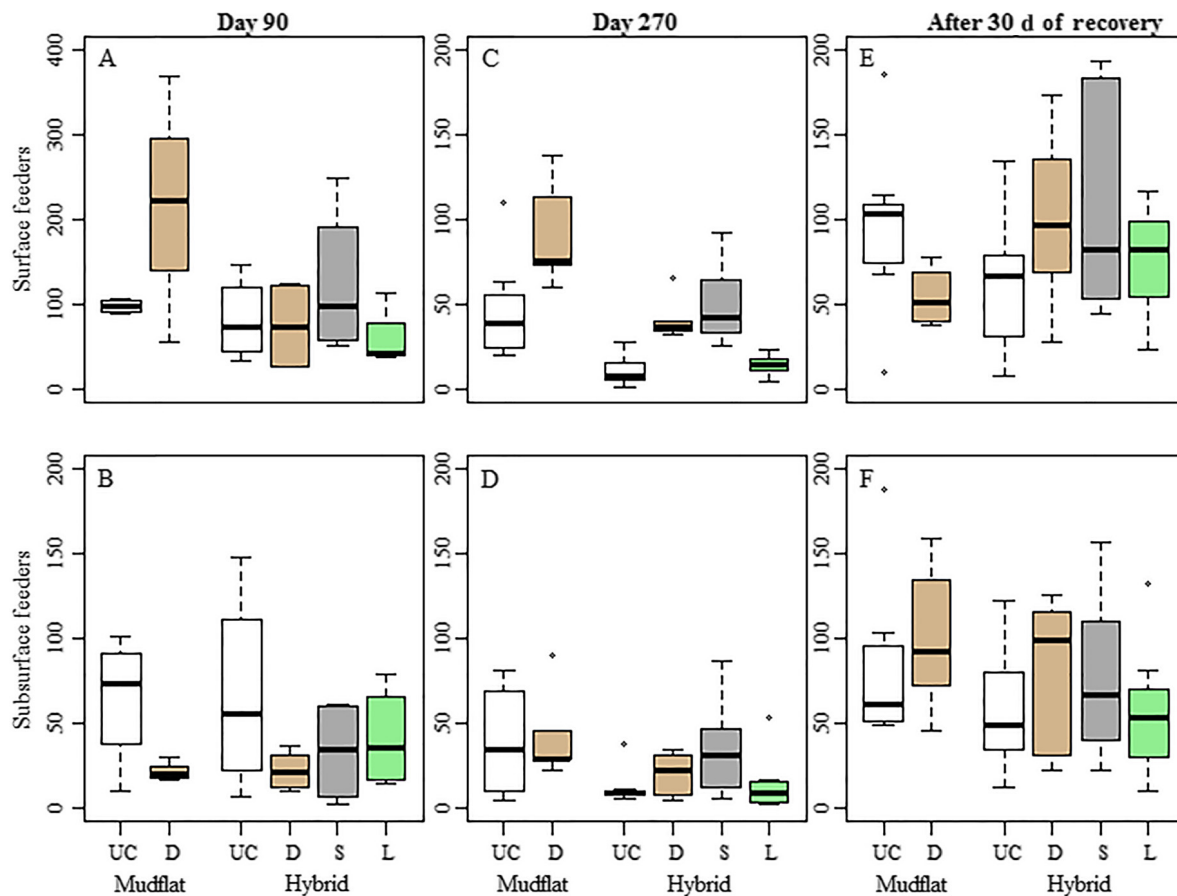
Fig. 2. Response of taxa by trophic mode per core after 90 (A, B) and 270 (C, D) days of treatment application. No treatment or habitat effects persisted 30 d after experimental removal (E, F). UC, unmanipulated control plots; and D, dowel; S, shade; L, litter addition.

and habitats (Fig. 3F). These species readily disperse across mudflats and are present only at low density except within structured habitat (Appendix S4: Table S1). For the predation assays, after 24 h, almost all tethered *Ilyanassa* were recovered alive (372 out of 378 total snails) regardless of whether they were inside dowel or UC plots across the mudflat and hybrid zone. However, very few non-tethered (freely moving) snails were recovered from any plots (four out of 400 individuals), indicating high dispersal potential for these adult snails.

Belowground biomass

Belowground biomass of the hybrid *Spartina* root mat in UC plots in the eradicated hybrid zone declined on average 51% from the start until the end (day 270) of the experiment ($P < 0.001$,

loss of 70.4 ± 30 g per plot). Structural manipulation, however, had no effect on the final abundance of decaying root mat material ($F_4 = 0.270$, $P = 0.896$), which differed across blocks ($F_1 = 9.000$, $P = 0.005$). We find that this rate of decline in belowground biomass is similar to the rate of breakdown measured in long-term plots at three other sites, which shows that belowground biomass may take 6 yr or more to completely break down (Appendix S5: Fig. S1).

Benthic microalgae

Benthic chlorophyll-*a* was not affected by treatment, but did vary across blocks and was greater in the hybrid compared to the mudflat zone at 90 d (Table 2, Fig. 4A). Thirty days following structure removal, benthic microalgae was again influenced by spatial block and was greater in the

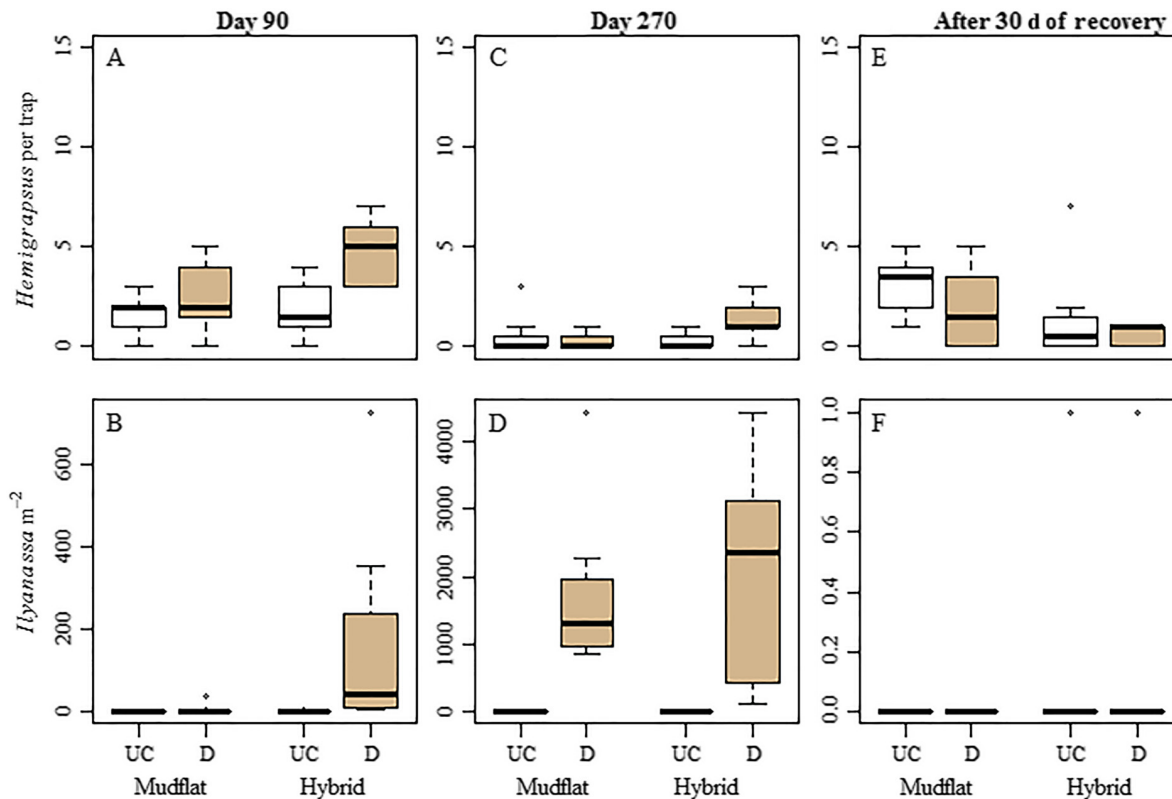Fig. 3. The two most abundant epifauna species, the crab *Hemigrapsus oregonensis* per pit fall trap (A, C, E) and the snail *Ilyanassa obsoleta* per m^2 in surveys (B, D, F) within experimental plots at the middle (day 90) and end (day 270) of the experiment, and 30 d after the aboveground structure (dowels), were removed. *Ilyanassa* were rare to absent at day 0 and after 30 d of recovery. The day 90 and the recovery samplings occurred in early fall and spring, respectively, when the crabs are active. The day 270 sampling occurred in the winter when crabs are burrowed and less active. UC, unmanipulated control plots; and D, dowel plots.

hybrid compared to the mudflat and was lower in plots previously exposed to belowground manipulation (Table 2, Fig. 4C).

Sediment organic content

After 90 d, sediment organic matter was greater in the hybrid zone compared to the mudflat (Table 2, Fig. 4B). This pattern persisted after 270 d, but did not vary among structural manipulations (Table 2, Fig. 4D). This result was also observed at 90 and 270 d for sediment grain size fractionation (greater silt accumulation in the hybrid). Thirty days after the structure removals, sediment organic content remained higher in the hybrid compared to the mudflat habitat (Table 2, Fig. 4F); this result was consistent with the greater fraction of silt found in the sediment in the hybrid.

Porewater sulfide

Porewater sulfide levels were significantly affected by habitat type. Sulfides were higher in the hybrid zone (6.561 ppm ± 5.344 SD) relative to the mudflat (1.645 ppm ± 1.359 SD; t test: $t = -2.424$, df = 12.933, $P < 0.031$).

Discussion

Our results show that the ghost of invasion past is present in this system through persistent legacy effects that can strongly influence habitat recovery and the potential for future restoration. By comparing eradicated hybrid *Spartina* habitats to nearby uninvaded (i.e., pre-invasion condition) mudflat, we found that the legacy effects of invasive ecosystem engineers can persist for
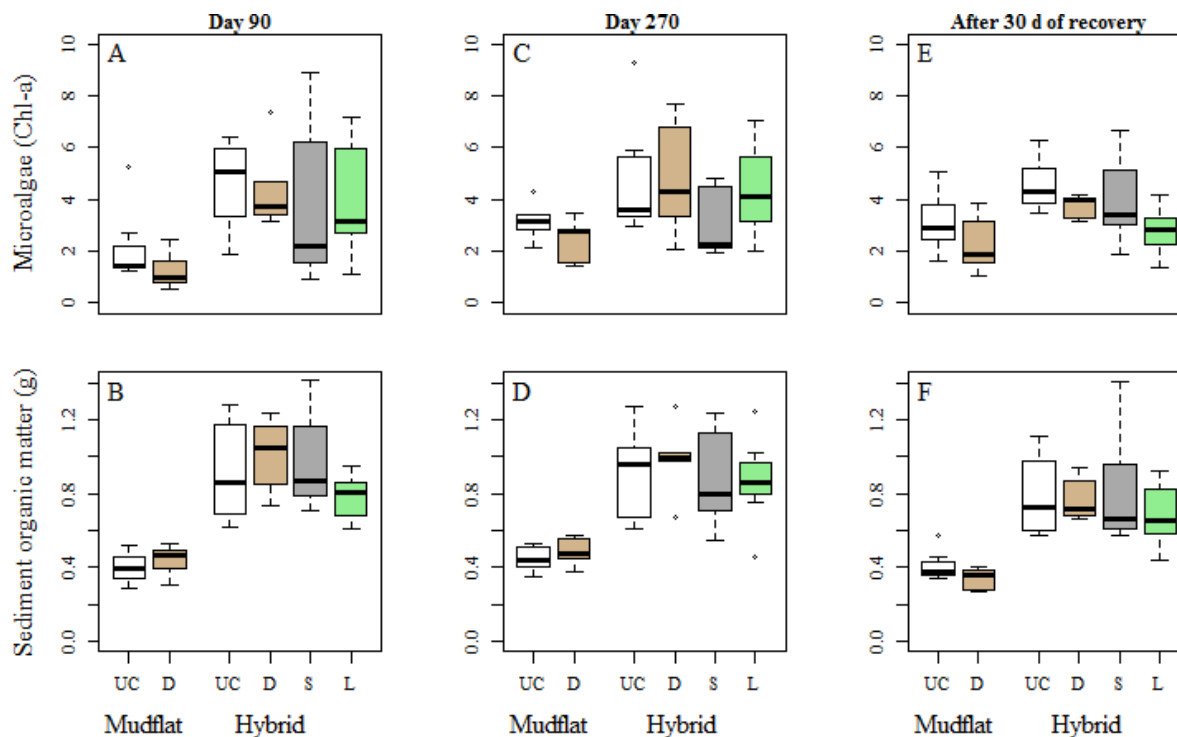
Fig. 4. Local heterogeneity (i.e., block effects) had a larger effect on benthic microalgae (A, C, E) across time points (see Appendix S2: Tables S1–S3). Habitat type and/or structural manipulations influenced sediment organic matter (ash-free dry mass per core; B, D, F) after 270 d and 30 d after manipulation removal. The pattern for the ratio of sediment silt to sand (not pictured) followed the same patterns as sediment organic matter. UC, unmanipulated control plots; and D, dowel; S, shade; L, litter addition.

several years post-eradication as a function of both belowground impacts that are slowly disappearing, but still present, and aboveground effects that disappeared quickly but whose impact continues in the form of surviving long-lived epifaunal invader populations. We suggest that both of these mechanisms are likely to be general in systems involving invasive plants as ecosystem engineers. Our work is among the first to quantify the change, or lack of change, in food web and community processes in an estuarine/marine system following the removal of an ecosystem engineer, as well as to quantify several of the mechanisms that contribute to persistent engineering effects after invader eradication.

Our manipulative field experiments showed distinct differences between habitats as well as differences among taxa in response to experimental additions of aboveground structural mimics. In the hybrid zone (where *Spartina* had

been eradicated), we found that a much broader range of species, including annelids (mostly polychaetes) as well as crustaceans (mostly amphipods), increased in abundance in response to experimental aboveground structure additions. By contrast, only crustaceans (mostly amphipods) showed a significant increase in abundance in response to the dowel manipulation in the mudflat zone. These results agree with our predictions that subsurface feeders, like many annelids, would recruit to dowel treatments if the belowground conditions were still similar to the invaded conditions as the result of legacy effects. By contrast, we saw no increase in the subsurface feeders in the mudflat despite adding dowels, likely because the belowground conditions were not conducive for these species. The recruitment of crustaceans to both habitats supports the idea that highly mobile epibenthic species like amphipods, which used refugia

provided by *Spartina* stems during the invasion (Neira et al. 2006), would now rapidly recruit to experimentally re-created aboveground structure if still in the system. We found that many of these species are still present in large numbers, although now, in the absence of the aboveground refugia, are widely dispersed at low density. Overall, these results support the idea that the effects of the roots and rhizomes are undergoing slow decay, and that their persistent effects on sediment characteristics and porewater chemistry are maintaining a legacy effect of the invasion in the hybrid zone strongly affecting the benthic community and food web. This raises the possibility of rapid re-assembly of the invaded community if this habitat is reinvaded by hybrid *Spartina* or another comparable plant in the near future, which may have consequences for native *Spartina foliosa* restoration activities.

Our experimental results point to two mechanisms as most important in contributing to the observed delays in recovery of the invaded system to pre-invaded conditions following eradication of hybrid *Spartina*. The first is the effect of the belowground structure consisting of an extensive network of roots and rhizomes that can remain for several years as they undergo slow breakdown in the highly reduced sediments typical of these habitats. This can produce persistent effects where the decaying roots and rhizomes provide trophic support and belowground habitat for small detritivores, but also persistent elevated levels of porewater sulfide, which can also negatively affect infaunal communities (Neira et al. 2006). We found that some sediment characteristics were slow to change, such as sediment organic matter and the silt-to-sand ratio. Additionally, despite several years post-hybrid *Spartina* eradication significant differences persisted across control plots in the two habitats. Thus, the slow breakdown of this root/rhizome mat, as also observed at other locations throughout San Francisco Bay (Appendix S5: Fig. S1), may dictate the equally slow transition of the benthic food web from dominance of subsurface detritivores to the pre-invasion community dominated by surface-feeding consumers. This mechanism may be most likely in hypoxic or anoxic soils or sediments where anaerobic processes dominate and breakdown of roots and rhizomes is slow.

The second mechanism concerns the presence of long-lived members of the invaded community that were facilitated by the effects of the aboveground structure (Neira et al. 2006, Grosholz et al. 2009). Species facilitated by the hybrid *Spartina* invasion included long-lived non-native species, such as the eastern ribbed mussel (*Geukensia demissa*), the eastern mudsnail (*Ilyanassa obsoleta*), the eastern whelk *Urosalpinx cinerea*, and the European green crab (*Carcinus maenus*). In their native range, the mussel can live for more than a decade (Bertness and Grosholz 1985), the whelk can live 6–10 yr (Franz 1971), the green crab can live up to 6 yr, and the mudsnail can live for as long as 70 yr (Curtis et al. 2000). Given that there is relatively little predation pressure on invasive mussels and snails in this system (Fig. 3; Weiskel 2012), adult survival may be high. While the persistent belowground structure still maintains populations of the mussel, the absence of aboveground structure may over time have negative effects on epifaunal reproduction and survivorship by removing important egg-laying habitat for snails and sediment stabilization for the mussel. Despite the now complete absence of the aboveground effects of hybrid *Spartina* at this site, even if reproduction was substantially reduced (or even failed completely), long-lived adult populations of invasive epifauna could persist for many years or, in the case of the invasive mudsnail *I. obsoleta*, for many decades beyond the aboveground engineering effects of the hybrid *Spartina*. We found support for this contention due to the rapid recruitment of adult mudsnails into our experimental plots with the addition of the structural manipulations, despite the time since the eradication of their hybrid *Spartina* habitat. Therefore, measuring eradication success may require intensive monitoring combined with targeted experimental approaches to capture changes occurring at slower-than-expected rates.

Previous studies of the consequences of removing invasive ecosystem engineers typically involve terrestrial plant species and their impact on native plants (reviewed in Corbin and D'Antonio 2012). For example, hysteresis in the recovery of a variety of different ecological functions, such as the reestablishment of ecological interaction networks of native birds, was found following removal of invasive honeysuckle (Rodewald et al. 2010). However, in coastal marine and estuarine systems,

there are few examples of the complete eradication of invasive ecosystem engineers and even fewer examples of systems that have experimentally tested the consequences of removal on entire communities (McGrorty and Goss-Custard 1987, Hacker and Dethier 2009). Most research examining restoration and recovery of marine or estuarine systems has focused on removal of other factors, such as fishing (Blackwood et al. 2012, Collie et al. 2013) or contaminants (Valega et al. 2008), likely due to the logistical challenges of complete invader removal and the difficulty in evaluating invader impacts. In general, research conducted on invasive species removal in these habitats, whether or not they were engineers, supports the idea that these systems may be unable to return to the pre-invaded condition. For instance, the removal of *Caulerpa racemosa* in the Mediterranean Sea resulted in the failure of the original macroalgal community to reestablish (Piazzi and Ceccherelli 2006). As in most other cases, the mechanisms underlying this failure to regain the pre-invasion community remain untested. Other studies have examined recovery of native plants after removal of another invasive *Spartina* species (*Spartina anglica*), and, while the specific mechanisms remain undocumented (Hacker and Dethier 2009), we assume that they are similar to our findings.

The distinct roles of both above- and belowground plant structure that we have demonstrated are likely to generalize to other similar systems involving invasive plants. In other systems such as bogs, swamps, or boreal habitats where breakdown of belowground plant biomass (roots, rhizomes, etc.) is delayed, this could also lead to persistent effects of ecosystem engineers well beyond the date of eradication. Additional impacts on nutrient cycling and enhancement of porewater sulfide could further add to delays in recovery. As we documented in our experimental manipulations, these delays could influence soil fauna and characteristics along with the recovery of native vegetation in systems with prolonged belowground breakdown. The effects of aboveground structure are likely to be more shortlived with respect to the physical characteristics, although it may have the potential for long-term effects dependent on the rate of breakdown of leaves, shoots, branches, etc., in the surface litter. We suggest that one of the most important long-term impacts

of aboveground structure may be the persistence of secondary invaders and other species for which that structure played a facultative role. Despite the relatively immediate loss of that habitat, long-lived species (such as the invasive mudsnails) may continue to persist, often in more resistant adult stages, even if conditions are not conducive to reproduction in the absence of the habitat created by the engineer. While surveys may reveal low levels of the secondary invaders and the restoration thereby determined a success, this designation may be premature as the secondary invaders may be retained in the system and their populations grow rapidly with the reestablishment of the invasive ecosystem engineer or a functionally similar native or exotic vegetation.

Finally, we argue that the delayed transition to the pre-invasion state we have documented may complicate evaluations of restoration success. Most of the current theory regarding the failure to reestablish the pre-invasion community, whether native or a mix of native and non-native, has focused on the presence of alternate states (or even alternate stable states) and the problems this may pose for evaluating restoration success (e.g., Suding et al. 2004). The slow transition to the pre-invasion state may suggest the presence of alternate states, especially when the eradicated invader was an ecosystem engineer with strong legacy effects. If a system, such as that examined here, required many years to recover the pre-invasion condition and was monitored with inadequate frequency or duration, it could be mistaken for one that is in a persistent alternate state rather than one moving slowly toward recovery of the pre-invasion state.

In summary, we conclude that the ghost of invasion past is operating in this system through persistent legacy effects of both above- and belowground effects that not only influence the state of recovery but also the potential for future restoration. These legacy effects arise from belowground processes that include the slow breakdown of roots and rhizomes creating belowground detritus and high levels of porewater sulfide that support the persistence of the invaded belowground community. Legacy effects also arise from long-lived epifaunal species that were facilitated by the refugia created by the aboveground structure and that now can persist

for many years, if not decades, despite the disappearance of this refugia. We suggest that both of these mechanisms are likely to be general in many similar systems involving invasive plants that are ecosystem engineers. This includes many terrestrial systems and aquatic habitats with soils that are poorly aerated and have limited capacities for breakdown of belowground plant material. Also, invasive plants in many other systems may also attract longer-lived non-native species, including beetles, fishes, reptiles, and rodents. Our work also points to the likelihood that many systems may respond much more slowly to the removal of invasive ecosystem engineers than expected, and may follow a slower-than-expected trajectory toward recovery of the pre-invasion food web. This slow transition would be missed if the monitoring interval or duration is insufficient to capture the rate of change. We suggest that short-term manipulation of either above- or belowground engineering structures are an efficient means of determining how far a system is from both the invaded and pre-invasion community, and may provide insights into the time required for recovery and restoration success.

Acknowledgments

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