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Effect of propagule pressure on recovery of a California grassland after an extreme disturbance

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Disturbance; Drought; Fire; *Nassella pulchra*; Patch dynamics; *Stipa pulchra*; Seed rain

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Abstract

Questions: How is natural regeneration of a patchy landscape affected by within-patch species interactions and among-patch dispersal after an extreme disturbance? Do landscape dispersal processes facilitate the invasion of native-dominated patches by exotic species in adjacent patches?

Location: Irvine Ranch Natural Landmark, Irvine, California, USA.

Methods: We monitored plant community composition in paired grassland patches that were initially dominated by native or exotic grasses at eight sites. We followed recovery of native and exotic grassland species over time, starting in a record drought year prior to an intense fire, and then for 3 yr with more typical rainfall patterns after the fire. Additionally, we compared seed rain of native and exotic species across native and exotic patches, quantifying how seed rain influenced species abundance in the following year. Multivariate and regression analyses were used to assess the potential homogenization of the landscape.

Results: Following the extreme drought/fire disturbance, the exotic annual grasses quickly recovered in abundance in patches that they dominated prior to the disturbance. However, the native grass, *Stipa pulchra*, was not able to recover in the patches it once dominated. As the exotic grasses gradually increased in the native patches, the paired patch types became more similar in composition over time. Exotic grasses produced up to 28 times more seed than the native dominant grass, *Stipa*; even in the patches initially dominated by *Stipa*, exotic seed rain was equivalent or greater than the native. Seed rain was positively correlated with the following year's abundance for both exotic and native species.

Conclusions: After an extreme disturbance, recovery of native patches can be stalled by an influx of propagules from neighbouring exotic patches. This exotic seed rain can allow the invasion of areas once dominated by natives, thus inhibiting regeneration. The matrix surrounding remnant native stands can be a critical factor in determining whether an extreme disturbance enhances native diversity vs. increasing its susceptibility to invasion.

Introduction

Disturbances play an important role in shaping communities and ecosystems (Jentsch 2007; Fukami & Nakajima 2011). Large-scale disturbances can initiate successional dynamics, ensuring the persistence of many species via the subsequent stages of recolonization (Clements 1916; Connell 1978) and enhancing diversity at the landscape scale (Collins 1990; Cook et al. 2005). These dynamics are particularly critical in invaded landscapes of conservation concern (Buckley et al. 2007), as these same disturbances can provide windows of opportunities for invasion of exotic species, whose subsequent effects may shift the successional trajectory (Hobbs & Huenneke 1992; Huston 2004; MacDougall & Turkington 2005). These interactions will likely become even more critical as the frequency of extreme climate events (e.g. flood, drought) increases (Turner 2010). To effectively manage resilience to these future disturbances, it is important to understand the complexity of disturbance regimes and their ecological impact (Mori 2011). An integral part of this is understanding the relative responses of species within a landscape to disturbance (D'Antonio et al. 2001).

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Initial recovery after a disturbance commonly depends on the species present prior to a disturbance leaving residual individuals, either vegetatively or in the seed bank (Noble & Slatyer 1980; Turner et al. 1998; Meiners et al. 2002). Residuals from the seed bank are often dominated by annual species that grow faster than perennial species growing from seed (Cook et al. 2005); however, residual perennial plants can reestablish vegetatively after a disturbance and achieve large sizes more quickly than those that start from seed (Gleeson & Tilman 1994). In cases where natives and exotics differ in life history, this balance of residual components (vegetative, seed bank) is thought to influence interactions between native and exotic species during the 'invasion window' following a disturbance (Meiners 2007; Tognetti et al. 2010) and to result in a classic competition–colonization trade-off (Levins & Culver 1971). While these trade-offs could strongly influence invasion dynamics, there have been few explicit tests (but see Keeley et al. 2005).

Our understanding of how interactions between species characteristics and propagule pressure impact invasion success following a disturbance is limited (Zouhar et al. 2008). Propagule pressure, either from residual plants or new colonists from surrounding patches, can strongly influence post-disturbance regeneration and invasion success (Lockwood et al. 2005; Colautti et al. 2006). While dispersal from surrounding intact communities can influence recovery of an area after disturbance (Connell & Slatyer 1977), large disturbances can isolate areas and initiate within these isolated areas nucleation processes as residuals, either vegetative or from the seed bank, become the foci for colonization and expansion of populations (Zobel et al. 1993; Turner et al. 1998). Recovery of the native species in a patch can stall if recovering neighbouring patches are dominated by exotics with high dispersal capabilities that colonize the native patch before the native patch is able to recover (Moody & Mack 1988; D'Antonio et al. 2001; Platt & Connell 2003).

Here, we investigate how propagule pressure influences invasion following an extreme disturbance (an intense fire following a record drought). We focus on a situation common in invasion, where exotics and natives differ in both their regeneration strategies and dispersal abilities, and investigate how these differences may alter early successional dynamics in a patchy, invaded landscape (Cook et al. 2005; Meiners 2007). We predict that if the exotic annual is able to disperse into and establish within the native patches, the colonization window following a disturbance should result in a homogenization of the landscape over time towards exotic annual dominance. In contrast, if dispersal among patches is limited, both native and exotic patches should be maintained in the landscape, as local competition dynamics determined by residual individuals (both vegetative and seed bank) would determine recovery (Fig. 1).

Fig. 1. The relative influence of propagule pressure from neighbouring invaded patches and survival of native residual individuals on the competition–colonization trade-off following a disturbance. Scenario depicts invasion of a good colonizer (e.g., exotic annuals, in black) into patches dominated prior to the disturbance by a good competitor (e.g., native perennials, in grey). The expected competition–colonization trade-off is shown in solid lines. With high propagule pressure and/or low survival of perennial individuals following a disturbance (dashed lines), the expected trade-off may not occur due to the strong propagule pressure of the colonizer and the strong dispersal limitation of the competitor.

Throughout California, large portions of native grasslands have been invaded by exotic annual grasses from the Mediterranean area (Heady 1977). Traditionally this invasion is thought to be a result of the exotic grasses competitive advantage over the native grasses (Dyer & Rice 1997, 1999); however, recent research within California suggests that these invaders may be the 'passengers' not the 'drivers' of change (HilleRisLambers et al. 2010). If disturbance does favour these invaders then understanding the mechanisms by which the invader is able to capitalize during recovery is important for management (Firn et al. 2008). Furthermore, weather perturbations, such as drought, can alter the intensity of a disturbance and the community's response to the compounded events (Paine et al. 1998).

We focus on the effects of an extreme disturbance – a record drought followed by a large-scale fire – on a patchy, invaded grassland landscape in California. The goal of this study was to evaluate (1) the temporal pattern of native perennial and exotic annual grassland recovery after the disturbance and (2) how landscape (i.e. propagule pressure) dynamics following disturbance contribute to the recovery of native grasslands or the spread of exotic annuals.

Methods

Study site

We conducted our study at Loma Ridge in Irvine, California, within the Irvine Ranch Land Reserve (33.7501N, 117.71787W). The climate is mediterranean, with a growing season from November to June, as determined by rainfall (e.g. the 2010 growing season was from November 2009 to June 2010). Average growing season rainfall from 1991 to 2010 was 330 mm and average growing season temperature over the same period was 20.9 °C. Annual precipitation over the course of the study (2007–2010) was 68, 211, 214 and 175 mm, respectively (California Irrigation Management Information Services, http://www cimis.water.ca.gov/cimis/welcome.jsp). The first growing season (November 2006–June 2007), just prior to the studied burn (October 2007), was one of the driest years on record (Keeley et al. 2009).

Loma Ridge is a topographically complex site with a string of grassland vegetation on the ridge top and on north- and west-facing slopes, a steep erosional cliff on the southern edge, and coastal sage scrub vegetation to the north on south-facing slopes. While variable, most of the grassland area was <0.3 km in width, delimited by the cliff and sage scrub vegetation to either side. During the 2007 growing season (prior to the fire), we identified eight grassland sites each containing paired patches dominated by either native or exotic species. These eight sites were within 2 km of each other along the ridge. Patches were designated by the dominance (>80% abundance) of the native perennial grass, *Stipa pulchra*, or the exotic annual grasses, *Avena fatua* and *Bromus diandrus*, and were at least 20 m^2 in size. We used paired patches to minimize possible differences in environmental characteristics, such as slope and aspect, and paired patches did not differ in soil texture (Larios unpubl. data). A small two-track road provided access along the ridge but was limited to researchers and security patrols. At each of the eight sites, we set up two 1 m^2 plots randomly within each native and exotic patch (a total of 32 plots). Plots in paired patches within a site were 10–15 m apart, while plots within a patch were 2–5 m apart.

All of these sites were burned in the 2007 arson-caused Santiago wildfire, which occurred from 21 October to 4 November 2007, and was the most disastrous fire in Orange County in over 30 yr (OCFA 2008; Fig. 2). The fire was intense; it completely removed all above-ground vegetation and litter from the study site and in total burned 28 517 acres (OCFA 2008), leaving no unburned intact grassland communities within 5 km. Due to the scale of the fire as well as the timing of the extreme drought, we focus on temporal dynamics of recovery following 2007. While we were not able to include comparison with areas that did not burn or experience the intense drought, observational evidence indicates that the patchy mosaic within the eight grassland sites had been present on Loma Ridge for at least a decade prior to the burn (T. Smith, pers. comm.).

Measurements

We measured above-ground biomass and species composition annually from 2007 to 2010 (the drought year prior and 3 yr following the fire). Each year, at peak biomass, we clipped all above-ground biomass at ground level within a 25 × 25-cm subplot and sorted the biomass to species (nomenclature after Baldwin et al. 2012). Native perennial biomass was additionally sorted as either adult or seedling to distinguish between residual vegetation and newly colonizing vegetation. A subplot was never sampled twice. After sorting, samples were dried at 60 °C for 48 h and weighed.

To estimate propagule pressure, we measured seed rain along transects that ran between paired native and exotic

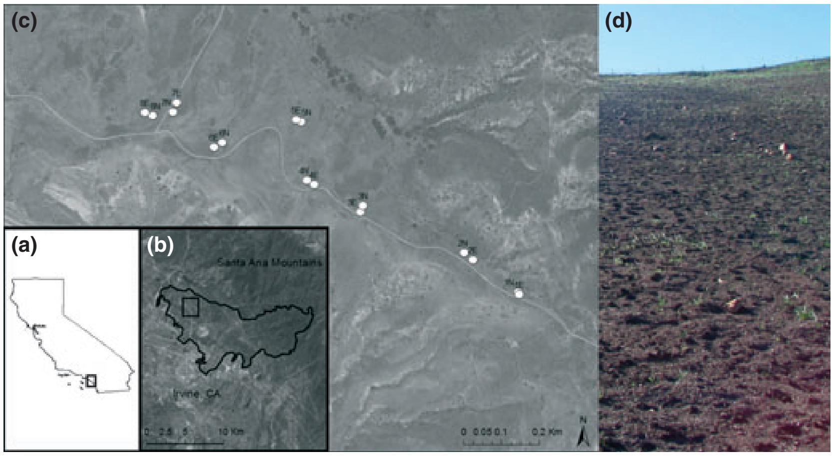

Fig. 2. Map of paired native (N) and exotic (E) patches within eight grassland sites in Irvine, CA (**c**). Inset (**a**) shows the map of California with our study sites in the boxed area and (**b**) shows the perimeter of the 2007 Santiago Wildfire and the rectangle within the perimeter highlights the location of the grassland sites. Across the ridge, the fire removed all above-ground vegetation (Inset '**d**', photo credit: L. Larios).

patches. We took these measurements in five additional sites that had also burned in the Santiago fire and were adjacent to the sites where we measured species composition. At these five sites, we set up three 8-m transects that extended from the centre of a native patch, across the patch edge, and into the centre of an exotic patch. To collect seed rain, we placed Petri dishes (8.5-cm diameter) filled with sticky resin (Tanglefoot^{TM}; Conotech Enterprises, Canada) every 80 cm along the 8-m transect. We collected seed rain over the entire seed dispersal period during the first year after the fire (April–October 2008), checking traps biweekly and replacing them once in July. We identified and counted all seeds within each trap using a reference seed collection. Additionally, we counted seedlings (stem counts) in a 25 × 25-cm subplot at each of the above-mentioned sampling points in the following growing season (2009) to estimate how seed rain related to subsequent recruitment.

Analyses

To compare above-ground biomass and species richness over time between native and exotic patches, we used a linear mixed effects model with Patch Type and Year as fixed effects, and Site as a random factor. We additionally included Precipitation as a continuous variable to account for inter-annual variability related to rainfall; however we did not include the three-way interaction of Year, Type and Precipitation. When Precipitation was not a significant variable, we dropped it from the analyses. For all analyses we averaged the values for the two plots within each patch and used R statistical software (v. 2.15.0; R Core Development Team, Vienna, AT). All linear mixed effect analyses were run using the 'nlme' package.

To evaluate recovery of the native and exotic patch types (designated prior to the fire), we first grouped species into three abundance categories (dominants, sub-dominants and rare) based on species rank abundance curves within each patch type (Grime 1998). Using the 'BiodiversityR' package, we calculated a rank abundance curve within each patch for each year following the fire (2008–2010). We did not use abundance from 2007 to classify species groups, as several of the less abundant species were notably absent due to the drought. We classified a species as 'dominant' if it was present in a patch in all 3 yr with 20% or higher abundance each year. A sub-dominant was defined as present with abundances between 1 and 20% within any year. A rare species was defined as present with a maximum abundance of 1% within any year. Note that these groupings were based on rank abundance curves in exotic and native patches, not on the origin (exotic or native) of the species. To incorporate origin, these groupings were subdivided based on species origin (either native or exotic; Table S1). Using this classification, the perennial bunchgrass, *S. pulchra*, was the only native dominant, while three annual grasses (*A. fatua, B. diandrus* and *Festuca perenne*) comprised the exotic dominant grouping.

To assess recovery of the species groups, we ran a linear mixed effects model for each group with initial Patch Type (native or exotic) as a fixed effect, Year (2007–2010) as a continuous effect and Site as a random effect. We conducted post-hoc contrasts to compare groups when a significant interaction (Patch Type × Year) was present. There were many cases where a species group was frequently absent in a given patch type (e.g. native dominants in exotic patch type); therefore, to assess how the abundance of the native and exotic species groups shifted through time, within each patch type we additionally conducted a similar linear mixed model as described above but with species Origin (native or exotic) instead of Patch Type as a fixed effect. If a group still lacked adequate representation, we dropped the comparison that was lacking adequate representation. To account for the lack of independence between plots over time, we estimated effects based on maximum likelihood estimations (Everitt & Hothorn 2011).

To determine propagule pressure, we averaged seed rain at each distance among the three transects within each sampling site. We compared exotic (*A. fatua, B. diandrus* and *F. perenne*) and native (*S. pulchra*) seed rain within each distance with paired *t*-tests. To assess how this seed rain related to abundance in the following growing season, we conducted a linear mixed effects model for the abundance of each of the native and exotic dominants with Seed Rain as a continuous factor, Block as a fixed factor, and Distance along the transect as a random factor.

Lastly, to determine the dependencies between abundances in paired patches within a site (i.e. an indicator of dispersal among patches), we calculated Bray–Curtis dissimilarity (Bray & Curtis 1957) between the paired native and exotic patches within each site using the species abundance groups. We compared dissimilarity over time using a linear mixed effects model, with Year as a continuous factor and Site as a random effect. We interpreted a decrease in dissimilarity over time as evidence of homogenization across sites. We then examined three factors that could explain dissimilarity patterns across sites: average site above-ground biomass, species richness (i.e. total number of species) and the abundance of exotic dominants establishing in native patches.

Results

Environment

Above-ground biomass was lowest during the drought year (29.34 $g{\cdot}m^{-2}$; 2007) and increased after the fire

(607.67, 738.75 and 586.08 $g{\cdot}m^{-2}$; $F_{1,53} = 18.02$, $P < 0.001$). It also was higher in patches initially dominated by exotics compared to natives ($F_{1,53} = 4.44$, $P = 0.04$; Fig. S1a). Species richness increased over time (2.4 in 2007 to 4.7 in 2010; $F_{1,53} = 13.07$, $P < 0.001$) and was significantly higher in the native patches than in exotic patches in 2009 and 2010 (Year × Type interaction, $F_{1,53} = 6.81$, $P = 0.01$, Fig. S1b). Precipitation did not consistently influence above-ground biomass or species richness ($F_{1,50} = 1.76$, $P = 0.19$ and $F_{1,50} = 0.65$, $P = 0.43$); however, the low precipitation in 2007 was likely responsible for the very low biomass and low richness (particularly in the native patches) during this year.

Response of native and exotic dominant species

Following the drought and fire, abundance of the dominant species in native patches changed, with exotics invading native patches (Table 1, Fig. 3). However, the exotic dominants maintained high abundances in the exotic patch type in each of the 3 years after the disturbance. In the native patch type, exotics increased from <2% abundance during the drought year to 25% in the year after the fire, and reached 80% 2 yr after the fire. The native dominant *Stipa* was absent from all but one exotic patch. In the native patches, *Stipa* abundance decreased from almost 100% prior to the fire, to 60% the year following the fire, to ca. 25% in the subsequent years (Fig. 3b). Additionally, within the native patches, no *Stipa* seedlings were present in the drought year (2007) or the year immediately after the intense fire (2008); however, they made up 37% and 14% of the *Stipa* biomass in 2009 and 2010 (non-drought years 2 and 3 yr after the fire), respectively.

By the second year after the fire, the abundances of exotic dominant grasses did not significantly differ between patches that they initially dominated and patches where *Stipa* initially dominated (Year × Type interaction; Table 1, Fig. 3a,b), and by the second and third years after the fire (2009, 2010), exotic dominants had higher abundance than *Stipa* even in the initially designated native patch type (Origin × Year interaction; Table 1, Fig. 3a).

The native dominant, *Stipa*, never produced more seed rain than the exotic dominant grasses, regardless of patch type. Within native patches where *Stipa* abundance was still on average more than 50%, seed rain was similar for both the native dominant and exotic dominants ($t = 0.49$, $P = 0.65$ at 0 m, the start of the transect in the native patch core; Fig. 4a). The seed rain of the natives was also positively correlated with the density of native seedlings in the following year ($r^2 = 0.79$, $P < 0.001$; Fig. 4b). In the exotic patch type, exotic dominant seed rain was approximately 28 times higher than seed rain from native dominants. The seed rain of the exotics was positively correlated with density of exotics (stem counts) in the following year ($r^2 = 0.74$, $P < 0.001$; Fig. 4b).

Response of native and exotic sub-dominant species

The abundance of sub-dominant species did not consistently shift after the disturbance within either community type. These species were similarly abundant (10% abundance) in native and exotic patches across all years, except for the year following the fire, where they increased in abundance in exotic patches (from 10% to almost 30%, Year × Type interaction; Table 1). The abundance of

Table 1. Mixed effects model table summarizing how species relative abundance was influenced by year (2007–2010), initial patch type (native or exotic) or origin (native or exotic) and their interaction with year. Site was included as a random effect in all models.

Response Variables	Year		Type		Year*Type	
	F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Among patches						
Exotic dominants	$32.384_{1,53}$	**<0.001**	$51.291_{1,53}$	**<0.001**	$24.251_{1,53}$	**<0.001**
Native dominants*						
Native sub-dominants *						
Exotic sub-dominants	$0.000_{1,53}$	0.99	$21.575_{1,53}$	**<0.001**	$4.328_{1,53}$	**0.04**
	Year		Origin		Year*Origin	
Within native patches						
Dominants	$0.068_{1,53}$	0.80	$0.135_{1,53}$	0.71	$100.29_{1,53}$	**<0.001**
Sub-dominants	$1.970_{1,53}$	0.16	$0.432_{1,53}$	0.51	$0.430_{1,53}$	0.51
Within exotic patches						
Dominants*						
Sub-dominants	$1.464_{1,53}$	0.23	$68.91_{1,53}$	**<0.001**	$1.464_{1,53}$	0.23

*Models were not run because the group was not present within some patch types. Significant results in bold, numerator and denominator *df* shown as subscripts.

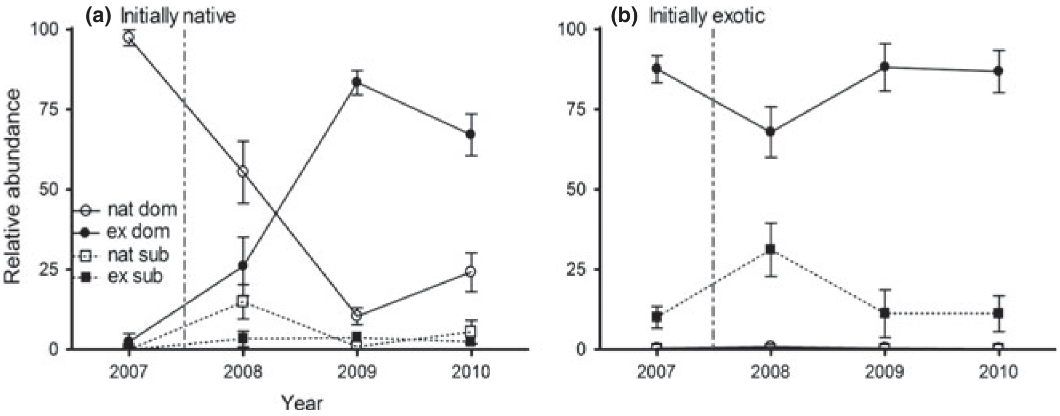

Fig. 3. Relative abundance of species (means ± SEM) before and after fire (indicated by vertical dashed line; 2007 was a drought year) within initially native (**a**) and exotic (**b**) patch types. Species are grouped by origin (native, nat; exotic, ex) and abundance (dominant, dom; sub-dominant, sub). Within native patch types, dominance shifted from native to exotic species, while exotic dominants quickly recovered within exotic patches. Rare species are not shown. Specific species in each group are found in Table S1.

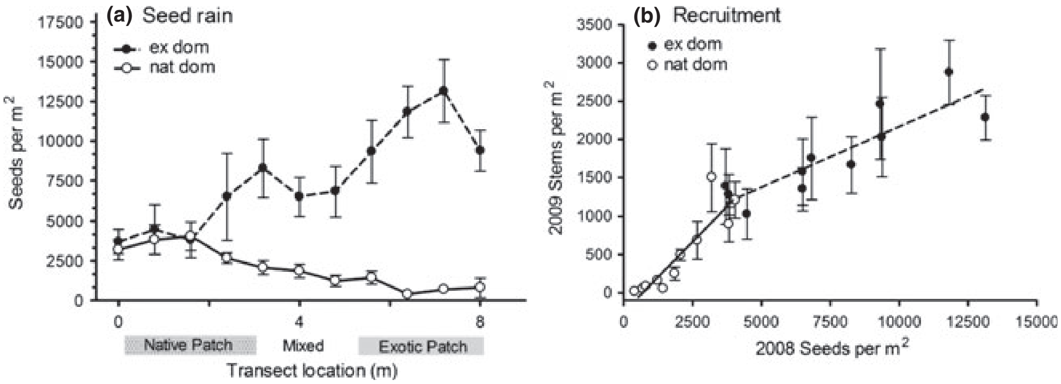

Fig. 4. (**a**) Seed rain of native and exotic dominants along an 8-m transect bisecting native and exotic patches (n = 5, for each point). While few native seeds made it to the interior of exotic patches, seed rain for the exotic (ex dom, filled circles) and native dominants (nat dom, open circles) was similar in the interior of the native patches. (**b**) Seed rain of the exotic and native dominants was a strong predictor of recruitment in the following year (n = 5, for each point, lines represent significant relationships). For natives, because they are perennial, only seedling stem counts are reported. This distinction was not necessary for the exotics because they have an annual life history. Errors bars represent 1 SEM.

native sub-dominant species was variable within the native patches, and they were rarely present in the exotic patch types (Fig. 3a,b).

Community response

The paired native and exotic patches, while initially very different from one another, became less dissimilar (i.e. more similar) to each other after the disturbances ($F_{1,23}$ = 60.96, $P < 0.001$; Fig. 5). This decreased dissimilarity was positively correlated with the abundance of exotic dominants in the native patch type ($F_{1,21}$ = 124.70, $P < 0.001$; Fig. 5) and was not correlated with average site above-ground biomass or species richness (P = 0.54, P = 0.60, respectively).

Discussion

Recovery after a disturbance is often highly dependent on the presence of residuals (Turner et al. 1998). In this case, after a record drought followed by an intense arson-caused fire, the native perennial residuals did not translate to a recovery of the native community type, as would be predicted by the classic competition–colonization trade-off (Fig. 1, solid lines). Instead, we observed a homogenization of the landscape over time, as the abundance of exotic dominants increased within the initially native patches (Fig. 1, dashed lines). While annual exotics were not abundant in the seed bank within the native patches immediately after this extreme disturbance, a large influx of exotic annual seed from the neighbouring exotic annual

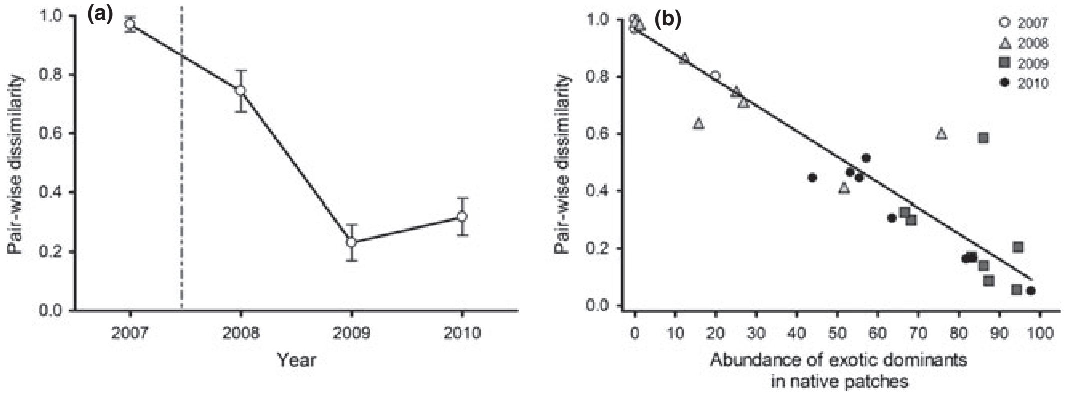

Fig. 5. (**a**) Pair-wise (Bray–Curtis) dissimilarity between paired native and exotic patches (means ± SEM) within the eight grasslands sites over time (fire indicated by vertical dashed line). Pair-wise dissimilarity was negatively related to the abundance of the exotic dominants establishing in the native patches (**b**).

patches occurred in the first year following the fire. This strong propagule pressure resulted in high recruitment of exotic annuals and possibly an increased competitive environment for native perennial seedlings in subsequent growing seasons. These results suggest that dispersal among patches is a strong mechanism governing recovery trajectories and can likely initiate 'replacement competition' dynamics between new propagules (*sensu* Yu & Wilson 2001).

Competition–colonization trade-offs traditionally argue for the displacement of the inferior competitor/better colonizer over time (Levins & Culver 1971). However the superior competitor is often more susceptible to extinction following habitat loss because it is strongly recruitment-limited (Tilman et al. 1994, 1997). While we were not able to measure mortality rates of individual *Stipa* plants, it is possible that the fire immediately following a record drought led to a more intense and thus severe fire and caused higher mortality of *Stipa* individuals than would be expected by either the fire or drought alone. Bunchgrasses can continue burning after a fire has swept through an area, making them vulnerable in a high-intensity fire (Dyer 2003; Keeley et al. 2011).

Limited *in-situ* regeneration of the perennial grasses can create gaps of bare ground that could provide viable microsites for colonization by incoming propagules, increasing the relative importance of dispersal and subsequent recruitment for the recovery of the native community (Kotanen 1997; Paine et al. 1998). These 'colonization windows' created by disturbances can increase the susceptibility of a community to invasion (D'Antonio et al. 2001). Within our exotic patches, we observed that seed rain in the year after the fire (2008) was dominated by the annual exotic dominants, such that there was little native dominant seed input into the exotic patches. Conversely, within native patches, we observed comparable seed rain for native and exotic dominants; however, this seed rain translated to double the recruitment of exotic annuals compared to native perennial seedlings the subsequent year (2009) and a high abundance of exotic annuals in the following year. Additionally, studies have shown that *Stipa* has a limited seed bank (Major & Pyott 1966; Cox & Allen 2008), and the lack of any *Stipa* seedlings during the first growing season after the fire suggests that the *Stipa* seed bank is likely susceptible to intense fires, which would limit the population's recovery to vegetative adults during the first year. While we were not able to fully isolate the effect of propagule pressure by experimentally manipulating seed inputs, these results support previous work showing limited seed dispersal and propagule pressure of the native perennials and high propagule pressure and dispersal ability of the exotic annuals (Seabloom et al. 2003; DiVittorio et al. 2007; Seabloom 2011). Furthermore, these results support that the dominance of exotic annuals is the result of the highly fecund annuals being able to recover quickly after a disturbance and capitalize on the 'colonization window' (Corbin & D'Antonio 2004; HilleRisLambers et al. 2010).

Within 3 yr of the drought and fire we observed homogenization of the two types of grassland patch. Evidence suggests that these trajectories will be maintained, as natural recovery of native perennials is rare and has only been shown consistently in California's coastal prairies (Hatch et al. 1999; Kotanen 2004). While we cannot attribute the cause of this homogenization to any single factor, we expect similar dynamics following events that cause large-scale mortality of the native perennial species.

Recruitment of native perennial seedlings is likely constrained by factors quite different than those maintaining resistance to invasion in established native perennial grasslands. While previous research within California has shown that the native perennial bunchgrass, *Stipa pulchra*, is a superior competitor to exotic annual grasses (Corbin & D'Antonio 2004), our observed recruitment dynamics support previous research that native seedlings are unable to grow quickly enough to effectively compete against the exotic annual grasses and transition into adults (Dyer et al. 1996). This new competitive hierarchy is possible within stage-structured populations like that of a perennial bunchgrass, which have multiple growth stages (e.g. seed, seedling, adult; Yu & Wilson 2001).

California's grassland species composition and biomass fluctuates with the variable rainfall in California (Pitt & Heady 1978), and as a result abiotic factors can be more important in determining grassland species composition than biotic factors (Jackson & Bartolome 2002). In 2007, biomass and species richness were lowest across both patch types, likely due to the severe drought during that growing season. Although we did not find precipitation was a good predictor of biomass and diversity over time, this is likely due to the fact that annual growing season rainfall did not vary much in the years following the fire.

Fire has been an integral part of California's grassland ecosystem (Reiner 2007); it can increase the fecundity and establishment of native perennial grasses like *Stipa* (Ahmed 1983; Langstroth 1991) and reduce the fecundity of invaders (DiTomaso et al. 1999), depending on the timing of the fire (Meyer & Schiffman 1999). Therefore, prescribed burns are often advocated as a tool to restore native grasslands (Menke 1992). While we cannot conclude with certainty the relative importance of the drivers responsible for the dramatic changes we observed, it may be that large-scale wildfires may result in dynamics different from those of prescribed burns, particularly if they interact with weather perturbations.

Sequential disturbances acting upon a system can interact to produce synergies that can alter a community's response and resilience to a disturbance (Paine et al. 1998; Davies et al. 2009). Identifying when these interactions will occur and understanding the potential synergistic effects is critical for land management under continuing global change (Turner 2010). Southern California is predicted to experience more severe droughts (Bell et al. 2004; Hayhoe et al. 2004) and is already experiencing altered fire regimes due to increased human activity (Syphard et al. 2007). Understanding how native perennial grasslands respond to these combined disturbances will be important to their future management and conservation.

While disturbances can promote native communities in some cases, our work suggests that it is important to consider landscape context as well as its interaction with other disturbances or weather patterns. Moreover, a less-intense fire following a particularly wet year may have facilitated native expansion rather than the contraction. Native perennial recruitment is highly limited by seed availability (Seabloom et al. 2003; Seabloom 2011) and can be easily thwarted by the rapid colonization of exotic annuals in invaded landscapes (Seabloom et al. 2003). Understanding the relative importance of dispersal limitation on recovery of the native species can have significant impacts on management efforts. Furthermore, management strategies to enhance vegetative regeneration of natives and decrease propagule pressure from exotics, such as low-intensity prescribed fires, and to introduce native species via seed addition with consideration of weather patterns will be key in maintaining these remnant grasslands.

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References

Ahmed, E.O. 1983. *Fire ecology of Stipa pulchra in California annual grassland*. Ph.D. Dissertation. University of California, Davis.

Baldwin, B., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T. J. & Wilken, D.H. 2012. *The Jepson Manual: vascular plants of California*. University of California Press, Berkeley, CA.

Bell, J.L., Sloan, L.C. & Snyder, M.A. 2004. Regional changes in extreme climatic events: a future climate scenario. *Journal of Climate* 17: 81–87.

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 326–349.

Buckley, Y.M., Bolker, B.M. & Rees, M. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters* 10: 809–817.

Clements, F.E. 1916. *Plant succession*. Carnegie Institution of Washington, Washington, DC, US.

Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8: 1023–1037.

Collins, S.L. 1990. Patterns of community structure during succession in tall grass prairie. *Bulletin of the Torrey Botanical Club* 117: 397–408.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302–1310.

Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119–1144.

Cook, W.M., Yao, J., Foster, B.L., Holt, R.D. & Patrick, L.B. 2005. Secondary succession in an experimentally fragmented landscape: Community patterns across space and time. *Ecology* 86: 1267–1279.

Corbin, J.D. & D'Antonio, C.M. 2004. Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology* 85: 1273–1283.

Cox, R.D. & Allen, E.B. 2008. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. *Plant Ecology* 198: 37–46.

D'Antonio, C., Levine, J.M. & Thomsen, M. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *Journal of Mediterranean Ecology* 2: 233–245.

Davies, K.W., Svejcar, T.J. & Bates, J.D. 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications* 19: 1536–1545.

DiTomaso, J.M., Kyser, G.B. & Hastings, M.S. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. *Weed Science* 47: 233–242.

DiVittorio, C.T., Corbin, J.D. & D'Antonio, C.M. 2007. Spatial and temporal patterns of seed dispersal: an important determinant of grassland invasion. *Ecological Applications* 17: 311–316.

Dyer, A.R. 2003. Burning and grazing management in a California grassland: growth, mortality, and recruitment of *Nassella pulchra*. *Restoration Ecology* 11: 291–296.

Dyer, A.R. & Rice, K.J. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* 7: 484–492.

Dyer, A.R. & Rice, K.J. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80: 2697–2710.

Dyer, A.R., Fossum, H.C. & Menke, J.W. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madrono* 43: 316–333.

Everitt, B. & Hothorn, T. 2011. *An introduction to applied multivariate analysis with R*. Springer, London, UK.

Firn, J., Rout, T., Possingham, H. & Buckley, Y.M. 2008. Managing beyond the invader: manipulating disturbance of natives simplifies control efforts. *Journal of Applied Ecology* 45: 1143–1151.

Fukami, T. & Nakajima, M. 2011. Community assembly: alternative stable states or alternative transient states? *Ecology Letters* 14: 973–984.

Gleeson, S.K. & Tilman, D. 1994. Plant allocation, growth-rate and successional status. *Functional Ecology* 8: 543–550.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.

Hatch, D.A., Bartolome, J.W., Fehmi, J.S. & Hillyard, D.S. 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* 7: 376–381.

Hayhoe, K., Cayan, D., Field, C.B., Frumhoff, P.C., Maurer, E.P., Miller, N.L., Moser, S.C., Schneider, S.H., Cahill, K.N., Cleland, E.E., Dale, L., Drapek, R., Hanemann, R.M., Kalkstein, L.S., Lenihan, J., Lunch, C.K., Neilson, R.P., Sheridan, S.C. & Verville, J.H. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences of the United States of America* 101: 12422–12427.

Heady, H.F. 1977. Valley Grassland. In: Barbour, M.G. & Major, J. (eds.) *Terrestrial Vegetation of California*. pp. 491–514. John Wiley & Sons, New York, NY, US.

HilleRisLambers, J., Yelenik, S.G., Colman, B.P. & Levine, J.M. 2010. California annual grass invaders: the drivers or passengers of change? *Journal of Ecology* 98: 1147–1156.

Hobbs, R.J. & Huenneke, L.F. 1992. Disturbance, diversity, and invasion – implications for conservation. *Conservation Biology* 6: 324–337.

Huston, M.A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions* 10: 167–178.

Jackson, R.D. & Bartolome, J.W. 2002. A state-transition approach to understanding nonequilibrium plant community dynamics in Californian grasslands. *Plant Ecology* 162: 49–65.

Jentsch, A. 2007. The challenge to restore processes in face of nonlinear dynamics – on the crucial role of disturbance regimes. *Restoration Ecology* 15: 334–339.

Keeley, J.E., Baer-Keeley, M. & Fotheringham, C.J. 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications* 15: 2109–2125.

Keeley, J.E., Safford, H., Fotheringham, C.J., Franklin, J. & Moritz, M. 2009. The 2007 Southern California Wildfires: lessons in Complexity. *Journal of Forestry* 107: 287–296.

Keeley, J.E., Franklin, J. & D'Antonio, C. 2011. Fire and Invasive Plants on California Landscapes. In: McKenzie, D., Miller, C. & Falk, D.A. (eds.) *The landscape ecology of fire*. pp. 193–221. Springer, New York.

Kotanen, P.M. 1997. Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies. *Canadian Journal of Botany-Revue Canadienne De Botanique* 75: 352–361.

Kotanen, P.M. 2004. Revegetation following soil disturbance and invasion in a Californian meadow: a 10-year history of recovery. *Biological Invasions* 6: 245–254.

Langstroth, R.P. 1991. *Fire and grazing ecology of Stipa pulchra grassland: a field study at Jepson Prairie*. MS Thesis. University of California, Davis.

Levins, R. & Culver, D. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the United States of America* 68: 1246–1248.

Lockwood, J.L., Cassey, P. & Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20: 223–228.

MacDougall, A.S. & Turkington, R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86: 42–55.

Major, J. & Pyott, W.T. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. *Plant Ecology* 13: 253–282.

Meiners, S.J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88: 1098–1104.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography* 25: 215–223.

Menke, J.W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20: 22–25.

Meyer, M.D. & Schiffman, P.M. 1999. Fire season and mulch reduction in a California grasslands: a comparison of restoration strategies. *Madrono* 46: 25–37.

Moody, M.E. & Mack, R.N. 1988. Controlling the spread of plant invasions – the importance of nascent foci. *Journal of Applied Ecology* 25: 1009–1021.

Mori, A.S. 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. *Journal of Applied Ecology* 48: 280–292.

Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant-communities subject to recurrent disturbances. *Vegetatio* 43: 5–21.

OCFA (Orange County Fire Authority). 2008. After action report Santiago Fire. Available at http://www.ocfa.org/Content/NewsEvents/OCFAReports.aspx Accessed October 2011.

Paine, R.T., Tegner, M.J. & Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535–545.

Pitt, M.D. & Heady, H.F. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59: 336–350.

Platt, W.J. & Connell, J.H. 2003. Natural disturbances and directional replacement of species. *Ecological Monographs* 73: 507–522.

Reiner, R.J. 2007. Fire in California grasslands. In: Stromberg, M.R., Corbin, J.D. & D'Antonio, C.M. (eds.) *California grasslands ecology and management*. pp. 207–217. University of California Press, Berkeley, CA, US.

Seabloom, E.W. 2011. Spatial and temporal variability in propagule limitation of California native grasses. *Oikos* 120: 291–301.

Seabloom, E.W., Harpole, W.S., Reichman, O.J. & Tilman, D. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* 100: 13384–13389.

Syphard, A.D., Radeloff, V.C., Keeley, J.E., Hawbaker, T.J., Clayton, M.K., Stewart, S.I. & Hammer, R.B. 2007. Human influence on California fire regimes. *Ecological Applications* 17: 1388–1402.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65–66.

Tilman, D., Lehman, C.L. & Yin, C.J. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. *American Naturalist* 149: 407–435.

Tognetti, P.M., Chaneton, E.J., Omacini, M., Trebino, H.J. & Leon, R.J.C. 2010. Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. *Biological Conservation* 143: 2494–2503.

Turner, M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833–2849.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1: 511–523.

Yu, D.W. & Wilson, H.B. 2001. The competition–colonization trade-off is dead: long live the competition–colonization trade-off. *American Naturalist* 158: 49–63.

Zobel, K., Zobel, M. & Peet, R.K. 1993. Change in pattern diversity during secondary succession in Estonian forests. *Journal of Vegetation Science* 4: 489–498.

Zouhar, K., Smith, J.K., Sutherland, S. & Brooks, M.L. 2008. Wildland fire in ecosystems: fire and nonnative invasive plants. Gen. Tech. Rep. RMRS-GTR-42-vol 6. pp. 7–32. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Supporting Information

Additional Supporting information may be found in the online version of this article:

Figure S1. Above-ground biomass (a) and species richness (b; mean ± SEM) of native and exotic patches over time.

Table S1. List of species occurring within each vegetation type during the course of the study.