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Long-term propagule pressure overwhelms early community determination of invader success in a serpentine grassland

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By

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Accepted in Partial Completion
of the Requirements for the Degree
Master of Science

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Master's Thesis

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A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

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ABSTRACT

The role of plant diversity in reducing invasions has generated decades of debate. Diverse communities might be more resistant to invasion because the communities contain resident species that are functionally similar to the invader (limiting similarity/sampling effect), or the residents use the range of available resources more effectively (complementarity) than single species. However, the resistance of diverse communities to invasion appears to decline with increasing spatial and temporal scale, in a phenomenon called the “invasion paradox.” I addressed two groups of hypotheses related to this paradox, broadly that: (1) functional diversity and functional identity resist invasion initially, via complementarity or limiting similarity; and (2) disturbance and propagule pressure interact to weaken the effects of functional diversity and identity on invader success through time. Using long-term data from experimental assemblages in a serpentine grassland of California, I examined the abundance of a high impact invader, yellow starthistle (*Centaurea solstitialis*), in response to functional diversity (functional dispersion), functional dissimilarity, extent of pocket gopher disturbance, and propagule pressure. Neither diversity, nor dissimilarity, nor disturbance significantly impacted the success of *C. solstitialis* at any point in the study. Instead, propagule pressure was the single most important predictor of *C. solstitialis* abundance. These findings suggest that continued dispersal may eventually outweigh community resistance when considering a longer-term view of invasion. Thus, conservation efforts focused on preventing the introduction and establishment of invasive species should recognize that even diverse communities are susceptible to invasion over time.

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INTRODUCTION

Species invasions have occurred throughout the history of life on Earth. Only recently have humans played a large role in spreading organisms outside their native ranges (Elton 1958, Di Castri 1989, Vitousek et al. 1996, Lockwood et al. 2013). Most invasions fail, due to biotic and abiotic barriers to survival and reproduction in a new environment (Tilman 2004, Blackburn et al. 2011). However, some invasions are remarkably successful, as evidenced by the tens of thousands of species established outside their native ranges across the globe (Vitousek et al. 1996, Pimentel et al. 2005). Many cultivated and managed exotic species are beneficial to humans and native, ecological communities (Pimentel et al. 2005, Sax et al. 2007). Other non-natives alter the processes and functioning of entire ecosystems; these invasions reduce native biodiversity at rates second only to habitat loss, and cause an estimated $1.4 trillion in damages each year worldwide (Vitousek et al. 1996, Vitousek et al. 1997, Pimentel et al. 2000, Pimentel et al. 2005). Continued access to many ecosystem services depends on the ability of ecological communities to resist the advance of these high impact, invasive species (Cardinale et al. 2012). Decades of research have identified a variety of potential mechanisms determining invader success, including similarities in climate between the donor and recipient regions, release from natural enemies, fluctuations in resources, interactions with native species, propagule pressure, and disturbance (Davis et al. 2000, Mack et al. 2000, Lockwood et al. 2013). Here, I focus on the latter three hypotheses, with an emphasis on their possible interactions through time.

The diversity-invasibility relationship and the invasion paradox

Complementary resource use (i.e., niche partitioning) influences multiple levels of ecological organization, from community structure (e.g., Tilman 1982, 1988) to ecosystem processes (e.g., Díaz and Cabido 2001, Cadotte et al. 2011, Hooper et al. 2012). From a community ecology perspective, complementarity allows species to coexist in time and space, and niche overlap (i.e., limiting similarity) drives interspecific competition (Tilman 1982, 1988, Huston and Huston 1999, Chesson 2000). Shea and Chesson (2002) applied these concepts of complementarity and limiting similarity to invasion ecology, suggesting that invading species only succeed in the presence of 'niche opportunities' in the resident community. For example, a niche opportunity might involve a situation in which the amount of limiting resources that are left unconsumed by the resident community exceeds the amount required for the invading population to sustain itself (i.e., Tilman's R*: Tilman 1982, Shea and Chesson 2002). Thus, highly diverse communities might be more resistant to invasion for three reasons: first, diverse communities are more likely to have at least one species that is particularly effective at repelling invaders (i.e., sampling effect) (Huston 1997, Levine and D'Antonio 1999, Dukes 2002). Second, diversity increases the probability of niche overlap and resource preemption between native residents and invaders (i.e., limiting similarity) (Chesson 2000, Shea and Chesson 2002). Lastly, the inclusion of species with non-overlapping niches allows for more comprehensive use of available resources by the native residents (i.e., complementarity) (Levine and D'Antonio 1999, Theoharides and Dukes 2007). These three mechanisms are not mutually exclusive, and some studies suggest their effects predominate as mechanisms of community assembly and invader success (e.g., Fargione and Tilman 2005, Hooper and Dukes 2010).

Despite general support from theory, empirical evidence for these mechanisms of ecological resistance varies by spatial and temporal scale (Levine and D'Antonio 1999, Levine et al. 2004, Fridley et al. 2007). Small-scale, short-term experiments tend to show strong effects of biodiversity in resisting invasions (e.g., Fargione and Tilman 2005, Maron and Marler 2007). For example, a meta-analysis of 18 experiments in terrestrial plant communities and aquatic microcosms found the number of invading species to decline as native species richness increased (Hector et al. 2001). Moreover, a study involving California serpentine plant assemblages suggested that both the diversity and identity of *a priori* functional (i.e., resource-use-related) groups significantly reduced initial invader success (Hooper and Dukes 2010). On the other hand, larger-scale, observational studies tend to show the opposite pattern (e.g., Planty-Tabacchi et al. 1996, Lonsdale 1999, Stohlgren et al. 1999). A comprehensive review of plant diversity-invasibility studies showed that above 30 m^2, the relationship between native and exotic species richness was consistently positive or nonsignificant (Herben et al. 2004). Most attempts to reconcile this so-called “invasion paradox” address the spatial discrepancies between the two methodologies. For example, another review identified eight ecological processes, including species interactions, immigration, and environmental heterogeneity, that affect the relationship between diversity and invasibility differently at fine and broad spatial scales (Fridley et al. 2007). However, processes that operate over longer time periods, such as natural disturbance regimes, are also typically absent from small-scale experimental studies (see Fridley et al. 2007 for review). These differences in time-scale between experimental and “natural” community studies remain largely unaddressed (but see Clark and Johnston 2011, Clark et al. 2013). Quantifying changes in the effect of diversity on invader success through time, and identifying the mechanisms driving that change, may have important implications for understanding long-term community assembly and resistance to invasion.

Disturbance disrupts biotic resistance?

Disturbance often facilitates invasion by removing residents and increasing resource availability (e.g., Davis et al. 2000, Shea and Chesson 2002, Lembrechts et al. 2016, Pinto and Ortega 2016). However, established native and exotic species frequently exhibit similar responses to disturbance, such that the inclusion of disturbance in diversity-invasibility models reverses or nullifies positive native-exotic richness relationships (NERRs) (Fridley et al. 2007, Clark and Johnston 2011). For example, a positive NERR quantified at the state-level for plants in the U.S. (Stohlgren et al. 1999) reversed direction (Rejmánek 2003) and disappeared (Taylor and Irwin 2004) when human disturbance metrics were included in the model. On a smaller spatial scale, the inclusion of fire frequency and grazing intensity explained an apparently positive NERR in 10 m^2 tallgrass prairie plots (Smith and Knapp 1999). Such studies are largely observational, but implicate disturbance as a potential mechanism of the invasion paradox.

Few experimental studies have directly manipulated disturbance within the context of the diversity-invasibility relationship. In one experiment involving grassland assemblages, researcher-induced drought and fire decreased the effect of diversity on invader establishment (Pinto and Ortega 2016). Similarly, the NERR of marine sessile invertebrate communities shifted from negative to positive in response to periodic removal of organisms (Clark and Johnston 2011). In both studies, the time-span of observation was short (two years for the grassland and ten months for the invertebrates), leaving the long-term impact of disturbance on the diversity-invasibility relationship unaddressed. A simulation model that spanned 100-time steps predicted a similar reversal in the NERR of terrestrial plant communities experiencing random disturbance events (Clark et al. 2013). However, the simulated events only removed resident individuals, without creating the resource pulse that frequently accompanies natural disturbance (Sousa 1984, Davis et al. 2000). Moreover, the model assumed that all species respond to disturbance in the same way, which likely does not hold in natural plant communities (McIntyre et al. 1995). For example, annual forbs, like the invasive yellow starthistle (*Centaurea solstitialis*) in California, tend to dominate disturbed sites, particularly in areas outside their native range (Maddox et al. 1985, McIntyre et al. 1995, Hierro et al. 2006). Assessing the long-term effect of disturbance on NERRs in general, and disturbance-loving invaders in particular, would help elucidate one potential mechanism underlying the invasion paradox.

Propagule pressure promotes invader success?

Successful establishment of invaders like *C. solstitialis* largely depends on the supply of propagules (i.e., colonizing individuals) entering the ‘recipient’ region from the ‘donor’ region (Lockwood et al. 2013). In general, the probability of invader establishment increases as propagule pressure (i.e., the number of colonizing individuals) increases (D'Antonio et al. 2001, Simberloff 2009, Lockwood et al. 2013). This relationship can be explained in two parts: (1) higher numbers of arriving individuals decrease the influence of random changes in birth and death rates (i.e., demographic stochasticity) on population establishment; and (2) higher numbers of colonization episodes decreases the likelihood that random climatic and disturbance events (i.e., environmental stochasticity) will eliminate a new population (Simberloff 2009). Reviews show widespread support for the positive effect of propagule pressure on invader success in both experimental and observational studies across a broad range of taxa (Lockwood et al. 2005, Colautti et al. 2006, Simberloff 2009). Moreover, incorporating propagule pressure into models of ecological resistance helps explain why invasions suddenly succeed in areas where they have failed in the past (Lockwood et al. 2013) or overcome local ecological resistance from diversity (Levine 2000, Von Holle and Simberloff 2005).

Interacting mechanisms drive the invasion paradox?

Propagule pressure likely interacts with other mechanisms, including diversity and disturbance, which may further explain discrepant patterns of invader success (D'Antonio et al. 2001, Lockwood et al. 2013). For instance, one conceptual model proposes that a) diversity increases biotic resistance, b) disturbance decreases it, and c) propagule pressure has a larger influence on invader success when biotic resistance is high than when it is low (D'Antonio et al. 2001). Furthermore, theory predicts that disturbance only promotes invader establishment if propagules are available, and disturbance decreases the number of propagules necessary for establishment (D'Antonio et al. 2001, Lockwood et al. 2013). However, few studies have addressed such interactions explicitly. Empirical evidence from eastern hemlock forests and marine algal communities suggests that elevated levels of disturbance increase the effect of propagule pressure on invader success, and higher propagule pressure amplifies the positive effect of disturbance (Britton-Simmons and Abbott 2008, Eschtruth and Battles 2009). The forest study also investigated the role of species richness in explaining invader success, but the authors did not explicitly consider the influence of disturbance and propagule pressure on the effect of diversity (Eschtruth and Battles 2009). Furthermore, each of these experiments spanned a relatively short time period (3 years for forests, 11 months for algae). Thus, the long-term interactions between propagule pressure and disturbance remain unexplored. Evaluating these interactions over an extended period of community assembly may offer a more holistic explanation for the mechanistic underpinnings of the invasion paradox.

Centaurea solstitialis as a focal species in the California serpentine grassland

Centaurea solstitialis (yellow starthistle) is one of the most widespread and economically disruptive invasive weeds in the western United States (Maddox et al. 1985, DiTomaso 2000). Native to Eurasia, the annual forb is considered a high impact invader by the California Invasive Plant Council based on its ability to disrupt ecosystem processes, its reproductive potential, and its association with human-caused dispersal (DiTomaso et al. 2007). Areas high in native diversity tend to suppress the establishment of *C. solstitialis* (Dukes 2001, 2002, Hooper and Dukes 2010). However, the invader readily colonizes disturbed areas (Maddox et al. 1985, Hierro et al. 2006). California's serpentine grassland, situated within the core of the introduced range of *C. solstitialis*, exhibits high native diversity, low levels of soil resources, and high levels of disturbance (Hobbs and Mooney 1991, Harrison and Rajakaruna 2011, Anacker 2014). Pocket gophers clear about 26% of the serpentine grassland annually (Hobbs and Mooney 1991). In addition, harvester ants concentrate seed chaff and other debris around their colonies, creating pockets of high nutrient availability in an otherwise nutrient-poor landscape (Hobbs and Mooney 1991, Wagner et al. 2004). Similar resource pulses induced by leaf-cutter ants in Argentina facilitated the invasion of exotic, annual herbs into areas of conservation concern (Farji-Brener and Ghermandi 2008). However, experimental evidence from California's serpentine grassland suggests that *C. solstitialis* responds minimally to high nutrient availability, and is, in fact, suppressed by resident species in recently disturbed areas, at least initially (Dukes 2002). Conversely, preliminary evidence from experimental serpentine plots suggested that *C.*

solstitialis abundance surged in association with disturbance by pocket gophers (Fig. 1, Hooper DU, *unpublished data*). The apparent, strong response of *C. solstitialis* to both disturbance and diversity, and the high reproductive potential of the species, provides a unique opportunity to investigate the long-term interaction of these mechanisms in explaining changes in invader abundance.

Experimental overview

I addressed these outstanding questions about the influence of diversity, disturbance, and propagule pressure on invader success using long-term data from experimental grassland assemblages in California. Established in 1991, the original, replicate blocks of native plant communities experienced eight years of controlled composition before researchers introduced new species in an experimental test of the diversity-invasibility hypothesis (Hooper and Dukes 2010). Here, I follow up on the results of that experiment using data spanning over a decade of subsequent natural community assembly and biotic disturbance events. Colleagues quantified species abundance, harvester ant disturbance, and sources of *C. solstitialis* seed annually from 2001 to 2007, but data were only collected at two time points (2012 and 2017) after the advent of pocket gopher disturbance. I thus used four years of data—incorporating pre- (2004, 2006) and post-gopher disturbance (2012, 2017) assemblages—to test two sets of hypotheses related to the effects of (1) community composition, and (2) disturbance and propagule pressure, on invader success.

First, I hypothesized that functionally diverse communities were initially more resistant to invasion. This resistance could have resulted from complementarity and reduced resource availability, or from the sampling effect and the increased likelihood of a community containing

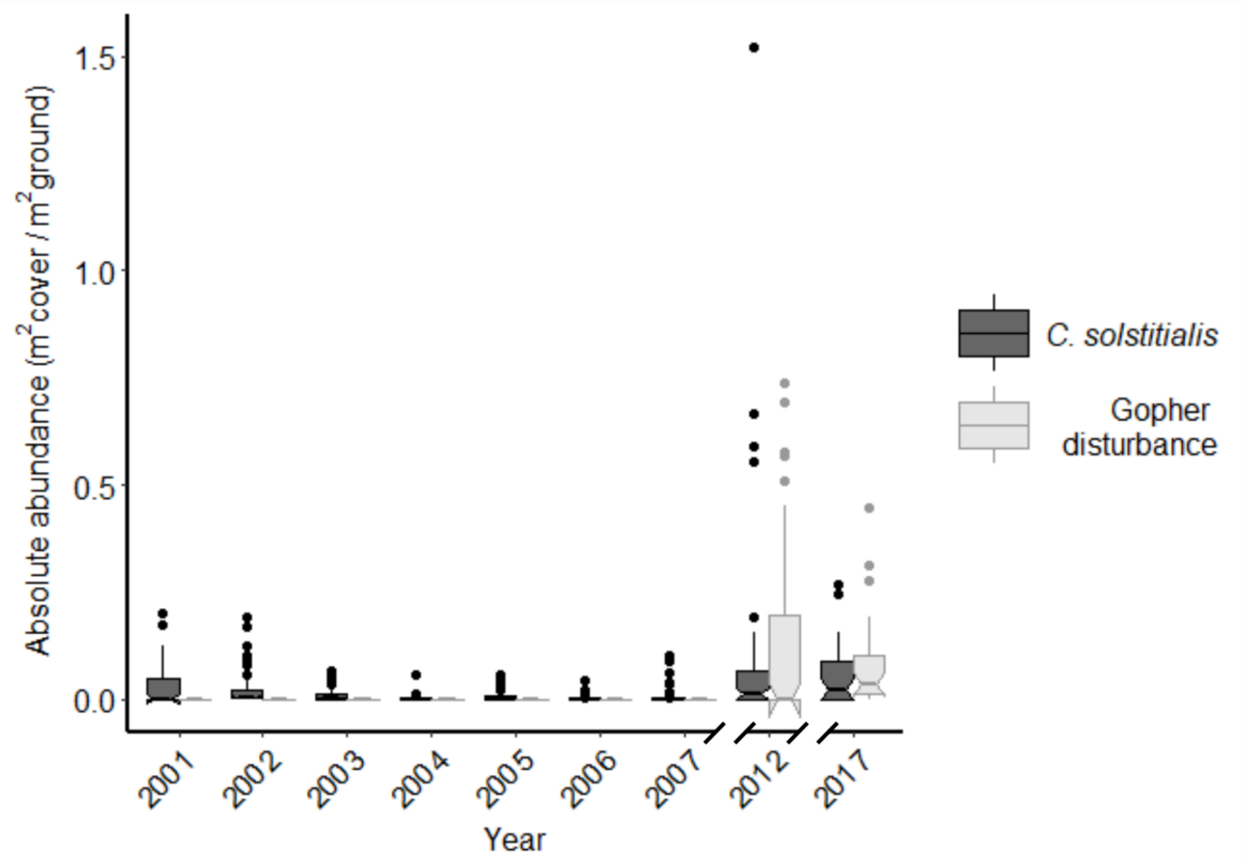

Figure 1. Absolute abundance of the invasive, annual forb *C. solstitialis* and pocket gopher disturbance in experimental assemblages of California serpentine plant species over time (Hooper DU, unpublished data). Gopher disturbance began in the area surrounding the plots in 2007, but was not measured within the plots until 2012. Data were not collected between 2007 and 2012, or between 2012 and 2017.

a functionally similar species. The latter mechanism related to my second hypothesis regarding functional identity, which was that limiting similarity reduced invasion success. If these hypotheses were supported, I predicted (1) a significant, negative relationship between functional diversity and *C. solstitialis* abundance, and (2) a significant, positive relationship between functional dissimilarity and *C. solstitialis* abundance. In both cases, I predicted the pattern in 2004 (i.e., early in *C. solstitialis* establishment), but not necessarily in years following gopher disturbance. If functional diversity and functional dissimilarity were not significantly correlated with each other, and/or only one had a significant effect on *C. solstitialis* abundance, I could also differentiate between the effects of complementarity and limiting similarity on invader success.

For the second theme of the study, I had three related hypotheses:

1. Disturbance and propagule pressure independently increased invader success. If this hypothesis was supported, I predicted significant, positive main effects of gopher disturbance and propagule pressure in all years they were present.

2. An interaction between disturbance and propagule pressure positively affected invader success. If this second hypothesis was supported, I predicted a significant interaction between disturbance and propagule pressure in both 2012 and 2017. For both of these first two, I also predicted no change in initial effects of functional diversity or identity over time.

3. The disturbance-by-propagule-pressure interaction weakened the effects of functional diversity and functional identity. If this last hypothesis was supported, I predicted a significant interaction between disturbance and propagule pressure during the same period that effects of functional diversity and identity declined.

STUDY AREA

The replicate plant communities examined for this study were originally established in 1991 by Hooper (1998) for an experiment investigating the relationship between functional composition and nutrient cycling. Situated at Kirby Canyon, near Morgan Hill, California, the experimental site experiences a Mediterranean-like climate, characterized by cool, wet winters and a dry season stretching from May to October (Hooper 1998). Morgan Hill receives an average of 403 mm precipitation per water year, with substantial inter-annual variation; between the years 2001 and 2007, Morgan Hill experienced a range of precipitation from 216 mm (observed in 2007) to 528 mm (observed in 2005) (Western Regional Climate Center 2016). These relatively low levels of rainfall, combined with low nutrient and high heavy metal content, typify the serpentine soils underlying this region’s native grassland (Harrison and Rajakaruna 2011, Anacker 2014). Due to the high stress environment, strong resource gradients, and recurrent dominance of native species, serpentine communities are considered a model system for studying competition theory and invasion ecology (Harrison and Rajakaruna 2011).

METHODS

Experimental design

Hooper (1998) covered 0.25 ha of previously denuded serpentinitic soil with ~30 cm of topsoil to create a homogeneous surface on which to plant the experimental communities. The communities contained four *a priori* functional groups: early season annual forbs (E), late season annual forbs (L), perennial bunchgrasses (P), and nitrogen fixers (N). All N-fixing plants had early-season reproductive phenology. These groups were chosen to capture complementary differences in resource acquisition traits relevant to nutrient cycling (e.g., growth form, phenology, rooting depth, litter C:N ratio). Each group was originally represented by two or three of the most common species (nine species total) in the surrounding serpentine landscape. The species were planted in ten treatments—B (bare plots), E, L, P, N, EL, EP, LP, ELP, and ELPN—generating an experimental gradient of functional group richness from zero to four, and species richness from zero to nine. Each plot covered 2.25 m^2 (1.5 m x 1.5 m) and was separated from other experimental communities by 0.5-1 m buffer strips. The configuration of the treatments was randomized within six replicate blocks, yielding a total of 60 experimental plots.

For eight years, Hooper and Dukes (2004) weeded out unplanted species to maintain the original species compositions, but not the densities or relative abundances. This allowed natural rank abundance curves to develop over that time (Hooper and Dukes 2004). In 1999, Hooper and Dukes (2010) introduced six new species of early and late annual plants representing common native and exotic “invaders” found in the surrounding serpentine landscape. Among those species planted was the nonnative, yellow starthistle (*Centaurea solstitialis*). The new species were initially seeded at densities comparable to native serpentine grasslands and were re-seeded at the start of the following growing season, such that propagule pressure throughout the experiment was carefully controlled (Hooper and Dukes 2010). As with the initial nutrient cycling experiment, the species compositions, but not relative abundances, were maintained for two years. When weeding of extra-experimental species ceased in 2001, plants from the surrounding landscape began colonizing the plots. Beginning in 2003, harvester ants disturbed portions of plots, creating pockets of high nitrogen availability (Wagner et al. 2004). Pocket gophers began disturbing the periphery of plots in 2007, and by 2012, less than 50% of the original 60 plots remained totally undisturbed by ants or gophers (DU Hooper, *unpublished data*).

For this study, I limited data to four years (2004, 2006, 2012, 2017), to capture two years before pocket gopher disturbance and two years after. The effect variables of interest were concurrent functional diversity (measured as functional dispersion), concurrent functional dissimilarity (measured as the multivariate distance in functional trait values between the community-weighted means [CWMs] and *C. solstitialis*), extent of concurrent gopher disturbance, and previous year's propagule pressure (measured as total seed input per plot). I also explored the independent effects of other late annual abundance (m^2 cover/m^2 ground), total annual precipitation (i.e., water year, previous October to current October; mm), and precipitation (mm) during the late annual growing season (May-October). In all cases, the response variable was the success of *Centaurea solstitialis*, measured in absolute abundance (m^2 cover/m^2 ground).

Data collection and measurements

Species abundance

Hooper and colleagues collected absolute and relative abundance data for all species on each plot using the point quadrat method (Goodall 1952). At every point on a 10 x 9 point grid, researchers passed a laser beam through a point frame and recorded all the species hit by the laser from the top of the canopy to the bare ground (Habenicht 2015). Absolute abundance was measured as the area of plant cover (m^2) per area of ground (m^2). Because a plant could be hit multiple times between the canopy and the ground, the absolute abundance could be greater than one. Relative abundance was the proportion of total cover, calculated by dividing the absolute abundance of each species by the total number of laser-hits per plot. For other species present but not captured by the point quadrat method, colleagues visually estimated their abundance as the midpoint in categories of percent of ground area covered: <0.01%, 0.01-0.05%, 0.05-0.1%, 0.1-0.5%, 0.5-1%, or 1-5%.

To capture the annual peak biomass of all species and functional groups (late March to early April for early-season species, mid-June for mid-season species, and mid-July to August for late-season species), abundance data were collected three times per year in 2004 and 2006, and twice in 2012 and 2017. In 2017, logistical constraints limited the sampling efforts to blocks 1, 3, and 5. Moreover, I only estimated percent cover for the most common early- and mid-season species in 2017, but I used the point quadrat method (Goodall 1952) to measure absolute abundance of late-season species. In 2004, 2006, and 2012, Hooper and colleagues recorded relative abundance on ant colonies separately from abundance off colonies and on the periphery (within ~30 cm of the mound). In 2012, community composition data were also collected separately on and off gopher mounds. Estimates of abundance for the entire plot were weighted by the proportion of disturbance type (e.g., no disturbance, ant mound, peripheral ant mound, etc.). I combined these estimates of relative species abundance with functional trait measurements to calculate functional dispersion and functional dissimilarity for each plot (below).

Community composition and diversity

I measured nine functional traits related to complementarity and limiting similarity (Hooper 1998, Díaz et al. 2007): phenology, life history, nitrogen-fixing capability, root type, maximum measured rooting depth, leaf dry matter content (LDMC), leaf C:N ratio, specific leaf area (SLA), and vegetative height (Table 1). Though a recent study suggested that several of these traits were not strongly correlated with niche differences (Kraft et al. 2015), extensive work in this system has found this suite of traits to be highly relevant to complementary resource use and coexistence (e.g., Hooper 1998, Hooper and Dukes 2004, Gonzalez 2007, Hooper and Dukes 2010, Habenicht 2015). Phenology, life history, and nitrogen-fixing capacities were determined *a priori* for all species by Hooper and colleagues using published sources (Mooney et al. 1986, Hickman et al. 1993). For the remaining traits, I aimed to measure species with at least 10% maximum relative abundance across all plots (33 species total). Where necessary, we relied on measurements previously collected on serpentine soils by Hooper DU (*unpublished data*), Spasojevic et al. (2012), or Fernandez-Going et al. (2012). Missing trait values were not included in the calculations of the community-weighted means (CWMs) or functional dispersion (FDis) (below). Final number of species measured was approximately proportional to the number of species in each *a priori* functional group (Table S1).

Table 1. Summary of functional traits measured to capture complementary resource use. Descriptions and units based on those recommended by Pérez-Harguindeguy et al. (2013). Range of values represent those observed here or collected previously on serpentine soils. All traits were included in the calculation of functional dispersion, but only quantitative variables were used to estimate functional dissimilarity between each community and *C. solstitialis*.

Trait	Description	Unit	Range of values	Source
Phenology	Timing of reproductive season	Category	Early, mid, late	Mooney et al. (1986)
Life history	Duration of survival	Category	Annual, perennial	Hickman et al. (1993)
Nitrogen-fixation	Symbiosis with nitrogen-fixing bacteria	Category	Nitrogen-fixing, non-nitrogen fixing	Hickman et al. (1993)
Root type	Morphology of root system	Category	Taproot, spreading fibrous, shallow diffuse, corm	This study (Fig. 2)
Rooting depth	Maximum measured depth of roots	m	0.04 - 0.43	This study
Leaf dry matter content (LDMC)	Oven-dry leaf mass divided by water-saturated leaf mass	mg mg^{-1}	0.09 - 0.35	This study, Hooper DU (*unpublished data*)
Leaf C:N	Ratio of carbon to nitrogen content per unit of dry leaf mass	unitless	9.85 - 66.15	Hooper DU (*unpublished data*), Fernandez-Going et al. (2012), Spasojevic et al. (2012)
Specific leaf area (SLA)	One-sided area of water-saturated leaf divided by oven-dry leaf mass	mm^2 mg^{-1}	10.29 - 66.70	This study, Hooper DU (*unpublished data*), Fernandez-Going et al. (2012), Spasojevic et al. (2012)
Vegetative height*	Distance between soil surface and uppermost, photosynthetic leaf	m	0.04 - 0.54	This study, Hooper DU (*unpublished data*), Fernandez-Going et al. (2012), Spasojevic et al. (2012)

*Height recorded for *C. solstitialis* was the reproductive, not vegetative, height; however, cauline leaves were present within the top 2-3 cm of the flower head.

All quantitative trait measurements, with the exception of rooting depth, were collected following standard protocols (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). Measurements required excavating approximately 6 individuals per species from the area around the plots or the nearby natural grassland and transporting them to Bellingham, WA, for processing. Early- and mid-season species were collected in mid-March, and late-season species were collected in late July. Where possible, individuals were selected at random intervals along a transect; however, in many instances, locating the plants required intensive searching throughout the landscape. In the latter case, average-sized, healthy, reproductively-mature plants were chosen haphazardly from the available specimens (per Pérez-Harguindeguy et al. 2013). In all instances, we ensured that plants sampled were at least 1 m apart to improve independence. After extracting the plant as completely as possible, root type was determined as one of the four following categories: (1) taproot, (2) spreading fibrous, (3) shallow diffuse, or (4) corm (Fig. 2). For rooting depth, I used maximum *measured* depth (m) due to our general inability to extract entire root systems from the clayey, rocky soil. When roots of an individual broke less than 0.1 m below the soil surface, and we had strong evidence from other specimens that the species rooted at least 0.2 m down, I conservatively changed the estimate to 0.2 m. While this approach provided relatively crude estimates of actual maximum rooting depth, it was sufficient, in combination with root type, to quantify the major differences in rooting strategies among the species in our experiment. Due to the extreme difficulty we encountered extracting intact specimens from the dry, summer soil, the height (m) of several of the late-season species was measured without extraction. For specific leaf area, I used ImageJ (Schneider et al. 2012) to measure area of 3-5 individual leaves per individual.

Figure 2. Examples of root types on 1 cm grid, from left to right: taproot (e.g., *Eschscholzia californica*), spreading fibrous (e.g., *Nassella pulchra*), shallow diffuse (e.g., *Lolium multiflorum*), and corm (e.g., *Muilla maritima*).

Using the above functional traits, I computed the functional dispersion (FDis) and community-weighted mean (CWM) trait values for each plot in R (R Core R Core Team 2017) using the package 'FD' (Laliberté and Legendre 2010, Laliberté et al. 2014). FDis is a diversity metric that measures the distance between the multivariate trait values of individual species and the centroid of all species, and weights the mean distance by species abundance (Laliberté and Legendre 2010). Unlike some other metrics of functional diversity, FDis is not constrained by 0 and 1, but typically does not exceed 2.5 (Laliberté and Legendre 2010). I chose FDis to represent functional diversity because of its relative insensitivity to both species richness and incomplete sampling of community traits (Laliberté and Legendre 2010, Pakeman 2014). The CWM of each quantitative functional trait was the average trait value across all species in a plot, weighted by the relative abundance of the species. CWMs and functional dissimilarity (below) were only calculated for quantitative traits, but FDis incorporated both quantitative and categorical traits. Both FDis and the CWMs of the experimental plots were calculated without *C. solstitialis*, to represent to the community with which *C. solstitialis* was competing.

To estimate functional dissimilarity, I calculated the difference between the CWM and *C. solstitialis* value of each functional trait for every plot. I then modified the Sørensen (Bray-Curtis) dissimilarity index to calculate the multivariate distance between the CWMs of all traits in a given plot and the values of all traits for *C. solstitialis*, such that

$$DFT_{i,h} = \frac{\sum_{j=1}^{n} |a_{ij} - a_{hj}|}{\sum_{j=1}^{n} a_{ij} + \sum_{j=1}^{n} a_{hj}}$$

where $DFT_{i,h}$ is the multivariate matrix of differences in functional traits (DFT) between community i and species h (i.e., *C. solstitialis*); n is the number of traits; a_{ij} is the CWM value of trait j in community i; and a_{hj} is the value of trait j in species h (*C. solstitialis*). The Bray-

Curtis dissimilarity index is bounded by 0 (most similar) and 1 (least similar) and offers a robust measure of compositional differences between ecological communities (Bloom 1981, Beals 1984, Faith et al. 1987).

Previous work on multimetric values of functional traits has raised concerns associated with incomplete trait sampling (Pakeman 2014), using too many traits (Bernhardt-Römermann et al. 2008, Pakeman 2011), or using traits irrelevant to the process of interest (Petchey and Gaston 2002, Gonzalez 2007). To assuage the fears of obscuring an effect of functional diversity or dissimilarity by using the wrong set of traits, I calculated FDis and DFT using two trait matrices: the first was larger, with more traits and species, but with gaps (i.e., not all traits were measured for all species). Phenology, life history, nitrogen-fixing ability, and root type were considered categorical, and thus excluded from the calculation of DFT. The second was smaller (i.e., fewer traits and species), but complete. Only traits directly related to complementary resource use (i.e., phenology, life history, nitrogen-fixing ability, root type, and root depth; e.g., Gulmon et al. 1983, Hooper 1998) were included in the matrix. Categorical variables were also made quantitative (Julian date of maximum flowering for phenology, and numerical codes for the remaining three variables), such that all variables were included in the calculation of DFT. I ran analyses using both metrics, and the results were the same. Thus, only results from the first, larger trait matrix are presented here.

In addition to measures of functional dispersion and dissimilarity, I explored the effect of total cover on *C. solstitialis* abundance to provide a measure of overall resource use, in the absence of niche-partitioning. I measured total cover for each plot as the absolute abundance (m^2 cover/m^2 ground) of all species in the community except *C. solstitialis*.

Disturbance extent

I used the point quadrat method (Goodall 1952) to quantify the proportion of each plot disturbed by harvester ants and pocket gophers, directly or peripherally. The extent of ant disturbance was first quantified in 2003, and peripheral gopher disturbance only was first found and quantified in 2007. The proportion of each plot disturbed directly by gopher mounds was recorded in both 2012 and 2017. Although my main hypothesis concerned the response of *C. solstitialis* abundance to gopher disturbance, I also explored two additional disturbance metrics: harvester ant activity (previous year in 2004 and 2006, concurrent in 2012, and absent in 2017) and cumulative ant and gopher activity (summed over all previous years—not just the four years of the study—and concurrent year). I did not consider peripheral disturbance of either ants or gophers in my analyses.

Propagule pressure

I used field survey data collected in 2003, 2005, and 2017 to parameterize a seed dispersal model that predicted probability of seed deposition from *C. solstitialis* as a function of the number and height of *C. solstitialis* seed sources (inflorescences), distance and direction of plots from source patches of *C. solstitialis*, and wind speed and direction (Fig. 3; details and methods for dealing with the absence of seed source data in 2012 are discussed below). I then summed the number of seeds predicted to enter each plot from all source patches as the propagule pressure for a given year. To map patches of *C. solstitialis* within the vegetated area surrounding the plots, we used Trimble Pro-XR (2003, 2005) and Trimble GeoXH 6000 (2017) GPS units (accuracy < 30 cm in overdetermined 3D mode). We started by mapping the location

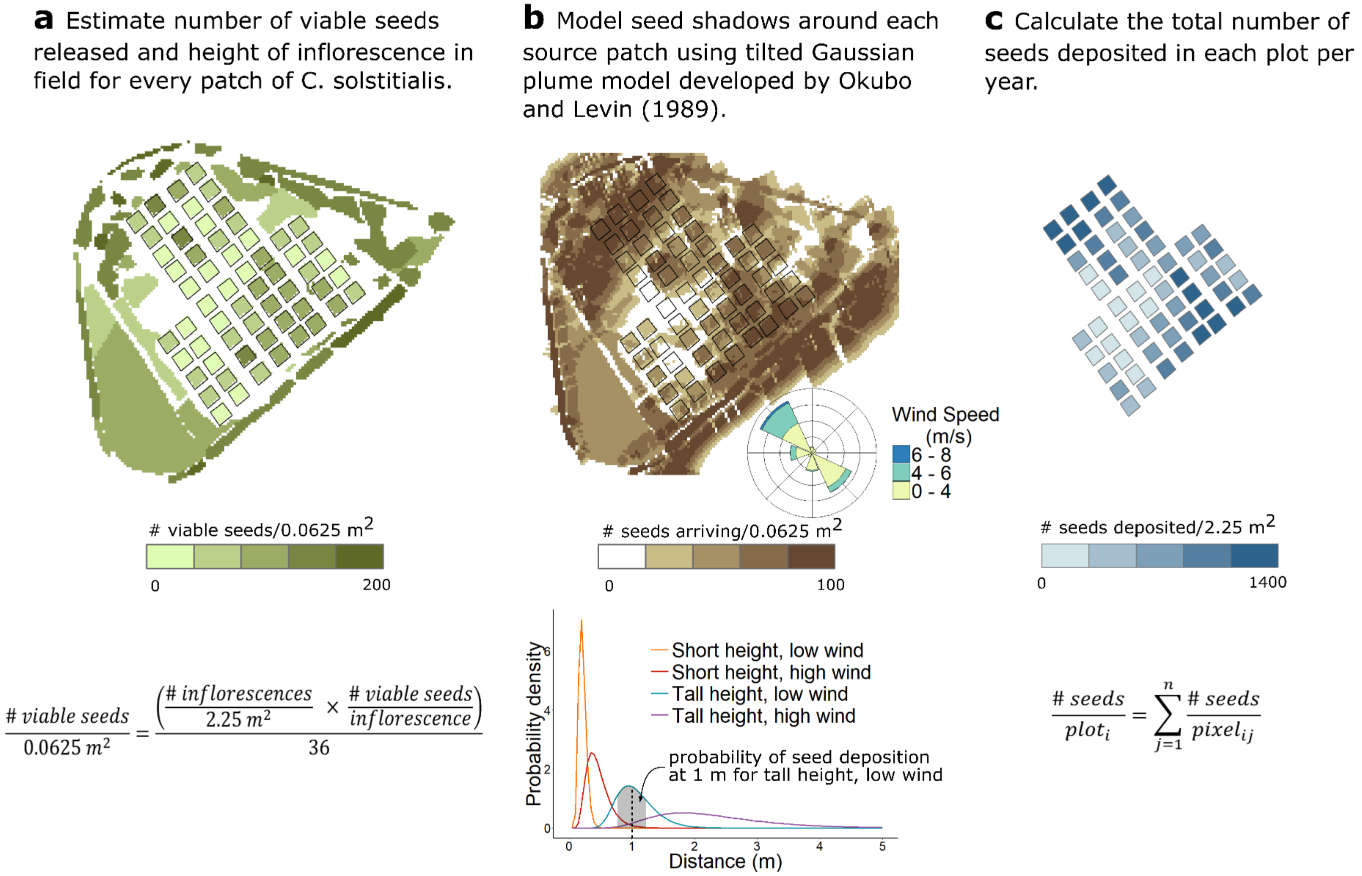

Figure 3. Propagule pressure (seeds/plot/year) estimated using a combination of (a) field surveys, (b) dispersal modeling, and (c) seed shadow summation. (a) Number of viable seeds per 0.25 m x 0.25 m pixel was calculated using the density of inflorescences within a plot-sized area (2.25 m^2) and the number of viable seeds per inflorescence. (b) The peak of the probability density function of seed deposition (i.e., dispersal model) shifted to greater distances as inflorescence height and wind speed increased. Multiplying the integrated probability density function by the number of seeds allocated to a given wind speed x direction yielded overlapping seed shadows around each source patch. (c) The number of seeds deposited within each pixel of the seed shadows were summed within each experimental plot to estimate the total seed input per plot per year. Maps for this figure were produced using actual seed and height data measured in 2017 and wind data averaged across years with a local weather station (2001-2007; California Irrigation Management Information System 2018).

of four, permanent, reference points, to ensure readings were consistent across years. Larger patches of *C. solstitialis* were mapped as areas, smaller patches (1-2 plants) as points. For each patch, we estimated the weighted average height (m) and density of inflorescences per 2.25 m^2 (i.e., the size of one experimental plot) on a scale of 1-5: 1 = 10-50 inflorescences; 2 = 50-100, 3 = 100-500, 4 = 500-1000, 5 ≥ 1000. In 2017, I modified this scale to better capture observed variation in that year: 1 = 10-50 inflorescences; 2 = 50-100, 3 = 100-300, 4 = 300-750, 5 ≥ 750. Inflorescence height and density were also recorded for *C. solstitialis* in each experimental plot for all years except 2003. For 2003, I used 2005 plot data to estimate (1) the median height of in-plot *C. solstitialis* (0.25 m), and (2) a relationship between absolute abundance and inflorescence density. I determined that in 2005 all plots with absolute abundance less than 0.03 had an inflorescence density of 1, and that the median density in plots with absolute abundance above 0.03 was 2. I used these values to convert 2003 cover estimates of *C. solstitialis* into inflorescence height and densities for dispersal modeling. Real-time differential correction for GPS improved the accuracy of the location data in the field for the years 2003-2005, but the service was not set up on the GPS unit used in 2017. Instead, I used post-processing differential correction, with a GPS receiver in San Jose, CA, serving as the reference station. Data files were post-processed and converted to ArcGIS format using the Trimble GPS Pathfinder Office v5.7 software (Trimble Navigation Limited 2015).

The raw files of *C. solstitialis* height and density for 2003, 2005, and 2017 were curated for analysis by amending the protocol outlined by Cookingham and Dukes (2008, *unpublished undergraduate thesis*, University of Massachusetts, Boston). For each patch, I calculated the number of seeds per 2.25 m^2 (the size of an experimental plot) as the product of the median inflorescence density and number of seeds per inflorescence. I estimated density as the median number of inflorescences in a density bin (bin 1 = 25 inflorescences, 2 = 75, 3 = 200, etc.). Because 72% of all inflorescences that we haphazardly surveyed (n = 43) were infected by one of two bio-control weevils (*Bangasternus orientalis* or *Eustenopus villosus*) and had few to no viable seeds, I estimated number of seeds per inflorescence as the weighted average of viable seeds per intact and weevil-infested seed head ($\bar{x}$ = 13 seeds/inflorescence). To achieve a pixel resolution of 0.25 m, I divided the number of seeds per 2.25 m^2 in each patch by 36 to yield the number of seeds per 0.0625 m^2. I used ArcMap 10.2.2 (ESRI 2014) to convert original point and polygon files to a single raster layer (0.25 m resolution) for each year, with each patch possessing a unique ID, average seed height (m), and number of seeds per 0.25 x 0.25 m cell (Fig. 3a).

I estimated the probability density of *C. solstitialis* seed deposition around each source patch using the tilted Gaussian plume model developed by Okubo and Levin (1989; Fig. 3b). I first generated raster layers where each cell had a value indicating the Euclidean distance from a given source patch and the direction to the patch in degrees (R package ‘raster’: Hijmans 2016). To estimate within-plot deposition, I reclassified all within-plot distances as the distance from the center of a plot to the perimeter (0.75 m). I then incorporated the distance layer into the tilted Gaussian plume model, which estimates the probability density of seed deposition as a function of distance (Okubo and Levin 1989). The model has a steady-state solution, implicitly assuming that wind velocity is constant in time and space (Andersen 1991, Levin et al. 2003). The solution estimates the rate of downwind seed deposition by integrating crosswind distribution of seeds (see Okubo and Levin 1989 for details), such that

$$Q(x) = \frac{W_S}{\sqrt{2\pi}\,\bar{u}\sigma_z} exp\left\{-\frac{(H-\frac{W_S x}{\bar{u}})^2}{2\sigma_z^2}\right\},$$

$$\text{with } \sigma_z^2 = \frac{k u^* H x}{\bar{u}},$$

where $Q(x)$ is the probability density function of seed deposition at ground-level ($z = 0$ m) as a function of distance from the seed source (x, measured in m); W_s is the terminal (i.e., settling) velocity of seeds (m/s); $\bar{u}$ is the mean wind speed (m/s); H is the release height of seeds (m); k is the von Kármán constant ($k \approx 0.41$, unitless); and u^* is the friction velocity ($u^* \approx 0.1\bar{u}$ m/s) (Okubo and Levin 1989, Andersen 1991, Levin et al. 2003). Cookingham and Dukes (2008, *unpublished undergraduate thesis*, University of Massachusetts, Boston) used the seed dropping method (Andersen 1993) to estimate the terminal velocity of *C. solstitialis* as W_s = 1.52 ± 0.03 m/s (mean ± 1 SE). Raw wind data were available from the California Irrigation Management Information System (CIMIS) station at Morgan Hill for the years 2001 to 2007, after which the station became inactive (CIMIS 2018). Due to absence of wind data in 2012 and 2017, for consistency, I pooled wind data from 2001 to 2007 for use in all four years of the study.

Although the model assumes that wind speed is independent of *z* (height above ground) (Andersen 1991), I incorporated the wind velocity profile into the equation by correcting measured wind speed to reflect wind speed at flowering height. Following other studies investigating the relationship between wind speed and seed release (e.g., Schippers and Jongejans 2005), I estimated wind speed at flowering height using a logarithmic wind profile, such that

$$u_F = u_M \frac{\ln(z_F - z_b)/z_0}{\ln(z_M - z_b)\,/z_0}$$

where u_F and u_M are the wind speeds at flowering height and measured height, respectively; z_F and z_M are flowering height and height of measured wind speed, respectively; z_b is a “zero-plane displacement,” or the height at which wind flow is zero (i.e., the height of obstacles such as trees or buildings); and z_0 is the roughness of the terrain (termed “roughness length”) (Holmes 2015). For the years of the study, the median flowering height of *C. solstitialis* within and around the plots was 0.42 m, and the height of the wind sensor was 2 m above the ground (University of California Integrated Pest University of California Integrated Pest Management 2018). Because the plots were on relatively open, grassy terrain with few trees or buildings blocking the primary directions of wind, I assumed a zero-plane displacement of 0 m and a median roughness length of 0.03 m, per Holmes (2015). To further improve the accuracy of the model, I limited the corrected wind data to the months during which *C. solstitialis* releases mature seeds (July-October) (Maddox 1981, as cited in Maddox et al. 1985). I then further reduced the data to only daylight hours (6:00 AM to 8:00 PM), reflecting the period of maximum desiccation and assumed maximum seed release.

The number of seeds dispersed from a parent plant, as well as the distance travelled by seeds, increase as wind speed increases (Jongejans et al. 2007, Borger et al. 2012, Savage et al. 2014). Moreover, many plants exhibit a seed release threshold, or a minimum wind speed required for seeds to abscise from the inflorescence (Schippers and Jongejans 2005, Skarpaas et al. 2006). Failure to incorporate such thresholds can significantly underestimate dispersal distance (Schippers and Jongejans 2005). Seed release thresholds are generally species specific. For example, the thresholds for two thistle species in the *Carduus* genus are 4.1 m/s and 6.1 m/s, respectively (Skarpaas et al. 2006). The morphologically similar seeds of a related species (*Senecio inaequidens*) abscise when wind speeds reach 5 m/s (Monty et al. 2008). However, other studies suggest a generic, catch-all initial release threshold of 10 m/s, decaying to 0 m/s ten days after the seed ripens (e.g., Schippers and Jongejans 2005). Since the threshold for *C. solstitialis* is unknown, I assumed that it exhibits the median threshold value of the other thistle species at 5 m/s. Over the period of data available for this study (2001 to 2007), wind speeds sufficient for *C. solstitialis* dispersal occurred at flowering height in the west, northwest, and southeast, directions (CIMIS 2018; Fig. 3b).

I estimated the probability density of dispersal in each of these wind speeds x directions to calculate the total seed input to each of the plots (Fig. 3b, c). To estimate the actual probability of deposition at distance x, I integrated the probability density function for an interval of 0.25 m around x (reflecting our raster resolution of 0.25 m) (Levin SA, *personal communication*). I then multiplied the probability of deposition at a given distance by the number of seeds available for dispersal. For each patch of *C. solstitialis*, I divided the total number of seeds released proportionally to the time spent within each wind speed-direction combination (Fig. 3b, Table S2). I summed these estimates of seed deposition within the plot boundaries to determine total seed input per plot per year (R packages 'rgdal' and 'raster': Bivand et al. 2013, Hijmans 2016) (Fig. 3c). Due to lack of contiguous data, I used average seed input across 2003, 2005 and 2017 as the metric for propagule pressure in 2012 and concurrent seed input in 2017. Using all three years was justified by the relative consistency of propagule pressure within each plot from year to year ($p \leq 0.10$ for each pairwise correlation). To reduce the likelihood of missing an effect by evaluating the wrong metric, I also explored the effect of cumulative seed input (summed over previous years in the study, and current year for 2017).

Though the relatively simplified process of dispersal modeling described here has several important caveats, I identified no consistent bias towards short- or long-distance dispersal. On the one hand, the model might have underestimated dispersal distance by ignoring secondary wind dispersal along the ground (i.e., post-landing crawl) or the importance of updrafts to long-distance dispersal (Tackenberg et al. 2003). Conversely, the model might have overestimated germination at longer distances, because larger, more viable seeds might have dropped more quickly (e.g., Vander Wall 2003), or because the model ignored the decline in wind speed with proximity to the ground below the seed release height (Okubo and Levin 1989). The predictive power of the model could be improved by allowing wind speed to vary by year and by consistently using estimates of the previous season's seed availability, though those data were not available for all years of this study. Logistical constraints also prevented me from evaluating the accuracy of the model using seed traps or wind tunnel experiments (e.g., Nathan et al. 2001, Monty et al. 2008). However, because the above simplifications made the model more general, without a clear, directional bias, effects of propagule pressure identified here were likely not spurious results of the dispersal modeling process.

Statistical analyses

All hypotheses were tested simultaneously using multi-model inference within an information theoretic framework (Burnham and Anderson 2002). To assess changes in parameter coefficients and importance at different stages of invasion and disturbance, I analyzed the data in each of the four years (2004, 2006, 2012, and 2017) independently. In addition to the main parameters of interest, each linear mixed model also contained an intercept term, a random intercept for each block, and residual error, such that the global model was

$$\mathrm{CS} = \mathrm{I} + \mathrm{FDis} + \mathrm{DFT} + \mathrm{GD} + \mathrm{PP} + \mathrm{GDxPP} + \mathrm{Block} + \mathrm{E}$$

where CS is *C. solstitialis* absolute abundance; I is the intercept; FDis is functional dispersion of the extant community (unitless); DFT is the multivariate difference in functional traits (i.e., functional dissimilarity) between the invader and the extant community (unitless); GD is gopher disturbance extent (proportion of plot disturbed); PP is propagule pressure (number of seeds per plot per year); GDxPP is the interaction between gopher disturbance extent and propagule pressure; Block is the random intercept for each block (1-6); and E is residual error. The range of propagule pressure was roughly 2000 times larger than the ranges of the other variables. To avoid biasing results towards propagule pressure and to ensure model convergence, I transformed propagule pressure to a scale of 0 to 1 by dividing each observed value by the maximum (max = 2090 seeds/plot/year). Regression coefficients were then back-transformed to reflect estimates for actual, not scaled, propagule pressure. For analyses involving exploratory metrics, I substituted each new metric for the original term independently. I did not interpret the effect of block in any model, but used it only to explain additional variation in the data. For all predictors, the error structures were approximately Gaussian, with some abnormally high residuals. I used the identity link function to have the flexibility to test multiple shapes of *C. solstitialis* abundance response to different parameters (below). All models were fit using R package ‘lme4’ (Bates et al. 2015).

Before assessing parameter effects, I used Akaike’s Information Criterion corrected for small sample sizes (AICc) to compare the factorial combinations of potential variable shapes (FDis = linear or saturating; DFT = linear; total cover = linear; disturbance = linear, saturating, or unimodal; propagule pressure = linear or saturating) (Burnham and Anderson 2002). Nonlinear shapes for FDis, disturbance, and propagule pressure were chosen based on theoretical and empirical support in the literature (FDis: Hector et al. 2001, Fargione and Tilman 2005; disturbance: Armesto and Pickett 1985, Petraitis et al. 1989; propagule pressure: Lockwood et al. 2005, Britton-Simmons and Abbott 2008). Assessment of shape was largely exploratory; the shapes themselves were not of intrinsic interest, but testing for nonlinearity provided the best chance of identifying an effect of a variable, if it existed. Thus, when nonlinear shapes yielded ecologically nonsensical predictions (e.g., negative abundances) as an artifact of our data distribution, I used the linear relationship instead.

After identifying the best base model for each year, I ranked all possible variable combinations by AIC_c (R package 'MuMIn': Bartón 2017). I then averaged the coefficients of the parameters across all models and calculated the relative importance of each variable (i.e., the sum of the Akaike weights of the models in which they appeared) (Bartón 2017). For the models that did not contain a given variable, the coefficient of that variable was assumed to be zero. Model-averaged coefficients were weighted by the likelihood of the models that contained a given variable. For each parameter, I defined statistical significance as $p < 0.05$, and "borderline" significance as $p < 0.10$. Because relative importance estimates alone can give spurious results about the relative effects of predictor variables, I focused on model averaged effect sizes and significance as metrics of variable importance (Galipaud et al. 2014, Galipaud et al. 2017).

The multi-model inference approach I used, with a balanced set of models (i.e., a model set in which all parameters appear with equal frequency), reduces bias towards individual variables and accounts for potential errors associated with model selection uncertainty (Burnham and Anderson 2002). Moreover, because all parameters were chosen to test specific hypotheses, I reduced the risk of selecting models and calculating coefficients that would be biologically nonsensical (Burnham and Anderson 2002). However, because the Gaussian distribution is not limited to positive values, the observed, large variance around measurements of low average abundance can lead to ecologically nonsensical predictions of negative abundance. Thus, after ascertaining that the intercepts did not deviate significantly from zero, I plotted the relationships with intercepts through the origin to better reflect ecological reality.

Lastly, I performed some additional, exploratory analyses to identify other potential mechanisms of *C. solstitialis* success. Using simple, generalized linear models, I regressed average *C. solstitialis* abundance in each year (n = 4) against (1) average, total, absolute abundance of other late annual species (m^2 cover/m^2 ground); (2) total growing season (water year) precipitation (i.e., from the start of the first fall rains in October of the previous year to the October of the year in which we estimated abundances (per Maddox et al. 1985), measured in mm); and (3) late growing season precipitation (i.e., between the measurements of peak biomass for early and late annual species, approximately mid-April to mid-August, measured in mm). If *C. solstitialis* abundance responded to annual climatic variation, I predicted other late annuals to respond similarly to such variation. Moreover, in such a moisture-limited environment, I predicted abnormally high precipitation, particularly late into the summer, to have a strong, positive effect on late annuals, like *C. solstitialis*, which exhibit most aboveground growth after the winter rains cease. Raw precipitation data were not available from the CIMIS station at Morgan Hill or the nearby town of Gilroy for all years of the study (CIMIS 2018). However, precipitation data were collected simultaneously in San Jose and Morgan Hill for the years 2001-2009, and in San Jose alone for the years 2012 and 2017 (Western Regional Climate Center 2016). I used simple, linear regressions to predict Morgan Hill precipitation from precipitation in San Jose for the late growing season ($\beta = 0.804$, $p < 0.001$) and the total growing season ($\beta = 0.540$, $p = 0.026$) between the years 2001 and 2009. Then, for the years of the study, I multiplied the San Jose precipitation values by the regression coefficients above to estimate precipitation in Morgan Hill.

RESULTS

Establishing appropriate shapes for response of *C. solstitialis* abundance

Semi-exploratory model selection identified the best shapes for the response of *C. solstitialis* abundance to the predictor variables as linear for FDis, unimodal for gopher disturbance, and linear for propagule pressure (Table S3). The best shapes were similar for the exploratory metrics as well: unimodal or saturating for ant and cumulative disturbance, and linear for cumulative propagule pressure (Tables S4, S5, S6). However, the unimodal shape for disturbance metrics yielded biologically nonsensical predictions (i.e., negative values of absolute abundance). I expect this resulted from the concentration of data points around zero abundance. Therefore, I used linear relationships with disturbance for all interpretations.

Effects of community composition and diversity on invader success

I predicted that higher functional diversity, measured as functional dispersion (FDis), would decrease invader success, measured as *C. solstitialis* abundance, and larger differences in functional traits would increase invader success. However, these analyses did not find evidence that FDis or similarity in trait values resisted invasion in any of the study years (Fig. 4a, b). FDis and functional dissimilarity were significantly correlated in two years of the study, rendering complementarity and limiting similarity effects indistinguishable (Fig. S2). Though the most likely model in 2004 contained both FDis and functional dissimilarity, the model only explained 12% of the variation in *C. solstitialis* abundance (Table 2). Moreover, although FDis was among the most important variables in both 2004 (RI = 0.83) and 2012 (RI = 0.84), the direction of the effect shifted from negative in 2004 ($p = 0.139$) to positive in 2012 ($p = 0.121$). Neither variable

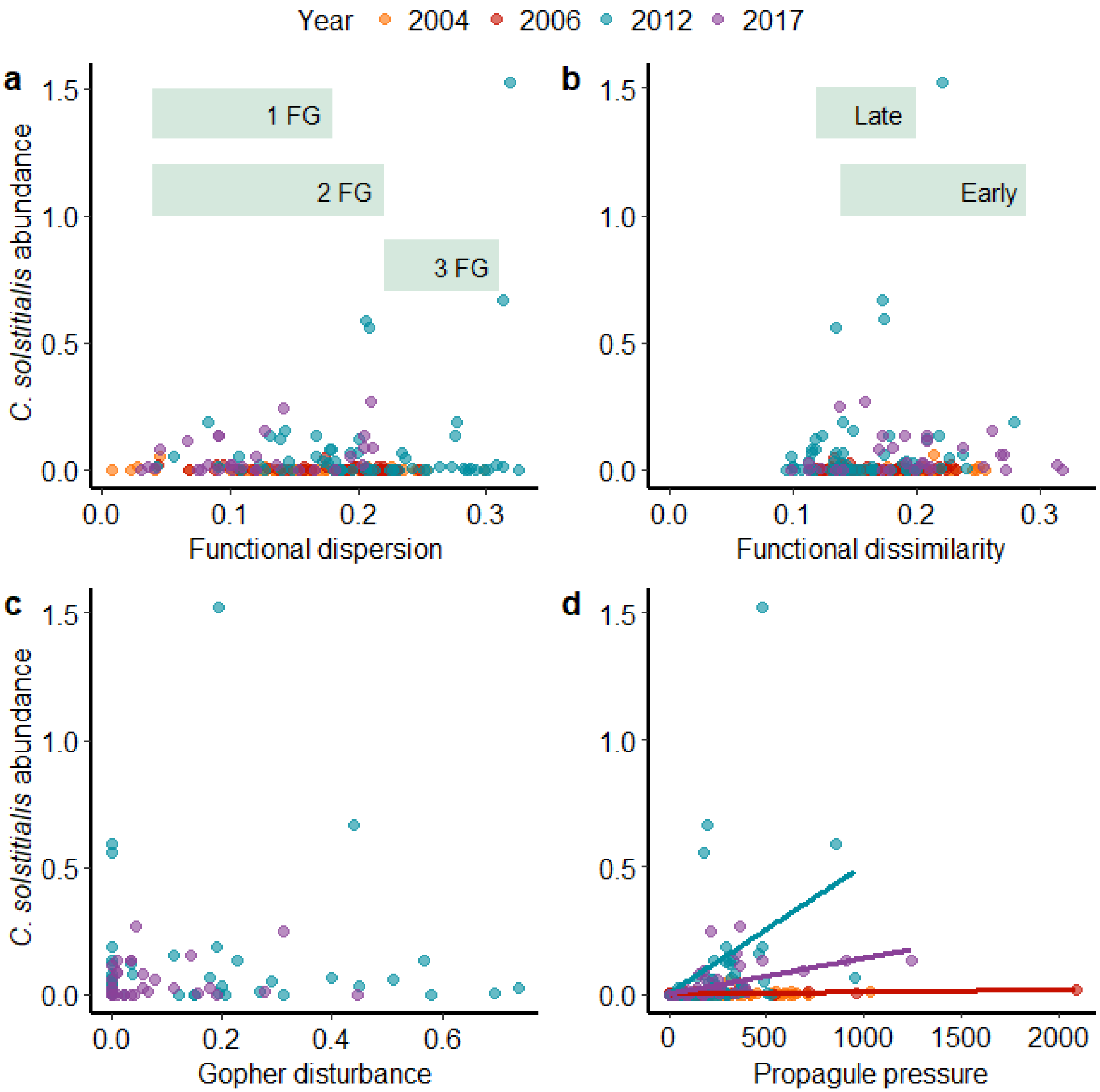

Figure 4. Main effects of (a) functional dispersion, (b) functional dissimilarity, (c) gopher disturbance (proportion of plot disturbed), and (d) propagule pressure (number of seeds/plot/year) on absolute abundance of *C. solstitialis* (m^2 cover/m^2 ground), by year. Scale bars provide reference values from 2001 (i.e., near-original functional treatments) for (a) range of functional dispersion across three levels of *a priori* functional group richness, and (b) range of functional dissimilarity for plots dominated by late annual species (expected to be most similar to *C. solstitialis*) and early annual species (expected to be least similar to *C. solstitialis*). Regression lines drawn for significant relationships only ($p < 0.05$).

Table 2. Model rankings for *C. solstitialis* absolute abundance (m^2 cover/m^2 ground) explained by factorial combinations of functional dispersion (FDis), functional dissimilarity (DFT), gopher disturbance (GD, 2012 and 2017 only, measured as proportion of plot disturbed), propagule pressure (PP, measured as seed input/plot/year), and the interaction between gopher disturbance and propagule pressure (2012 and 2017 only).

Year	n	Model	ΔAIC_c	w_i	R^2	K
2004	60	FDis + DFT	0.00	0.41	0.12	5
		FDis + DFT + PP	1.17	0.23	0.14	6
		FDis	2.48	0.12	0.05	4
2006	60	PP	0.00	0.40	0.16	4
		FDis + PP	1.10	0.23	0.17	5
		DFT + PP	1.48	0.19	0.17	5
		FDis + DFT + PP	2.45	0.12	0.18	6
2012	60	FDis + PP	0.00	0.38	0.19	5
		FDis + DFT + PP	1.28	0.20	0.20	6
		FDis + GD + PP	2.12	0.13	0.19	6
2017	30	PP	0.00	0.30	0.26	4
		FDis + PP	0.76	0.20	0.29	5
		GD + PP	2.41	0.09	0.26	5
		FDis + GD + PP	2.58	0.08	0.31	6
		FDis + DFT + PP	2.77	0.07	0.30	6
		DFT + PP	2.79	0.07	0.25	5

Notes: n is number of samples; ΔAIC_c is the difference in the Akaike Information Criteria (corrected for small sample sizes) of model *i* and the best-fitting model; w_i is the Akaike weight; R^2 is proportion of total variance explained by fixed effect variables only; and K is the total number of parameters (including intercept, random block effect, and residual error). Rankings presented for models with $\Delta AIC_c \leq 3$.

was significant in any year (Table 3). Exploratory analyses suggested that total cover did not significantly affect *C. solstitialis* abundance, either (Tables S7, S8). These nonsignificant effects are unlikely to reflect an insufficient range in community composition, because the values measured during this study covered the ranges observed in 2001, when the plots still resembled their original, strongly divergent functional treatments (Fig. 5). The higher values of functional dissimilarity observed in two plots in 2017 were driven by elevated abundances of *Lolium multiflorum*, an early annual grass with functional trait values that greatly differ from *C. solstitialis* (Table S1).

Effects of disturbance and propagule pressure on invader success

Independent effects

Contrary to my initial hypotheses, I found no evidence that gopher disturbance independently facilitated invader success (Fig. 4c). This lack of effect did not vary by metric for disturbance (Tables S9, S10, S11, S12). However, I did find relatively strong evidence that propagule pressure increased *C. solstitialis* abundance (Fig. 4d). Propagule pressure from the previous or concurrent growing season was the most important, and the only significant, predictor of invader success in all years except 2004 (Table 3). Moreover, the most likely models in 2006, 2012, and 2017 contained propagule pressure, though the models only explained 16-26% of the variance in *C. solstitialis* abundance (Table 2). The strongest effect was observed in 2012, when 200 additional seeds per plot increased the absolute abundance of *C. solstitialis* by 10% (0.10 ± 0.04 m^2 cover/m^2 ground, mean ± SE). This effect was not likely spurious, as the exploratory metric of cumulative propagule pressure was also the most important and only significant predictor in 2006 and 2012 (Tables S13, S14).

Table 3. Model-averaged parameter estimates, standard errors (SE), and relative importance (RI) for the effects of functional dispersion, functional dissimilarity, gopher disturbance, propagule pressure, and the interaction between gopher disturbance and propagule pressure, on the absolute abundance of *C. solstitialis* (variable abbreviations and units as in Table 2). Variables in bold were significant at $\alpha = 0.05$.

Year	Variable	Coefficient	SE	p-value	RI
2004	(Intercept)	-0.002	0.007	0.809	-
	FDis	-0.037	0.025	0.139	0.83
	DFT	0.049	0.044	0.275	0.69
	PP	1.81×10^{-6}	3.65×10^{-6}	0.623	0.36
2006	(Intercept)	0.005	0.005	0.317	-
	FDis	-0.011	0.020	0.584	0.40
	DFT	-0.009	0.022	0.679	0.32
	PP	**8.77×10^{-6}**	**3.78×10^{-6}**	**0.022**	**0.94**
2012	(Intercept)	-0.280	0.149	0.064	-
	FDis	0.885	0.564	0.121	0.84
	DFT	0.331	0.629	0.603	0.38
	GD	0.028	0.129	0.831	0.30
	PP	**5.06×10^{-4}**	**1.98×10^{-4}**	**0.012**	**0.97**
	GDxPP	-4.27×10^{-5}	3.51×10^{-4}	0.905	0.07
2017	(Intercept)	0.001	0.041	0.984	-
	FDis	0.157	0.232	0.508	0.45
	DFT	-0.032	0.127	0.807	0.31
	GD	0.015	0.082	0.858	0.22
	PP	**1.41×10^{-4}**	**5.64×10^{-5}**	**0.015**	**0.95**
	GDxPP	5.92×10^{-5}	2.82×10^{-4}	0.838	0.07

Notes: Coefficients were averaged over all models, weighted by model likelihood. In models that did not contain a given variable, the coefficient of that variable was assumed to be zero.

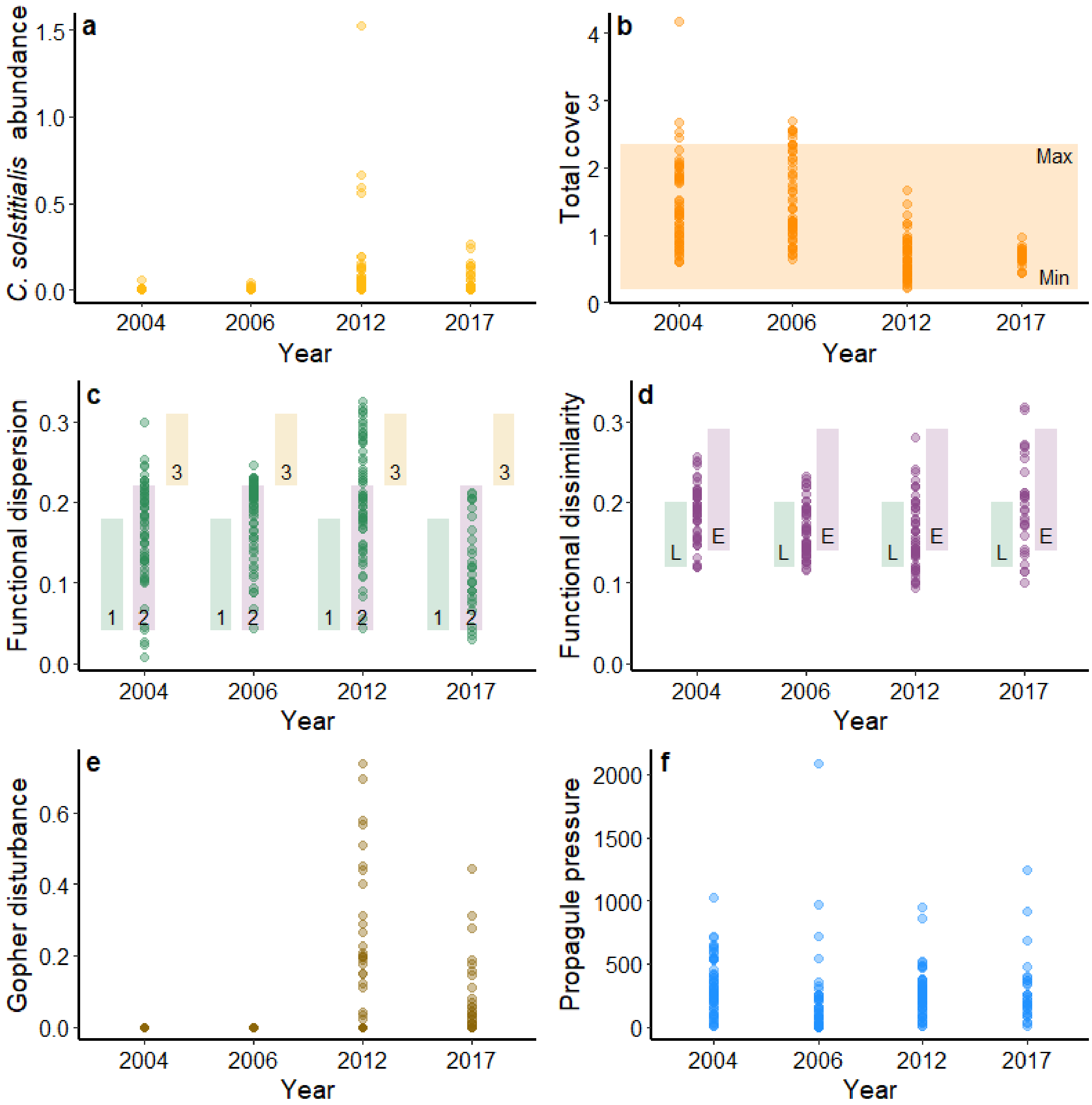

Figure 5. Observed values in each plot for (a) the absolute abundance of *C. solstitialis*, (b) total cover of all other species (m^2 cover/m^2 ground), (c) functional dispersion, (d) functional dissimilarity; (e) extent of pocket gopher disturbance, and (f) propagule pressure, in each year of the study (units as in Fig. 4). Scale bars in (b), (c), and (d) represent values from 2001 (i.e., near-original functional treatments): (b) range of total cover across all plots, (c) range of functional dispersion across three levels of *a priori* functional group richness, and (d) range of functional dissimilarity for plots dominated by late annual species (expected to be most similar to *C. solstitialis*) and early annual species (expected to be least similar to *C. solstitialis*).

Interaction effects

I found no evidence of an interaction between disturbance and propagule pressure impacting invader success (Fig. S1). The interaction effect was not significant or important in any year of the study, regardless of the metric of disturbance or propagule pressure (Tables 3, S10, S12, S14).

Exploratory regressions

Additional, exploratory analyses revealed no evidence for climatic variation or biomass of phenologically similar species driving invader success. *C. solstitialis* abundance was not significantly explained by the abundance of other late annuals, total growing season precipitation, or late growing season precipitation (Fig. 6).

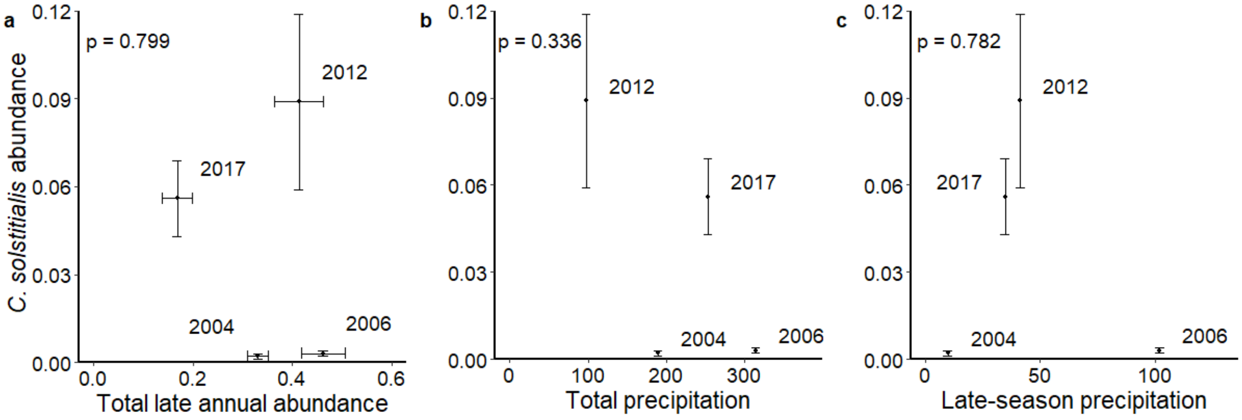

Figure 6. Exploratory regressions of absolute abundance (m^2 cover/m^2 ground) of *C. solstitialis* (mean ± 1 SE) explained by (a) total absolute abundance of other late annual species (mean ± 1 SE), (b) total growing season precipitation (mm), or (c) late growing season precipitation (mm).

DISCUSSION

My long-term analysis of experimental serpentine assemblages indicated that propagule pressure was the most important predictor of *C. solstitialis* success, except in the first year of my study. While this supports one of my primary hypotheses, the surprising absence of effects of community composition and pocket gopher activity on invasion in this study could reflect time-dependent effects of ecological resistance and disturbance (Hobbs and Mooney 1985, Levine et al. 2004). Because previous work on these plots found strong evidence of community composition and diversity affecting initial invader success (Hooper and Dukes 2010), my results suggest that (1) both complementarity and variation in dispersal rates contribute to community assembly, but they operate at different levels of community organization and/or temporal scales (e.g., Samuels and Drake 1997, Tilman 1997, 2004, Cadotte 2007); and (2) propagule pressure can overwhelm ecological resistance through time (Levine 2000, Von Holle and Simberloff 2005). These results indicate that differences in the duration of the invasion process and associated variation in dispersal rates among experimental and observational studies likely contribute to the invasion paradox (e.g., Fridley et al. 2007).

Based on previous work in this experimental system (e.g., Hooper and Dukes 2004, Gonzalez 2007, Habenicht 2015) and others (e.g., Dukes 2002, Fargione et al. 2003, Fargione and Tilman 2005), I predicted that *C. solstitialis* success would be inhibited by diversity (i.e., more efficient use of available resources) and enhanced by differences in resource use strategies (i.e., functional trait space). Indeed, when *C. solstitialis* was first experimentally introduced to these plots in 1999-2000, it was strongly suppressed by both diversity among and niche overlap with *a priori* functional groups (Hooper and Dukes 2010). After natural community assembly began, the functional compositions of the plots converged, commensurate with patterns of complementarity and limiting similarity (Habenicht 2015). This trend of functional convergence continued through at least 2007 (i.e., through the second year examined in this study), indicating persistent influence of complementarity and limiting similarity on community composition (Habenicht 2015). Why, then, did we not see an effect of either functional diversity or dissimilarity on invader success in this study?

Dispersal overcame ecological resistance

My results suggest that propagule pressure played a strong role in the declining effects of complementarity and limiting similarity on *C. solstitialis* abundance through time. Despite the simplifications necessary in my dispersal modeling process, propagule pressure, in the form of seed input per plot per year, was the most important predictor of invader success in all but the first year of my study (i.e., the fourth year of community assembly). Moreover, the effect of propagule pressure was apparently independent of pocket gopher disturbance (but see discussion of those results below). When *C. solstitialis* was first introduced to the plots, Hooper and Dukes (2010) carefully controlled seed input. As natural community assembly commenced, however, dispersal varied in association with the inherently high turnover of species in an annual grassland (Hobbs et al. 2007). The increasing influence of propagule pressure on *C. solstitialis* throughout the course of community assembly observed here supports two salient hypotheses in community and invasion ecology: (1) the relative importance of complementarity and dispersal rates depends on a) the duration of community assembly or invasion, and b) the level of community organization observed (e.g., Samuels and Drake 1997, Tilman 2004, Fukami et al. 2005, Cadotte 2007, Helsen et al. 2012); and (2) propagule pressure can overwhelm ecological resistance through time (e.g., Levine 2000, Von Holle and Simberloff 2005, Colautti et al. 2006).

First, former findings of complementarity at this site (Hooper and Dukes 2004, 2010, Habenicht 2015), combined with evidence of dispersal influencing invader success in this study, support the idea that these processes operate at different temporal scales (e.g., Leibold and McPeek 2006, Thompson and Townsend 2006, Adler et al. 2007, Cadotte 2007). Indeed, disparities in the duration of the invasion process observed by experimental and observational studies could explain the apparent reversal of the relationship between diversity and invader success described by the invasion paradox (see review by Fridley et al. 2007). Most experiments have found strong community resistance within the first two years of invasion (see review by Hector et al. 2001), capturing much different temporal extents than do observational studies, which have found consistent positive association between native and exotic species richness in areas with decades or even centuries of invasion (e.g., Planty-Tabacchi et al. 1996, Brown and Peet 2003, Stohlgren et al. 2003). By measuring the transition period between invader introduction and establishment, this study has the unique advantage of bridging the gap between experimental and observational studies. Moreover, this study supports previous results suggesting that the effect of complementarity on species (not functional—see below) composition declines through time (Inouye and Tilman 1995, Habenicht 2015). These results identify the need to consider temporal extent (i.e., not just spatial extent) as a factor influencing community determination of invader success.

Second, because complementarity shaped the functional composition of these plots through at least 2007 (Habenicht 2015), the success of *C. solstitialis* observed here supports the hypothesis that complementarity and dispersal operate at different levels of community organization. Multiple empirical studies (e.g., Gonzalez 2007, Helsen et al. 2012, Habenicht 2015) and simulation models (Tilman 2004, Gravel et al. 2006) suggest that complementarity and limiting similarity drive the functional compositions of communities, but variation in competitive fitness and dispersal shapes species identity within the available functional roles (Chesson 2000, Adler et al. 2007, Cadotte 2007, Gonzalez 2007). For example, nine years of natural assembly in initially manipulated experimental plots showed that functional compositions converged through time, following patterns commensurate with complementarity, but species compositions remained divergent (i.e., indicative of dispersal limitation and historical effects of experimental seeding) (Fukami et al. 2005). By the time my study began in 2004, functional convergence had already occurred to a large degree (Habenicht 2015). The subsequent reappearance of *C. solstitialis*, out of the pool of all potential late annual species, did not likely result from superior competitive fitness, because *C. solstitialis* abundance declined in the plots between 2001 and 2007 (Fig. 1). Instead, this study suggests that propagule pressure was the primary factor in the eventual success of *C. solstitialis*. Though the functional convergence observed by Habenicht (2015) contradicts the hypothesis by Kraft et al. (2015), that late annuals should competitively exclude early annuals, this study supports their hypothesis that outside forces, like dispersal, might contribute to coexistence at the local scale. These results corroborate previous findings for community assembly, and supply novel evidence that the effects of complementarity and dispersal on invader success depend on the level of community organization in combination with the duration of community assembly.

Finally, the increasing role of propagule pressure in this study indicates that dispersal can overwhelm ecological resistance through time. Several large reviews have demonstrated that propagule pressure outweighs the effects of other biotic and abiotic determinants of invader success across a wide range of taxa around the globe (Lockwood et al. 2005, Colautti et al. 2006, Simberloff 2009). Indeed, the consistency of dispersal patterns in predicting invader establishment and spread has led some researchers to suggest that propagule pressure should be a null model for invasion success (Colautti et al. 2006, Lockwood et al. 2013). Theory predicts that ecological resistance increases the number of propagules necessary for successful invasion (D'Antonio et al. 2001), but empirical evidence suggests that even strong effects of resistance cannot repel invaders completely (e.g., Levine 2000, Dukes 2001, Hooper and Dukes 2010; plus see reviews by D’Antonio et al. 2001, Levine et al. 2004). Multiple studies have found propagule pressure to implicitly or explicitly overwhelm abiotic or biotic resistance to invasion. For example, an observational study in California found that smaller patches of serpentine grassland were more heavily invaded by exotic plant species than were large, continuous outcrops, suggesting that high propagule supply from the surrounding area eventually overcame the harsh conditions of the serpentine soil (Harrison 1999). Similarly, two separate experiments that manipulated dispersal rates and community composition of riparian tussocks (Levine 2000) and riparian forest (Von Holle and Simberloff 2005) found that even strong local effects of diversity on invader success were overwhelmed by high propagule pressure. The results of this study support these findings, namely that continuous dispersal into the plots through time allowed *C.*

solstitialis to overcome initial resistance offered by complementarity and limiting similarity (Hooper and Dukes 2010). Future research should continue to integrate propagule pressure with facets of ecological resistance (e.g., community composition, disturbance) to understand when and why they interact to influence invader success (Britton-Simmons and Abbott 2008, Eschtruth and Battles 2009, Hufbauer et al. 2013, Duncan 2016, Vahsen et al. 2018).

Disturbance played a role?

Despite the lack of significant effects of pocket gopher activity in my results, I hesitate to conclusively say that disturbance by gophers did not facilitate the dispersal of *C. solstitialis* into the assemblages. Based on the temporal patterns of *C. solstitialis* and pocket gopher activity in the plots (Fig. 1), and the invader’s affinity for disturbed areas (Maddox et al. 1985, Hierro et al. 2006), the appearance of gopher disturbance between 2007 and 2012 is still a biologically plausible explanation for the resurgence of *C. solstitialis* seen when plots were resampled in 2012. Theory and empirical evidence suggest that by removing resident individuals and increasing resource availability, disturbance creates ‘niche opportunities’ for invaders to exploit in an otherwise resistant community (e.g., Davis et al. 2000, Shea and Chesson 2002, Hierro et al. 2006, Lembrechts et al. 2016, Pinto and Ortega 2016). In other words, periodic disturbance disrupts the competition-coexistence spectrum defined by complementarity and competitive ability (Tilman 1982, 1988, Chesson 2000), elevating the importance of dispersal variation among the competing species (Hobbs and Mooney 1991, Cadotte 2007).

If pocket gopher disturbance did indeed interact with propagule pressure to expedite the establishment of *C. solstitialis* in this study, I may have missed the signal for three reasons: (1) I missed the initial pulse of pocket gopher activity in the 2007-2012 hiatus in sampling; (2) I did not have estimates of the magnitude of gopher disturbance from the previous year; or (3) I did not have estimates of the timing of gopher disturbance from the previous year. With regard to the first point, a study involving marine sessile invertebrate communities found that disturbance facilitated invader establishment initially, but over time, it decreased invader abundance by removing invasive individuals at rates equal to natives (Clark and Johnston 2011). Thus, *C. solstitialis* may have increased in abundance when the initial onset of pocket gopher disturbance improved dispersal success, but the relationship declined once *C. solstitialis* became established in the plots. Second, a long-term study in the grassland surrounding our plots found that spatial location of gopher disturbance varied greatly from year to year (Hobbs and Mooney 1991). Thus, concurrent disturbance in the experimental assemblages may not have been representative of disturbance during the previous year (i.e., when seedling germination would have been most important). Finally, a study in the natural, serpentine grassland near the plots found that the response of annual species to gopher disturbance depended on when the disturbance occurred relative to the plants' reproductive seasons (Hobbs and Mooney 1985). Gopher disturbance that occurred early in the growing season freed up soil for early annual seeds to germinate, but late-season gopher activity buried the early seeds and increased resource availability for late annual seeds to germinate (Hobbs and Mooney 1985). In this study, mid-season gopher activity in 2011 (i.e., before *C. solstitialis* set seed) might explain the observed spike in *C. solstitialis* abundance in 2012. Moving forward, I hope that the issues encountered here might inform future studies investigating the interaction effects of dispersal and disturbance on long-term invasion trajectories and disruption of ecological resistance.

Some final caveats

A potential concern with the negative results of functional diversity and dissimilarity is that the suite of functional traits used in the analysis were irrelevant to invader success. Though all traits included in the metrics of functional diversity and dissimilarity were related to complementarity (Hooper and Vitousek 1997, 1998, Díaz et al. 2007), I did not take an iterative, statistical approach to determine the most parsimonious set of traits prior to analysis (e.g., Grime 1997, Bernhardt-Römermann et al. 2008). Failing to do so can potentially lead to spurious results, as previous studies have shown that including too many measures of functional strategies may obfuscate the effect of important traits within multivariate metrics (Bernhardt-Römermann et al. 2008, Pakeman 2011). However, I also ran my analyses using a smaller set of traits that aimed to capture variation in spatiotemporal resource use similar to the *a priori* phenological functional groups used in previous studies. Even with the more restricted set of traits, I still found no significant effects of composition or diversity on invader success (see Methods for details). The consistency of results among both sets of functional traits supports the conclusion that the absence of community composition and diversity effects on invader success resulted from the scale-dependence of those effects, not the obfuscation of important traits used in the metrics.

In addition to potential issues of composition metrics, I encountered a discrepancy between the large ranges of functional diversity and dissimilarity observed throughout this study and the continued functional convergence identified by Habenicht (2015). If the multivariate metrics used here captured the functional composition described in previous studies of this system (e.g., Hooper and Vitousek 1998, Gonzalez 2007, Habenicht 2015), I would have expected the ranges of functional diversity and dissimilarity to decline in association with the convergence of *a priori* functional group composition. Moreover, I would have expected functional dispersion at the beginning of community assembly (i.e., 2001) to differ strongly among plots containing primarily one *a priori* functional group and two functional groups, and among those with three and four functional groups. However, functional dispersion overlapped greatly among these *a priori* compositions (Fig. 5). These apparent inconsistencies cannot be explained by the inclusion of too many traits in the metrics of diversity and dissimilarity, as the ranges of metrics using the smaller set of traits revealed even more overlap of functional dispersion, and even higher values of functional dissimilarity in later years of assembly (data not shown).

What, then, might be driving these discrepancies? One potential answer is the large ranges in functional trait values observed within the *a priori* functional groups. Even among traits like vegetative height, which tended to increase gradually from early-season annuals to late annuals and mid-season perennials, there was substantial overlap of values among functional groups (Fig. S3). With large, within-group variation, two plots could have the same *a priori* functional group composition, with greatly different mean trait values, due to different relative abundances of species within those groups. In other words, the divergence in species (not functional) composition observed by Habenicht (2015) could explain the continued divergence of functional trait values observed here. Another potential answer is the differences in the type of community data analyzed by the two studies. Habenicht (2015) restricted her analyses to undisturbed portions of the plots, whereas I used species abundance data from the entire plots (i.e., disturbed and undisturbed areas). Because the extent of ant disturbance observed between

2003 and 2012 was quite large (up to 60% of the plot area; data not shown) and was covered almost exclusively by the invasive, early annual *Lolium multiflorum* (up to 95% relative abundance; data not shown), Habenicht (2015) and I likely had substantially different estimates of functional and species composition for some plots. An in-depth analysis of the exact species and traits contributing to these inconsistencies is necessary, but beyond the scope of this study.

Conclusions

This study contributes a unique, long-term analysis of invasion dynamics within a well-defined experimental system. In combination with previous work on these plots (Hooper and Dukes 2004, 2010, Habenicht 2015), these results suggest that both complementarity and variation in dispersal influence the timing and rate of invader success, but at different temporal scales and/or levels of community organization. While studies of primary succession suggest that stochastic dispersal events are more important at the onset of community assembly (i.e., priority effect: Ross and Harper 1972, Wilson 1988, Tilman 2004), the results of this study indicate that propagule pressure becomes relatively more important through time for species invading intact communities. These results suggest that continued propagule input can eventually overcome initial ecological resistance, potentially contributing to the shift in the diversity-invasibility relationship frequently observed when comparing experiments and observational studies (i.e., the invasion paradox: Fridley et al. 2007). The results of this study highlight the importance of considering community organization and temporal scale, and the perspective from which community assembly is viewed, when assessing factors influencing invasion success. Based on the importance of propagule pressure in explaining *C. solstitialis* abundance in this study, considering propagule supply as a prerequisite for invasion, and then evaluating the contribution of other biotic and abiotic factors, would likely improve predictive models of invader success (e.g., Colautti et al. 2006, Lockwood et al. 2013). Moreover, long-term experiments manipulating the variables modeled here (propagule pressure, community composition and diversity, and disturbance) in a factorial design would improve our understanding of when and why they interact to impact invasion. Land managers wishing to prevent exotic invasions may thus conserve and restore communities with diversity in mind, but understand that even initial ecological resistance can be overwhelmed by propagule supply, unless rates of introduction of nonnative propagules into areas of conservation concern are also reduced.

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Table S1. Functional trait values for species present in the experimental assemblages at any point between 2001 and 2017. Mean values for quantitative traits were calculated from data collected in this study or pulled from species summaries by Hooper DU (*unpublished data*), Mooney et al. (1986), Hickman et al. (1993), Fernandez-Going et al. (2012), or Spasojevic et al. (2012) (see Table 1). Abbreviations are as follows: phen = reproductive phenology, where E = early, M = mid, and L = late; life = life history, where A = annual and P = perennial; nitro = nitrogen-fixing capacity, where + = present and - = absent; RT = root type, where SD = shallow diffuse, SF = spreading fibrous, TR = taproot, and CO = corm; RD = maximum measured rooting depth (m); LDMC = leaf dry matter content (mg mg^{-1}); C:N = leaf carbon to nitrogen ratio; SLA = specific leaf area (mm^2 mg^{-1}); and height = vegetative height (m).

Species	Phen	Life	Nitro	RT	RD	LDMC	C:N	SLA	Height
Agoseris heterophylla	E	A	-	SD	0.05			42.15	0.10
Amsinckia menziesii	E	A	-						
Aphanes occidentalis	E	A	-						
Astragalus gambellianus	E	A	+	SD	0.08			26.65	0.16
Avena barbata	E	A	-	SD	0.08	0.24	34.84	29.46	0.37
Avena fatua	E	A	-						
Briza spp.	E	A	-						
Bromus diandrus	E	A	-						
Bromus hordeaceus	E	A	-	SD	0.06	0.26	66.15	29.56	0.16
Bromus madritensis ssp *rubens*	E	A	-	SD	0.06	0.29	32.73	30.96	0.18
Castilleja densiflora	E	A	-	SD	0.06	0.16		32.09	0.18
Claytonia perfoliata	E	A	-						
Crassula conata	E	A	-						
Cryptanthus spp.	E	A	-						
Cuscuta spp.	E	A	-						
Erodium spp.	E	A	-	SD	0.08				0.09
Euphorbia spp.	E	A	-	SD	0.08			66.7	0.17
Hesperevax sparsiflora	E	A	-	SD	0.10	0.15	20.57	61.26	0.04
Lasthenia californica	E	A	-	SD	0.04	0.22	16.26	21.5	0.07
Layia platyglossa	E	A	-	SD	0.13	0.12	20.12	26.04	0.17

Table S1, continued.

Species	Phen	Life	Nitro	RT	RD	LDMC	C:N	SLA	Height
Lepidium nitidum	E	A	-	SD	0.07	0.21	19.48	15.94	0.09
Lolium multiflorum	E	A	-	SD	0.09	0.22		38.25	0.23
Lotus subpinnatus	E	A	+	SD	0.06	0.13		23.74	0.14
Madia spp.	E	A	-						
Medicago polymorpha	E	A	+						
Melilotus spp.	E	A	+						
Microseris douglasii	E	A	-	SD	0.08	0.12	16.68	39.39	0.05
Oxalis oregana	E	A	-						
Plantago erecta	E	A	-	SD	0.05	0.21	28.87	21.02	0.09
Trifolium albopurpurea	E	A	+	SD	0.05				0.13
Trifolium microdon	E	A	+						
Trifolium tridentata	E	A	+						
Trifolium spp.	E	A	+						
Unknown early annual	E	A	-						
Uropappus lindleyi	E	A	-						
Vicia villosa	E	A	+	SD	0.14	0.17	12.67	32.40	0.30
Vulpia microstachys	E	A	-	SD	0.08	0.29	33.52	26.73	0.16
Vulpia myuros	E	A	-	SD	0.08	0.21	33.79	38.12	0.19
Allium sera	E	P	-						
Calystegia subacaulus	E	P	-	SD	0.10	0.13	9.85	21.29	0.13
Unknown corm	E	P	-						
Dichelostemma capitatum	E	P	-	CO	0.08	0.18	18.44	10.29	0.32
Eschscholzia californica	E	P	-	TR	0.31	0.16	10.57	20.42	0.32
Lomatium spp.	E	P	-						
Lupinus spp.	E	P	+						
Muilla maritima	E	P	-	CO	0.06	0.13		17.12	0.23

Table S1, continued.

Species	Phen	Life	Nitro	RT	RD	LDMC	C:N	SLA	Height
Sisyrinchium bellum	E	P	-	SF	0.26	0.24	19.03	15.38	0.37
Tritellia spp.	E	P	-						
Calycadenia multiglandulosa	L	A	-	TR	0.23	0.18		23.8	0.26
Centaurea solstitialis	L	A	-	TR	0.28	0.09	31.50	54.12	0.37
Epilobium brachycarpum	L	A	-	TR	0.26	0.16	15.71	23.63	0.24
Hemizonia congesta ssp. *lazulifolia*	L	A	-	TR	0.24	0.12	15.47	38.26	0.19
Lactuca saligna	L	A	-						
Lactuca seriola	L	A	-	TR	0.20	0.15	13.34	31.30	0.44
Lactuca virosa	L	A	-	TR	0.24			16.99	0.33
Lessingia micradenia	L	A	-	TR	0.25	0.16		41.11	0.35
Senecio vulgaris	L	A	-						
Sonchus oleraceus	L	A	-	TR					
Malacothrix spp.	M	A	-						
Achillea millefolium	M	P	-	SF	0.23	0.19	15.71	12.63	0.38
Chlorogallum pomeridianum	M	P	-						
Elymus multisetus	M	P	-	SF		0.30		20.72	0.54
Nassella pulchra	M	P	-	SF	0.43	0.35	37.16	16.23	0.28

Table S2. Proportion of time spent in each wind direction at speeds equal to or greater than 5 m/s in Morgan Hill, CA, during the period of maximum seed release by *C. solstitialis* (6:00AM to 8:00PM, July to October). Data were collected from 2001 to 2007 at the California Irrigation Management Information System station #132, managed by the State of California (California Irrigation Management Information System 2018). Values in bold were used to allocate seeds for dispersal modeling. Speeds observed less than 1% of the time were not included in estimates of dispersal.

Direction	5 m/s	6 m/s	Total
E	0.00	0.00	0.00
N	0.00	0.00	0.00
NE	0.00	0.00	0.00
NW	**0.50**	**0.19**	0.69
S	0.00	0.00	0.00
SE	**0.13**	0.00	0.13
SW	0.00	0.00	0.00
W	**0.13**	**0.06**	0.19
Total			1.00

Table S3. Shape selection for the response of *C. solstitialis* absolute abundance to original predictor variables (abbreviations and units as in Table 2). Model set contained the factorial combination of parameter shapes: linear for all variables, saturating for functional dispersion, propagule pressure, and gopher disturbance, and unimodal for gopher disturbance. No nonlinear shapes were tested for functional dissimilarity.

Year	n	Model	ΔAICc	R^2	w_i
2004	60	FDis + DFT + PP	0.00	0.14	0.80
		DFT + lnFDis + PP	3.41	0.15	0.15
		DFT + lnFDis + lnPP	5.71	0.14	0.05
2006	60	FDis + DFT + PP	0.00	0.18	0.87
		DFT + lnFDis + PP	4.26	0.18	0.10
		DFT + lnFDis + lnPP	7.56	0.17	0.02
2012	60	FDis + DFT + GD + GD^2 + PP + GDxPP + GD^2xPP	0.00	0.22	0.71
		FDis + DFT + lnGD + PP + lnGDxPP	3.38	0.20	0.13
		FDis + DFT + GD + PP + GDxPP	4.38	0.20	0.08
2017	30	FDis + DFT + GD + GD^2 + PP + GDxPP + GD^2xPP	0.00	0.34	0.61
		FDis + DFT + lnGD + PP + lnGDxPP	2.59	0.34	0.17
		FDis + DFT + GD + PP + GDxPP	3.22	0.34	0.12

Table S4. Selection of parameter shapes using exploratory metric of ant disturbance (AD, measured as proportion of plot disturbed). Model set consisted of the response of *C. solstitialis* absolute abundance to the factorial combination of variable shapes, as in Table S3 (abbreviations and units as in Table 2).

Year	n	Model	ΔAICc	R^2	w_i
2004	60	FDis + DFT + AD + AD^2 + PP + ADxPP + AD^2xPP	0.00	0.58	0.81
		lnFDis + DFT + AD + AD^2 + PP + ADxPP + AD^2xPP	2.91	0.59	0.19
		FDis + DFT + AD + AD^2 + lnPP + ADxlnPP + AD^2xlnPP	18.06	0.54	0.00
2006	60	FDis + DFT + lnAD + PP + lnADxPP	0.00	0.18	0.38
		FDis + DFT + AD + PP + ADxPP	0.67	0.18	0.27
		FDis + DFT + AD + AD^2 + PP + ADxPP + AD^2xPP	1.10	0.27	0.22
2012	60	FDis + DFT + AD + AD^2 + PP + ADxPP + AD^2xPP	0.00	0.20	0.92
		lnFDis + DFT + AD + AD^2 + PP + ADxPP + AD^2xPP	5.23	0.18	0.07
		FDis + DFT + lnAD + PP + lnADxPP	10.27	0.21	0.01
2017	30	FDis + DFT + PP	0.00	0.30	0.52
		FDis + DFT + lnPP	0.56	0.34	0.39
		lnFDis + DFT + PP	4.80	0.30	0.05

Table S5. Selection of parameter shapes using exploratory metric of cumulative ant and gopher disturbance (CD, measured as proportion of plot disturbed over all previous and concurrent years). Model set consisted of the response of *C. solstitialis* absolute abundance to the factorial combination of variable shapes, as in Table S3 (abbreviations and units as in Table 2).

Year	n	Model	ΔAICc	R^2	w_i
2004	60	FDis + DFT + CD + CD^2 + PP + CDxPP + CD^2xPP	0.00	0.74	0.88
		lnFDis + DFT + CD + CD^2 + PP + CDxPP + CD^2xPP	4.08	0.74	0.12
		FDis + DFT + CD + CD^2 + lnPP + CDxlnPP + CD^2xlnPP	18.92	0.71	0.00
2006	60	FDis + DFT + lnCD + PP + lnCDxPP	0.00	0.18	0.64
		FDis + DFT + CD + PP + CDxPP	2.01	0.18	0.24
		lnFDis + DFT + lnCD + PP + lnCDxPP	4.05	0.18	0.08
2012	60	FDis + DFT + lnCD + PP + lnCDxPP	0.00	0.21	0.71
		FDis + DFT + CD + PP + CDxPP	2.54	0.18	0.20
		lnFDis + DFT + lnCD + PP + lnCDxPP	5.27	0.21	0.05
2017	30	FDis + DFT + lnCD + PP + lnCDxPP	0.00	0.37	0.72
		FDis + DFT + CD + PP + CDxPP	2.96	0.36	0.16
		lnFDis + DFT + lnCD + PP + lnCDxPP	4.94	0.36	0.06

Table S6. Selection of parameter shapes using exploratory metric of cumulative propagule pressure (CPP, measured as total seed input per plot over all previous years). Model set consisted of the response of *C. solstitialis* absolute abundance to the factorial combination of variable shapes, as in Table S3 (abbreviations and units as in Table 2).

Year	n	Model	ΔAICc	R^2	w_i
2004	60	FDis + DFT + CPP	0.00	0.14	0.81
		lnFDis + DFT + CPP	3.41	0.15	0.15
		FDis + DFT + lnCPP	5.99	0.13	0.04
2006	60	FDis + DFT + CPP	0.00	0.18	0.86
		lnFDis + DFT + CPP	4.25	0.17	0.10
		FDis + DFT + lnCPP	6.79	0.14	0.03
2012	60	FDis + DFT + GD + GD^2 + CPP + GDxCPP + GD^2xCPP	0.00	0.21	0.67
		FDis + DFT + lnGD + CPP + lnGDxCPP	3.38	0.18	0.12
		FDis + DFT + GD + CPP + GDxCPP	4.38	0.18	0.08
2017	30	FDis + DFT + GD + GD^2 + CPP + GDxCPP + GD^2xCPP	0.00	0.21	0.51
		FDis + DFT + lnGD + CPP + lnGDxCPP	2.59	0.15	0.14
		FDis + DFT + GD + CPP + GDxCPP	3.22	0.15	0.10

Table S7. Top three models using exploratory metric of total cover (TC) of all other species (m^2 cover/m^2 ground) to explain *C. solstitialis* absolute abundance. Model set consisted of the factorial combination to total cover, gopher disturbance extent, and propagule pressure (abbreviations and units as in Table 2).

Year	n	Model	ΔAIC_c	w_i	R^2	K
2004	60	(Null)	0.00	0.49	0.00	3
		PP	1.16	0.28	0.02	4
		TC	2.36	0.15	0.00	4
2006	60	PP	0.00	0.50	0.16	4
		TC + PP	0.06	0.49	0.18	5
		(Null)	8.02	0.01	0.00	3
2012	60	TC + PP	0.00	0.49	0.16	5
		TC + GD + PP	2.29	0.15	0.16	6
		PP	2.47	0.14	0.09	4
2017	30	PP	0.00	0.41	0.26	4
		TC +PP	0.70	0.29	0.30	5
		GD + PP	2.41	0.12	0.26	5

Table S8. Model-averaged effects of exploratory metric of total cover and other original variables on *C. solstitialis* absolute abundance (abbreviations and units as in Tables 2, 3, S7). Variables in bold were significant at α = 0.05, and variables in italic were borderline significant at α = 0.10.

Year	Variable	Coefficient	SE	p-value	RI
2004	(Intercept)	0.001	0.002	0.494	-
	PP	1.81×10^{-6}	3.74×10^{-6}	0.632	0.36
	TC	1.64×10^{-4}	0.001	0.847	0.23
2006	(Intercept)	8.88×10^{-5}	0.003	0.973	-
	PP	**9.91×10^{-6}**	**3.15×10^{-6}**	**0.002**	**0.99**
	TC	0.001	0.002	0.480	0.49
2012	(Intercept)	0.090	0.096	0.356	-
	PP	*3.69×10^{-4}*	*2.01×10^{-4}*	*0.070*	*0.89*
	TC	-0.151	0.117	0.201	0.76
	GD	0.028	0.125	0.825	0.29
	GDxPP	-3.38×10^{-5}	3.33×10^{-4}	0.921	0.06
2017	(Intercept)	0.052	0.074	0.492	-
	PP	**1.48×10^{-4}**	**5.35×10^{-5}**	**0.007**	**0.96**
	TC	-0.057	0.095	0.558	0.39
	GD	0.001	0.073	0.986	0.26
	GDxPP	5.49×10^{-5}	2.72×10^{-4}	0.844	0.07

Table S9. Top three models using exploratory metric of ant disturbance to explain *C. solstitialis* absolute abundance. Model set consisted of the factorial combination of functional dispersion, functional dissimilarity, ant disturbance extent, and propagule pressure (abbreviations and units as in Tables 2, S4).

Year	n	Model	ΔAIC_c	w_i	R^2	K
2004	60	AD + PP + PPxAD	0.00	0.15	0.23	6
		FDis + DFT + AD	0.49	0.12	0.23	6
		DFT + AD	0.63	0.11	0.20	5
2006	60	PP	0.00	0.29	0.16	4
		FDis + PP	1.10	0.17	0.17	5
		DFT + PP	1.48	0.14	0.17	5
2012	60	FDis + PP	0.00	0.32	0.19	5
		FDis + DFT + PP	1.28	0.17	0.20	6
		FDis + PP + AD	1.42	0.16	0.20	6
2017	30	PP	0.00	0.43	0.26	4
		FDis + PP	0.76	0.29	0.29	5
		FDis + DFT + PP	2.77	0.11	0.30	6

Table S10. Model-averaged effects of exploratory metric of ant disturbance and other original variables on *C. solstitialis* absolute abundance (abbreviations and units as in Tables 2, 3, S4). Variables in bold were significant at $\alpha = 0.05$.

Year	Variable	Coefficient	SE	p-value	RI
2004	(Intercept)	-0.005	0.006	0.431	-
	FDis	-0.010	0.017	0.584	0.40
	DFT	0.034	0.038	0.373	0.60
	AD	0.013	0.028	0.636	0.98
	PP	3.68×10^{-6}	4.40×10^{-6}	0.410	0.66
	ADxPP	5.86×10^{-5}	9.69×10^{-5}	0.549	0.36
2006	(Intercept)	0.005	0.005	0.320	-
	FDis	-0.011	0.020	0.585	0.39
	DFT	-0.009	0.022	0.682	0.32
	AD	1.02×10^{-4}	0.005	0.985	0.28
	PP	**8.90×10^{-6}**	**4.07×10^{-6}**	**0.031**	**0.94**
	ADxPP	-4.60×10^{-7}	4.20×10^{-6}	0.914	0.06
2012	(Intercept)	-0.263	0.154	0.092	-
	FDis	0.847	0.569	0.141	0.82
	DFT	0.329	0.617	0.598	0.38
	AD	0.138	0.393	0.731	0.40
	PP	**4.61×10^{-4}**	**2.14×10^{-4}**	**0.033**	**0.94**
	ADxPP	4.04×10^{-5}	3.91×10^{-4}	0.919	0.08
2017	(Intercept)	0.004	0.039	0.917	-
	FDis	0.146	0.224	0.526	0.44
	DFT	-0.031	0.127	0.813	0.23
	PP	**1.41×10^{-4}**	**5.71×10^{-5}**	**0.017**	**0.94**

Table S11. Top three models using exploratory metric of cumulative ant and gopher disturbance to explain *C. solstitialis* absolute abundance. Model set consisted of the factorial combination of functional dispersion, functional dissimilarity, cumulative disturbance extent, and propagule pressure (abbreviations and units as in Tables 2, S5).

Year	n	Model	ΔAIC_c	w_i	R^2	K
2004	60	CD + PP + CDxPP	0.00	0.22	0.31	6
		DFT + CD + PP + CDxPP	0.67	0.16	0.32	7
		DFT + CD + PP	1.79	0.09	0.29	6
2006	60	PP	0.00	0.29	0.16	4
		FDis + PP	1.10	0.17	0.17	5
		DFT + PP	1.48	0.14	0.17	5
2012	60	FDis + PP	0.00	0.36	0.19	5
		FDis + DFT + PP	1.28	0.19	0.20	6
		FDis + CD + PP	2.17	0.12	0.19	6
2017	30	PP	0.00	0.25	0.26	4
		FDis + PP	0.76	0.17	0.29	5
		FDis + CD	2.03	0.09	0.26	5

Table S12. Model-averaged effects of exploratory metric of cumulative disturbance and other original variables on *C. solstitialis* absolute abundance (abbreviations and units as in Tables 2, 3, S5). Variables in bold were significant at $\alpha = 0.05$.

Year	Variable	Coefficient	SE	p-value	RI
2004	(Intercept)	-0.005	0.006	0.404	-
	FDis	-0.006	0.014	0.682	0.33
	DFT	0.029	0.035	0.405	0.57
	CD	0.006	0.014	0.683	1.00
	PP	4.12 x 10^{-6}	4.26 x 10^{-6}	0.341	0.77
	CDxPP	4.20 x 10^{-5}	4.83 x 10^{-5}	0.389	0.54
2006	(Intercept)	0.005	0.005	0.320	-
	FDis	-0.011	0.019	0.586	0.39
	DFT	-0.009	0.022	0.683	0.32
	CD	-9.90 x 10^{-5}	0.001	0.941	0.29
	PP	**9.00 x 10^{-6}**	**4.07 x 10^{-6}**	**0.029**	**0.94**
	CDxPP	-1.10 x 10^{-7}	9.58 x 10^{-7}	0.910	0.07
2012	(Intercept)	-0.272	0.151	0.077	-
	FDis	0.872	0.565	0.127	0.83
	DFT	0.329	0.627	0.604	0.38
	CD	-0.001	0.037	0.987	0.32
	PP	**4.85 x 10^{-4}**	**2.03 x 10^{-4}**	**0.019**	**0.96**
	CDxPP	1.61 x 10^{-5}	6.97 x 10^{-5}	0.819	0.10
2017	(Intercept)	-0.008	0.045	0.858	-
	FDis	0.228	0.294	0.447	0.52
	DFT	-0.031	0.125	0.810	0.22
	CD	0.016	0.028	0.588	0.42
	PP	1.33 x 10^{-4}	8.29 x 10^{-5}	0.116	0.84
	CDxPP	-9.83 x 10^{-6}	3.02 x 10^{-5}	0.749	0.13

Table S13. Top three models using exploratory metric of cumulative propagule pressure to explain *C. solstitialis* absolute abundance. Model set consisted of the factorial combination to functional dispersion, functional dissimilarity, gopher disturbance extent, and cumulative propagule pressure (abbreviations and units as in Tables 2, S6).

Year	n	Model	ΔAIC_c	w_i	R^2	K
2004	60	FDis + DFT	0.00	0.41	0.12	5
		FDis + DFT + PP	1.17	0.23	0.14	6
		FDis	2.48	0.12	0.05	4
2006	60	FDis + PP	0.00	0.39	0.17	5
		PP	0.81	0.26	0.13	4
		FDis + DFT + PP	1.77	0.16	0.18	6
2012	60	FDis + PP	0.00	0.20	0.15	5
		FDis + DFT + PP	0.00	0.20	0.18	6
		DFT + PP	0.53	0.15	0.14	5
2017	30	FDis	0.00	0.27	0.10	4
		(Null)	0.90	0.17	0.00	3
		PP	1.71	0.11	0.12	4

Table S14. Model-averaged effect of exploratory metric of cumulative propagule pressure and other original variables on *C. solstitialis* absolute abundance (abbreviations and units as in Tables 2, 3, S6). Variables in bold were significant at α = 0.05, and variables in italic were borderline significant at α = 0.10.

Year	Variable	Coefficient	SE	p-value	RI
2004	(Intercept)	-0.002	0.007	0.809	-
	FDis	-0.037	0.025	0.139	0.83
	DFT	0.049	0.044	0.275	0.69
	CPP	1.81×10^{-6}	3.65×10^{-6}	0.623	0.36
2006	(Intercept)	0.006	0.006	0.350	-
	FDis	-0.024	0.024	0.335	0.63
	DFT	-0.005	0.018	0.769	0.28
	CPP	*5.66×10^{-6}*	*2.94×10^{-6}*	*0.057*	*0.90*
2012	(Intercept)	-0.212	0.156	0.179	-
	FDis	0.533	0.533	0.322	0.65
	DFT	0.620	0.803	0.444	0.52
	GD	0.032	0.122	0.794	0.33
	CPP	**1.84×10^{-4}**	**8.99×10^{-5}**	**0.044**	**0.92**
	GDxCPP	7.87×10^{-6}	1.53×10^{-4}	0.960	0.07
2017	(Intercept)	0.020	0.046	0.671	-
	FDis	0.223	0.278	0.431	0.53
	DFT	-0.035	0.135	0.803	0.22
	GD	0.011	0.064	0.875	0.22
	CPP	2.01×10^{-5}	3.80×10^{-5}	0.602	0.30
	GDxCPP	2.09×10^{-7}	3.40×10^{-5}	0.995	0.01

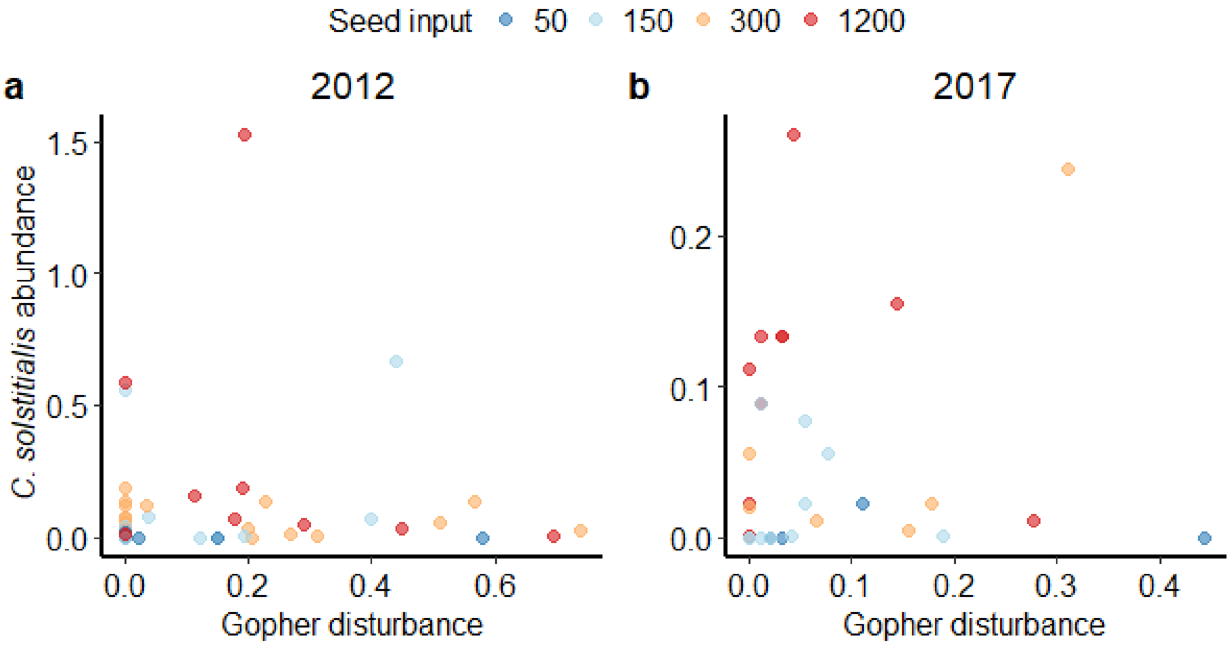

Figure S1. Interaction effect of gopher disturbance and propagule pressure on *C. solstitialis* abundance in (a) 2012 and (b) 2017 (variable units as in Fig. 4). Seed input values represent the median levels of propagule pressure for the 1st, 2nd, 3rd, and 4th quartiles across all years.

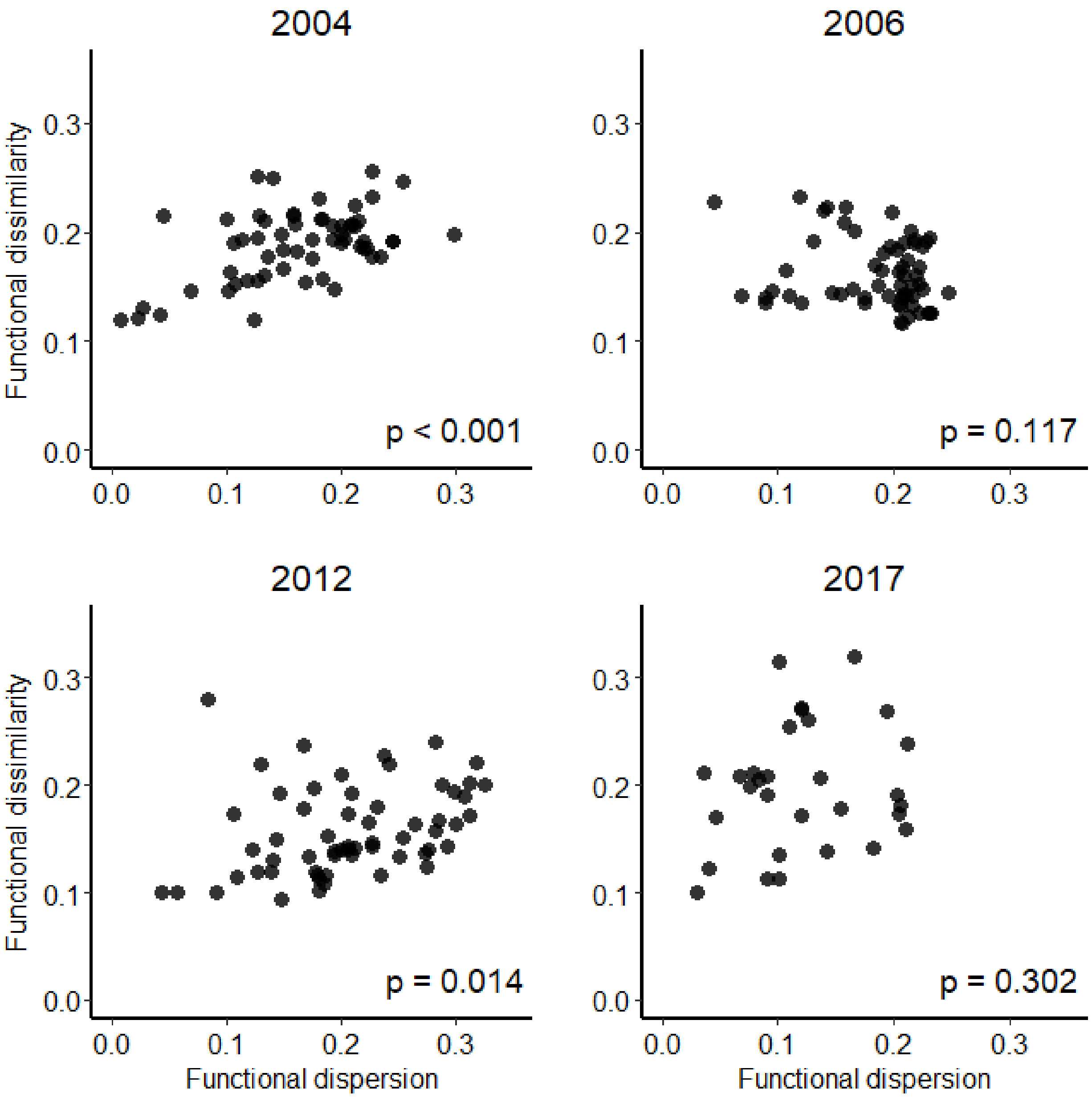

Figure S2. Correlations between functional dispersion and functional dissimilarity, by year.

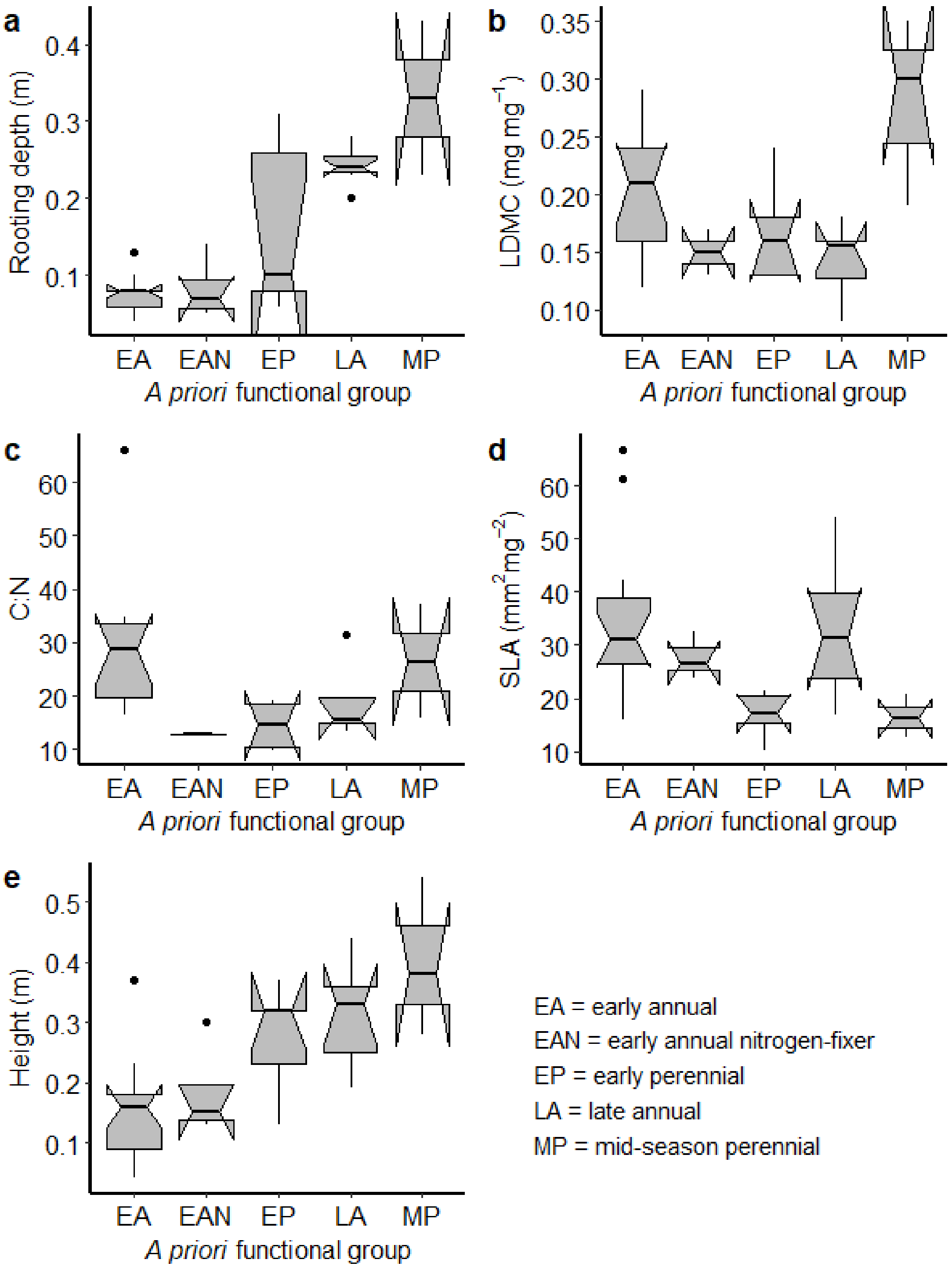

Figure S3. Range of quantitative functional trait values (abbreviations and definitions as in Table 1) within each *a priori* functional group (Hooper 1998, Hooper and Dukes 2004, Gonzalez 2007, Hooper and Dukes 2010, Habenicht 2015).