



The small-scale spatiotemporal pattern of the seedbank and vegetation of a highly invasive weed, *Centaurea solstitialis*: strength in numbers

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The dynamics of invasive plant populations are intriguing and informative of the importance of population and community-level processes. A dominant approach to understanding and describing invasion has been the development of unique hypotheses to explain invasion. However, here we directly explore the relevance of the small-scale, spatiotemporal pattern in seedbanks and plants of the highly invasive weed, *Centaurea solstitialis*, to determine whether pattern can be used to contrast predictions associated with the simple ecological hypotheses of seed versus microsite limitations. At three invaded grasslands in California, highly invaded (> 20 adult plants present), invaded (< 10 adults), and uninvaded (no *C. solstitialis* plants) sites were selected. The spatial pattern of the seedbank was assessed using fine-scale, 2 cm diameter contiguous cores and geostatistical statistics, and the number of *C. solstitialis* seeds in the seedbank was recorded in addition to the total community seedbank density. Three of the four critical predictions associated with the seed limitation hypothesis were clearly supported as an explanation for the patterns of *C. solstitialis* invasion observed in the field. The density of *C. solstitialis* seeds decreased from high to low extents of invasion, there was no relationship between the community seedbank and *C. solstitialis* seeds, and the distances between *C. solstitialis* plants was inversely related to the density of *C. solstitialis* seeds. However, both the persistent and transient seedbanks of *C. solstitialis* were spatially aggregated with autocorrelation up to 12 cm² which suggests that aggregation is a consistent attribute of this species in the seedbank regardless of extent of invasion. This basic pattern-based approach clearly detected an ecological signal of invasive seedbank dynamics and is thus a useful tool for subsequent studies of invasions in grasslands.

Invasion is both a process and a phenomenon. The dramatic success of some exotic species in becoming invasive, i.e. spreading widely or becoming numerically dominant in a new region, from a process perspective is described and tested primarily by the development of hypotheses specific to invasive species. The list of hypotheses is extensive including at least seven major theories proposed, tested to date, and reviewed to varying degrees (Mack et al. 2000, Rejmanek 2000, Sax and Brown 2000, Hierro et al. 2005). Admittedly, any of the proposed hypotheses explaining invasion are linked in some form to ecological principles or evolutionary explanations, yet it is tempting to invoke even more general, first-principle hypotheses to study invasion. For example, while enemy release or evolution of increased competitive ability both involve change following removal either 'naturally' or experimentally to explain the success of invasives (Blossey and Notzold 1995, Agrawal et al. 2005), the experimental methodology is explicitly linked to the absence of predators from the home range of the invasive species. It would be beneficial in many respects if an alternative, less specific, and proven approach to these types of hypothesis tests were available that

at the very minimum would rule out more parsimonious explanations. Many dominant ideas and approaches, albeit simple, in plant ecology have been modestly applied to 'native' species for numerous decades. It is reasonable to propose that in many respects the study of invasive species would benefit from the simplest of approaches used to understand and describe populations or communities such as the relevance of density and competition (Brown and Fridley 2003, Lortie et al. 2009), spatial pattern analysis (Silvertown et al. 1994, Fang 2005), indirect interactions (White et al. 2006), facilitation (Simberloff and Von Holle 1999, Sax et al. 2005), or revisiting community theory in general (Shea and Chesson 2002). That said, invasion as a phenomenon positively feeds back and informs ecology and evolution by challenging these direct, and sometimes simple, assumptions on what is community or what regulates a population (Callaway and Maron 2006). Nonetheless, here we use small-scale spatial analyses to explore and actively infer the process from the pattern for a highly successful invasive weed species.

Spatial pattern analysis is an extremely effective means to categorize the scale and pattern of population-level dynamics

(Tilman and Kareiva 1997). Arguably however, spatial pattern analysis if properly executed also has the capacity to speak directly to processes functioning within populations (Murrell et al. 2001, McIntire and Fajardo 2009). Furthermore, it has been proposed that, coupled with knowledge of a system, spatial pattern can be used more directly, even a priori, to predict patterns that can be parsimoniously explained by single processes (McIntire and Fajardo 2009) – provided the predictions are testable and specifically associated with each alternative. This is a compelling argument conceptually and a profound paradigm shift that elevates spatial pattern analysis from description to hypothesis testing. Whether the process of using spatial statistics is a priori as proposed for hypothesis testing (McIntire and Fajardo 2009) and sometimes empirically applied (Fajardo and McIntire 2007, Fang 2005) or posteriori as is more common (Fortin and Dale 2005), explicit spatial pattern analysis of invasive plants is rarely used as means to infer the dynamics associated with population level processes and invasion (Meirmans et al. 2003, Stohlgren et al. 2003, Fang 2005), particularly at the small scales relevant to plant–plant or seed–seed interactions such as the neighbourhood level (Garrett and Dixon 1998, Malkinson et al. 2003). This is an important opportunity to add a new/old tool to the study of invasion.

Seedbanks are a key component of understanding seed and plant interactions within grasslands (Harper 1977, Tilman 1993) for either native (Thompson 1987, Baskin and Baskin 1998) or introduced species (Tilman 1997, Brown and Fridley 2003). In a recent comprehensive review of studies on annual and perennial seeds, both were shown to use seedbanks as a mechanism to persist within grasslands (Thompson et al. 2003), the seed to plant transition has also been shown to be a significant and general limitation or filter in many systems (Turnbull et al. 2000, Caballero et al. 2008), and for invasive plants established within a community, it would be useful to ascertain whether local dynamics at the neighbourhood level are modified by seed or by microsite limitations. Furthermore, seedbanks are rarely studied at small-scales pertinent to the neighbourhood (Lortie and Turkington 2002). More directly, only three studies to date have successfully used spatial pattern analyses to contrast seed versus microsite limitation (Caballero et al. 2008, Fajardo and McIntire 2007, Stark et al. 2008) but not for invasive plant species.

In this study, we test the overarching hypothesis that seed versus microsite limitations can be contrasted for invasive weed species using appropriately structured seedbank and plant spatiotemporal analyses via gradients of invasion and transient versus persistent seedbank sampling (Fig. 1). The alternative general hypothesis is that invasion dynamics within a grassland are not linked to the seedbank. Seed limitation is generally conceptualized as absence or inadequate densities of seeds (Turnbull et al. 2000) often associated with an aggregated seedbank, i.e. patches and gaps (Dale 2000, Stark et al. 2008). Microsite limitation is best conceptualized as biotic or abiotic limitations that prevent seeds from persisting or establishing at a given site, i.e. heterogeneity in availability of appropriate microsites and not seed availability (Eriksson and Ehrlén 1992). To explore these hypotheses, the following predictions (visually depicted in Fig. 2 for clarification) are tested using the highly invasive weed, *Centaurea solstitialis*. The predictions are grouped into four categories, and the

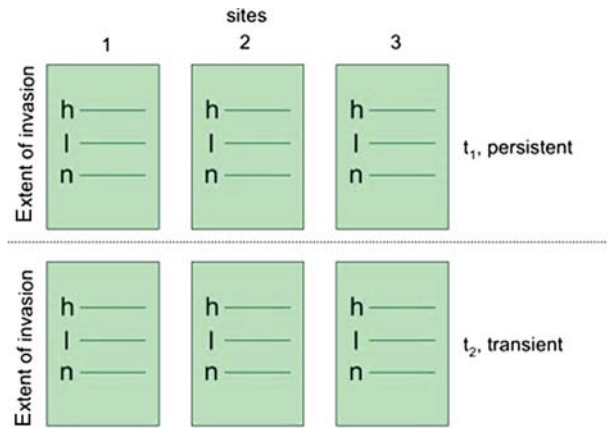


Figure 1. The sampling design for spatial surveys of *C. solstitialis* seedbank spatiotemporal dynamics. Site refers to independent grasslands sampled. Extent of invasion within each site refers to patches at least 500 m² in size that were either highly invaded (> 20 adult plants), invaded (< 10 plants), or uninvaded (no adult plants) within each grassland. The strata at each site was sampled twice to characterize the persistent and transient seedbanks. The letters, h, l, and n refer to the densities of *C. solstitialis* plants (high, low, and none), and the horizontal lines to the 400 m transects used to sample seedbanks and record the vegetation aboveground.

associated logic is provided after each pair in parallel, i.e. seed versus microsite. (1) Seed density: seed limitation predicts that *C. solstitialis* seed densities decrease with decreasing density of mature plants (i.e. extent of invasion); microsite limitation predicts no relationship between seed densities and the density of mature plants. The logic of the former prediction is that the availability of seed is associated with the density of plants depositing seeds to a system since more plants directly leads to more seeds present. The logic of the latter prediction is that even with high densities of seeds, i.e. availability is not limiting, it does not necessarily follow that there will be concurrent availability in appropriate microsites for these seeds to persist or establish since availability of seed need not map onto the availability of sites. (2) Spatial pattern: seed limitation predicts that *C. solstitialis* seed aggregation decreases with decreasing density of mature plants (i.e. extent of invasion); microsite limitation predicts no relationship between seed spatial pattern and plants. The logic of the former prediction is that the likelihood of sampling seeds increases with extent of invasion since more seeds are present thereby decreasing the likelihood of sampling gaps. More seeds and less gaps inflates the estimate of aggregation. The logic of the latter hypothesis is that seeds are universally aggregated or stationary. (3) Seed–seedbank: seed limitation predicts no relationship between *C. solstitialis* seed densities and the density of the local community seedbank; microsite limitation predicts that *C. solstitialis* seed densities decrease with increasing local seedbank density. The logic of the former prediction is that since availability of *C. solstitialis* seeds is the critical limitation there should be no relationship with the local community. The logic of the latter prediction is that biotic interactions between *C. solstitialis* and the local species is negative for at least two reasons. Seed–seed or plant seed interference prevails thereby directly limiting the density of *C. solstitialis* seeds present or available microsites are modified by the local community

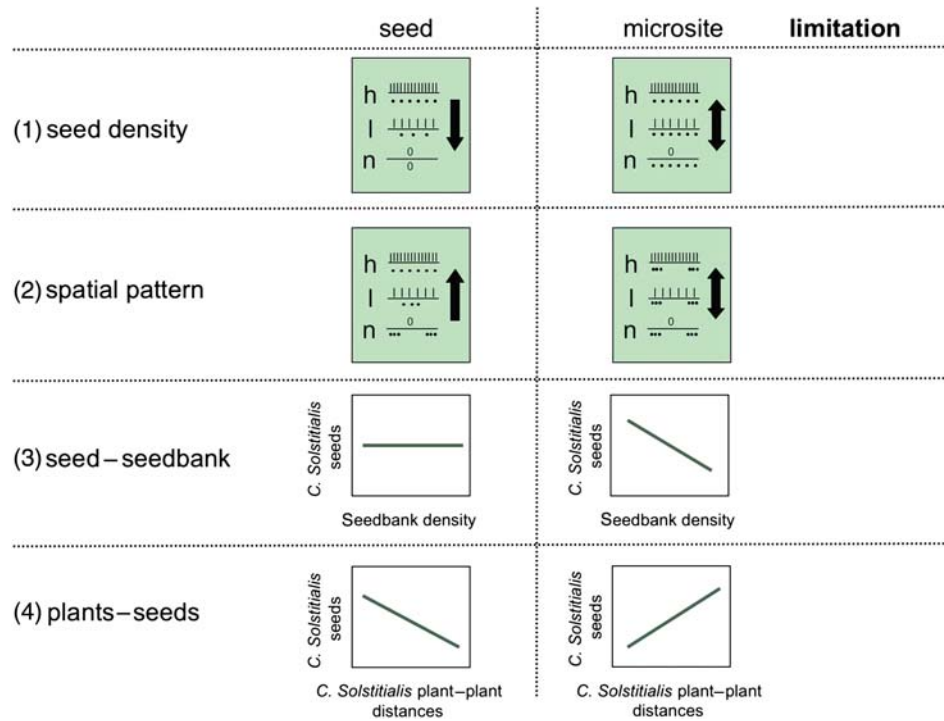


Figure 2. Predictions associated with the pattern analysis of *C. solstitialis* seedbank dynamics in the soil (see Introduction for predictions described).

which also reduces availability for *C. solstitialis*. (4) Plants-seeds: seed limitation predicts that *C. solstitialis* seed densities decrease with increasing distances between mature *C. solstitialis* plants; microsite limitation predicts that *C. solstitialis* seed densities increase with increasing distances between mature plants. The logic of the former prediction is that mature plants further apart generate more gaps without available seed.

The logic of the latter prediction is that mature *C. solstitialis* plants further apart produce more seeds since the capacity for interference is reduced as dispersion increases.

Methods

Study species

Centaurea solstitialis is a highly invasive weed in California grasslands (Maddox et al. 1985, Pitcairn et al. 1998). An individual plant can produce up to 85 000 seeds (Benefield et al. 2001), it is a seedbanking species (Joley et al. 2003), and seeds can persist in the soil for at least two years (Callihan et al. 1993, Benefield et al. 2001). Previous research has explored density of seeds (over 10 000 seeds per m² in the persistent seedbank) in the soil over time but these patterns have not been documented at small spatial scales (DiTomaso et al. 1999).

Experimental design

In 2007, three grasslands (without cattle present) no more than 2 km² in size were selected that were at least 1 km apart to sample the spatiotemporal patterns of *C. solstitialis* in Yolo County, California. At each grassland within this region invaded by *C. solstitialis*, three strata were identified corresponding to the extent of invasion within the site. For

instance, each grassland was invaded, yet there was heterogeneity in the abundance of plants present, and surprisingly there were even patches with no *C. solstitialis* adults present from previous years. To sample this gradient within a grassland, transects were placed in large areas that were either highly invaded (> 20 adult standing plants per 0.25 m² present from last season), invaded (< 10 plants), or uninvaded (no adult plants). If more than one representative area (per extent of invasion) was available within the grassland, the transect location was selected using a random number table.

Within each patch, a 400 m transect was centrally located, and contiguous 2 cm diameter cores, 5 cm deep were used to sample the soil seedbank. The distance from every fifth sampling point to the nearest *C. solstitialis* adult plant was recorded, and the distance from this plant to the next nearest *C. solstitialis* plant was recorded. A resolution of every fifth interval for plants (vs every interval for seeds) was selected since the plants are much larger than the seeds of this species, and this distance also ensured that distinct plants were sampled at each point. This entire sampling regime was repeated twice to characterize both the persistent and transient seedbanks. The persistent seedbank is the seeds that remain in the soil following the germination of that particular growing season (i.e. in California following the first winter rains, peak germination had completed by January), and the transient seedbank is the seeds that remained in the soil and also the new seed rain subsequently added by the end of that same growing season (by October 2007 all plants have flowered, produced seeds, and completed dispersal) (Thompson 1987, Baskin and Baskin 1998). All cores were weighed, seeds were separated from the soil using a series of sieves ranging in size from 2000 µm to 500 µm as this is a highly effective extraction method for small seeds (Baskin and Baskin 1998, Goldberg et al. 2001), and total seed mass

was recorded. Mass of the general community seedbank was used for analyses since it was not possible to differentiate and separate individual seeds from the remainder of the seedbank, but *C. solstitialis* seeds were individually extracted from the seedbank, visually inspected, counted and weighed.

Statistics

A generalised linear model (GLM) was used to test for differences in the seed density of *C. solstitialis* by census, extent of invasion within sites, mass of the community seedbank, and plant-plant distances between adults of *C. solstitialis*. A priori interaction effects were also included in the model (primarily interactions with census, i.e. transient versus persistent seedbanks) and census was modeled as a random, independent effect while extent of invasion was treated as a fixed effect. A mixed effect GLM was used to test for differences in the number of *C. solstitialis* seeds using a log link function for a Poisson probability model (Sokal and Rohlf 2003). Conservatively, transect was considered the smallest scale of appropriate sampling for these broad comparisons and not every individual point within a transect ($n = 18$ transects vs 4000 cores, respectively). Regression analyses were subsequently used to explore the shape or sign of relationships both at the transect and within transect scales (Underwood 1997).

To characterize seed spatial patterns, a geostatistical technique was used. Semivariograms provide a means to graphically assess both the intensity and scale of spatial pattern of contiguously sampled point processes (Rossi et al. 1992, Robertson and Augspurger 1999, Fajardo et al. 2008). The variation associated with resampling points adjacent to one another iteratively is plotted for increasing distance classes, and the attributes of these plots are used to infer degree and scale of spatial autocorrelation within the data (Dale 1999, 2000). The following elements are described for the best fit model semivariogram: the lag which is the distance between the samples, the nugget which is the y-intercept, the sill which is the asymptote, and the range which is the scale of the autocorrelation or patch size depending on the semivariance model fit (Lortie and Turkington 2002). Semivariograms can be calculated for the entire length of the samples collected; however conservatively, the maximum scale of resolution is approximately half the total number of samples pooled per transect (and in this study we set active distance to 125 lags) (Journel and Huijbregts 1978). There was no anisotropy in the data, and the best objective fit was selected as the instance that minimized the residual sum of squares (Aubry and Debouzie 2001). In addition to the scale of spatial patterns, the intensity of aggregation is calculated as dependence ((nugget – sill)/sill) and generally values less than 50% are considered weakly aggregated (Rossi et al. 1992). Geostatistical analyses were done with the application G+ ver. 9 (Gammadesign 2008) and all other statistics with JMP 7.02 (SAS 2007).

Results

Prediction 1. Differences in *C. solstitialis* seed densities

Both the persistent and transient seedbank densities of *C. solstitialis* decreased with decreasing extent of invasion

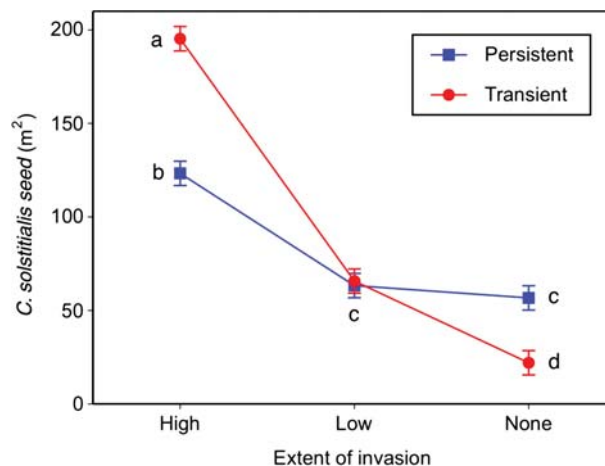


Figure 3. The density of the *C. solstitialis* seedbanks present in the soil at two census intervals (persistent – prior to germination and transient – following seed production and seed rain at the end of the growing season) by extent of invasion within grasslands. The extent of invasion refers to the sampling of large patches within each site wherein adult densities of *C. solstitialis* plants varied from the previous season. The mean \pm 1 SE is shown. Different letters denote significant post hoc contrasts at $p < 0.05$.

(Fig. 3, Table 1). The relative differences were greater in the transient seed densities of *C. solstitialis* sampled, and the transient seedbank of *C. solstitialis* was significantly larger particularly at the highest extent of invasion (Fig. 3, Table 1, census \times extent with post hoc contrast of highly invaded to other extents, alpha at $p < 0.05$). Interestingly, the lowest densities recorded were however in the transient seedbank at uninvaded patches.

Prediction 2. Spatial pattern of *C. solstitialis* seedbank

The seedbank of *C. solstitialis* is aggregated in the soil with the semivariograms accurately describing the spatial pattern in 12 of the 18 instances tested (Fig. 4, Table 2, spatial dependence values $> 50\%$). The scale of spatial

Table 1. A summary of the generalized linear model used to test for broad differences in the density of *C. solstitialis* seeds in the seedbank by important factors and appropriate contrasts identified *a priori*. The smallest appropriate sample unit defined for these analyses was conservatively set at the scale of transect and not the extensive sampling done within each transect (therefore $n = 18$). Census is modeled as a random, independent effect and sampled the persistent and transient seedbanks. Extent of invasion was ordinal and fixed from high to low to none describing the abundance classes of *C. solstitialis* adult plants present at each site sampled. Seedbank density is the total mass of the inclusive community of seeds present, and plant-plant distances describes the mean distances between *C. solstitialis* adult plants. The DF was 1,4 for each factor. Bold numbers denote significance at $p < 0.05$.

Factor	χ^2	Prob $> \chi^2$
Census	8.5	0.003
Extent of invasion	137	0.0001
Seedbank density	0.42	0.52
Plant-plant distances	0.93	0.33
Census \times extent	31.9	0.0001
Census \times seedbank density	0.94	0.33
Census \times plant-plant distances	10.1	0.0015

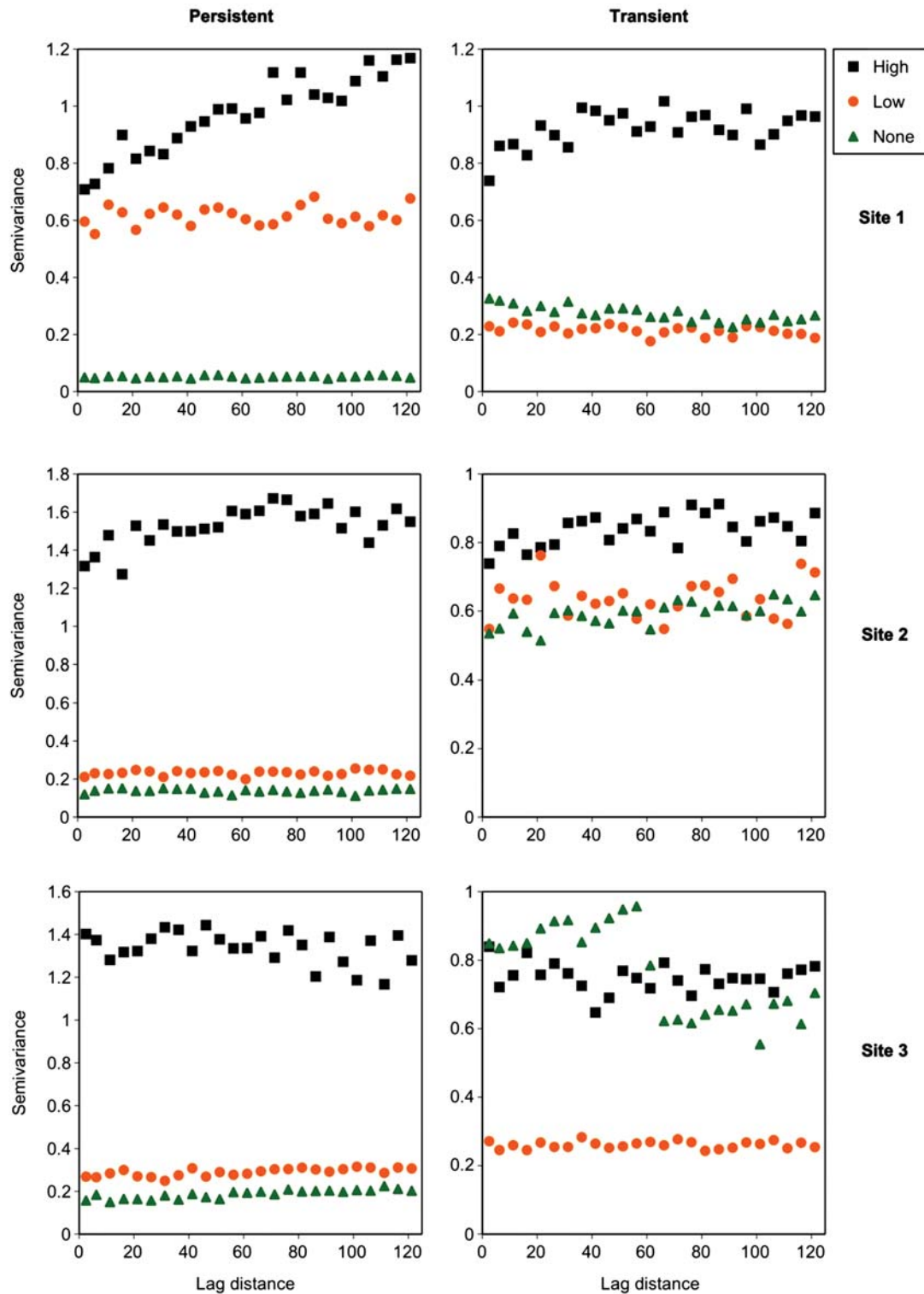


Figure 4. A fine-scale spatial pattern analysis of the seedbank of the invasive plant species *C. solstitialis*. Seedbank cores were collected contiguously on transects. Each plot is a semivariogram for the variance associated with resampling various lag distances along each transect (see text for description). The extent of invasion refers to large patches sampled within sites with various density classes of adult *C. solstitialis* plants present including high, low, and none denoted by the letters h, l, and n respectively. Three sites were sampled and two censuses were used to assess the persistent and transient seedbanks.

autocorrelation was up to and including 3.7 lags or approximately 12 cm² in one instance (number of lags by surface area of core), but *C. solstitialis* seeds were more frequently aggregated at even finer scales nearer 1.5 lags

or approximately 4.5 cm² (Table 1, range values associated with a significant fit). There were no consistent differences in the scale nor intensity of spatial patterns between the persistent and transient censuses nor between

Table 2. The model parameters for the fitted semivariograms describing the spatial dependence of the *C. solstitialis* seedbank. Site refers to independent grasslands sampled, persistent and transient to the census corresponding with each seedbank present in the soil at those sites at that time, and high, low, and none to the extent of invasion of *C. solstitialis* as estimated by density of plants from previous season. The best fit model was selected based on percent variance explained and parameters are explained in detail in the text. However, range is the number of lags, i.e. cores at which spatial dependence ends. Models successful fit included linear, exponential (exp.), and spherical (sph.).

Site	Census	Extent	Model	Nugget	Sill	Range	Dependence
1	persistent	high	exp.	0.72	1.44	130	50%
	persistent	low	exp.	0.019	0.62	0.8	97%
	persistent	none	exp.	0.006	0.05	0.8	89%
	transient	high	exp.	0.03	0.93	1.7	97%
	transient	low	linear	0.21	0.21	121	0%
	transient	none	linear	0.28	0.28	121	0%
2	persistent	high	exp.	0.26	1.54	1.6	83%
	persistent	low	sph.	0.02	0.23	3.4	93%
	persistent	none	linear	0.03	0.14	1.9	81%
	transient	high	exp.	0.13	0.84	1.3	85%
	transient	low	sph.	0.001	0.64	3.7	99%
	transient	none	exp.	0.07	0.60	1.2	88%
3	persistent	high	linear	1.33	1.33	121	0%
	persistent	low	exp.	0.05	0.29	1.1	85%
	persistent	none	exp.	0.05	0.19	1.7	77%
	transient	high	linear	0.75	0.75	121	0%
	transient	low	exp.	0.04	0.26	0.1	85%
	transient	none	linear	0.77	0.77	121	0%

the extents of invasion with aggregation being a consistent feature of the *C. solstitialis* seedbank (Fig. 4). Generally, the spatial dependence of the semivariograms was high (Table 1, dependence greater than 80% in 10 instances), and the highly invaded patches had larger estimates of semivariance (Fig. 4). For instance, these patches were described by semivariograms with higher levels of variance (Fig. 4 asymptotes, Table 1 larger sills in 5 of the 6 instances) and larger estimates of the sampling error (Fig. 4 y-intercepts, Table 1 nugget of highly invaded > other extents in 4 of 6 instances).

Prediction 3. Relationship between community seedbank and *C. solstitialis* seeds

There was no significant relationship between the density of the community seedbank and that of *C. solstitialis* (Fig. 5, Table 1). This likely independence was consistent for both seedbanks assayed, i.e. persistent and transient, and across all extents of invasion tested (Table 1, census × seedbank density n.s.).

Prediction 4. Importance of *C. solstitialis* plant–plant distances

The mean distance between the nearest *C. solstitialis* plants to the seedbank core collected significantly predicted the density of *C. solstitialis* seeds in the soil in the transient seedbank but not in the persistent seedbank (Fig. 6, Table 1, census × plant–plant distances). The actual distance of the *C. solstitialis* plants from the core was also tested for each census and was not significant (GLM, χ^2 -square = 0.009, $p = 0.92$).

Discussion

Invasive plant species have the capacity to inform population and community ecology at large through tests of specific sets

of potential explanations (Callaway and Maron 2006). However, hypotheses exploring invasive plant species are often tested independently from one another, and arguably (but justifiably) sometimes the link to basic plant ecology is left for the reader to infer. Here, this theme is explored via the application of pattern analysis to contrast four specific predictions associated with the general ecological hypotheses of seed versus microsite limitations. The seed limitation hypothesis (Turnbull et al. 2000) was clearly supported as an explanation for the patterns observed in the field for the invasive plant species *C. solstitialis*. The seed densities of *C. solstitialis* decreased concomitantly with extent of invasion which indicates that *C. solstitialis* seeds are not universally present or stationary within invaded regions. Simply put, more plants lead to more seeds with no evidence for biotic interactions through interference (Lortie et al. 2004). The *C. solstitialis* seedbank was unrelated to the density of the community seedbank which also fails to provide evidence for potential negative interactions or microsite limitations imposed by the greater plant community at the seedbank level (Eriksson and Ehrlén 1992). Lastly, decreasing the nearest neighbour distances between *C. solstitialis* adult plants increased the density of *C. solstitialis* seeds present in the transient seedbank which further suggests that there was no microsite effects via intra-specific interference between *C. solstitialis* plants as estimated by natural seed rain into the seedbank. The persistent and transient seedbanks of this invasive plant species in California grasslands were however consistently aggregated in the soil which suggests that seed limitation is not necessarily manifested through changes in the patch-gap dynamics (Dale et al. 2002) associated with extent of invasion. Importantly, the use of spatial pattern analyses herein with explicit and multiple predictions places this set of techniques on a comparable playing field with manipulative studies of invasive plant species. Furthermore, this study provides a tangible means to directly characterize invasion by plant species in grasslands and includes an estimate of the plant–seed dynamics and recruitment processes.

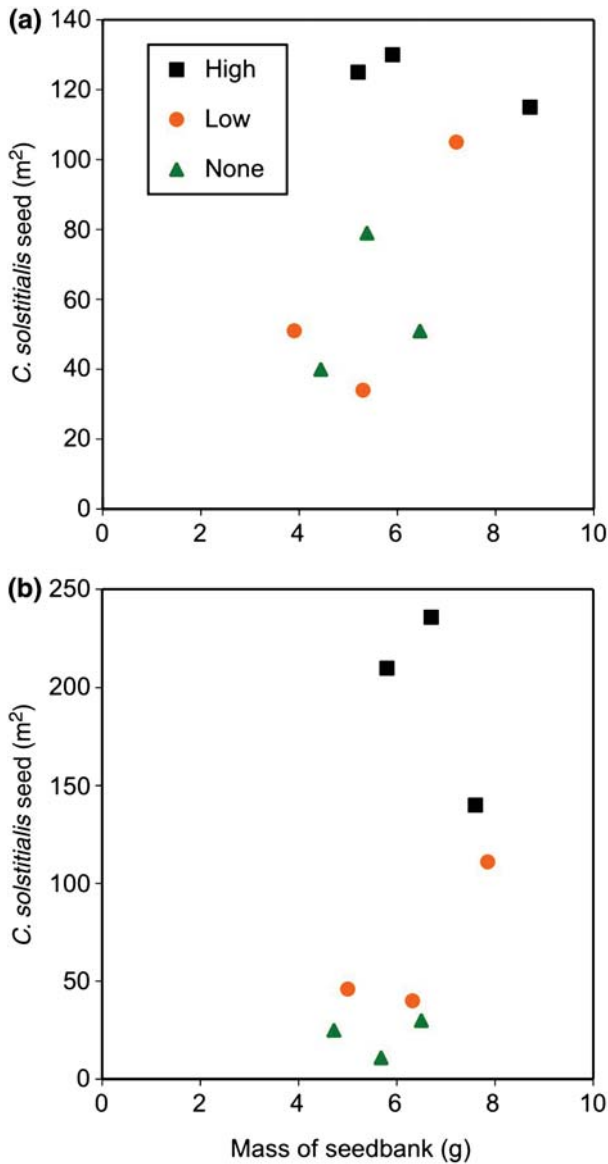


Figure 5. The density of the *C. solstitialis* seedbanks at two census intervals, (a) persistent and (b) transient, by the mass of the general community seedbank (less *C. solstitialis* seeds). The grand mean per transect for each site for each extent of invasion class of *C. solstitialis* is plotted. A GLM with subsequent regression analyses were done on the entire set of samples to assess whether community seedbank estimates predicted representation of *C. solstitialis* in the seedbank (and there were no significant trends), and as such, for simplicity grand means are plotted for each transect.

Pattern-based analyses do have the capacity to speak to process provided more than one statistical test is applied to explore the pattern data (Dale et al. 2002) and more than one hypothesis is proposed a priori to explain potential patterns (Fajardo and McIntire 2007). This is an extremely attractive and intuitive approach to using ecological patterns since it is akin to the approaches and assumptions associated with well-designed manipulative experiments. Both concepts were integrated into this study to contrast the importance of seed versus microsite limitations in establishment. A limited number of studies have successfully applied this set of spatial

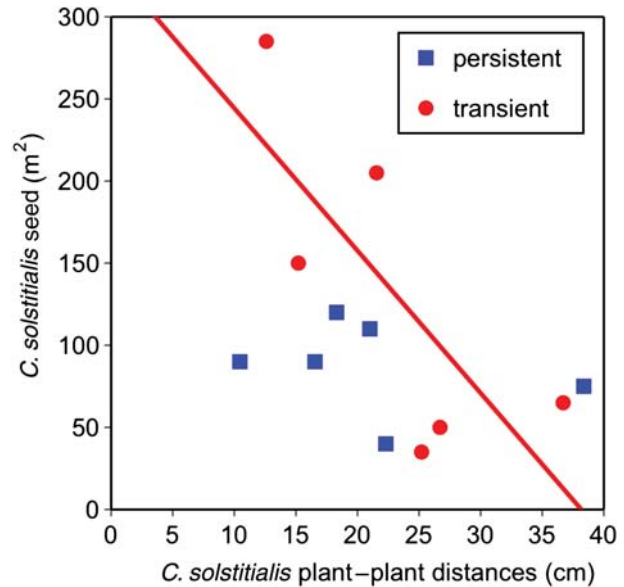


Figure 6. The relationship between the mean distance between adult plants of *C. solstitialis* and the number of *C. solstitialis* seeds in the seedbank. The grand mean per transect for each site for each census (persistent and transient seedbanks) is plotted. A GLM with subsequent regression analyses were done to assess whether distances between plants (as an estimate of interactions) influenced number of seeds in the soil. A significant relationship is shown with a fitted curve for the transient seedbank census ($r^2 = 0.57$, $p = 0.05$).

concepts to test the seed limitation hypothesis. Caballero et al. (2008) used explicit spatial pattern analyses to assess structure in the seedbank and vegetation over time to explore the transition from seed to plants in both annuals and perennials. This spatiotemporal design detected consistent differences between the persistent and transient seedbank with the transient seedbank expressing a stronger signal of spatial aggregation, greater seed densities, and relatively greater importance for the annual plants, i.e. seed limitation (Caballero et al. 2008). Here, the plant species studied *C. solstitialis* is an annual, and we similarly detected higher seed densities in the transient seedbank at the highest densities of plants. There was also the signal of temporal persistence in the seedbank for this species via relatively higher densities of persistent seed relative to the transient seedbank in patches without adult plants. Hence, the seed limitation hypothesis applies to this invasive annual plant species as changes in the extent of invasion relate to the presence of seedbank but unfortunately persistence through time is highly likely by resident seed throughout an invaded region including currently uninvaded local patches.

Two other studies have used a similar conceptual approach to explore seed limitation and scale. Firstly, Stark et al. (2008) used coarse and fine-scale spatial analyses appropriately structured to explore the process of disturbance on tree seedbank composition, and secondly, Fajardo and McIntire (2007) used semivariograms on the growth rate of trees to contrast biotic versus abiotic limitations over time in structuring the population. In both instances, contrasting the patterns detected by scale and time clearly characterized the processes associated with the population dynamics. In the former instance, the scale of sampling detected differences in

the relative importance of the type of disturbance, i.e. disturbance by logging had a homogenizing effect on seedbank composition at coarse scales but fire had an effect at smaller spatial scales (Stark et al. 2008). In the latter instance using tree ages, spatial pattern analyses identified seed limitation as an important process in early stand development stages, and with increasing stand development, the importance of competition as a filter increased (Fajardo and McIntire 2007). Taken together, these studies clearly demonstrated that intensive sampling over time is required to effectively link pattern analyses to processes. Here, while the transient and persistent seedbank expressed similar patterns, a negative relationship between *C. solstitialis* plant–plant distances and seed densities was only evident in the transient seedbank. However, the absence of a relationship between plant distances and seed densities in the persistent seedbank parallels these two studies in trees in that limitations need not function at every demographic transition identically nor similarly at every scale. In this study, plant–plant distances predicted the density of the transient seedbank but not the persistent. Over time, the tight spatial structure between vegetation and seeds evident immediately after seed deposition began to drift and decouple. The highly spatially dependent nature of the *C. solstitialis* seedbank, aggregated, certainly introduced a long term storage effect (Chesson and Huntly 1997, Chesson 2000) or residency to the patterns. Nonetheless, the variability in aggregation increased with increasing densities. Hence, seed limitation in invasive plant species is likely important but dependent on spatial scale and time. Importantly, seed and microsite limitations need not function in isolation. It is possible that appropriately structured sampling along such gradients could reveal that in some invasive species the local context determines which set of limitations prevail. Hence, effective sampling must be both intensive and include transient and persistent seedbank estimates, particularly in grasslands, since the dynamics have the capacity to shift over time (Stohlgren et al. 2008) and management of invasives will be most successful if targeted to the highly local scales.

Despite its apparent utility, only a handful of studies have used spatial pattern analyses to explore the importance of ecological drivers on invasive plant species. Studies include tests at different levels of organization such as the spatial correspondence of invasives with patterns of diversity at multiple, larger scales (Stohlgren et al. 2003), identification of the spatial genetic structure of an invasive weed species (Meirmans et al. 2003), and more recently, the use of spatial statistics by age class to determine the rate and extent of invasion in long-lived tree species (Fang 2005). No studies to date however have explored the fine-scale seedbank dynamics of invasive plant species. Unfortunately, seedbanks in general have also not been extensively studied at fine scales (Lortie and Turkington 2002) in spite of the fact that most plant and seed interactions occur at very local scales in grasslands (Turkington and Harper 1979, Garrett and Dixon 1998, Malkinson et al. 2003). Support for the seed limitation hypothesis here suggests that there is no intra-specific interference on seed production in the field. This corresponds with previous manipulative research on *C. solstitialis* wherein all performance measures recorded in intra-specific density series including germination, survival, and relative growth rate were

independent of seed density in California (Lortie et al. 2009). Importantly, the independence of this invasive plant species to increasing density evident in the field and greenhouse may also be compounded in that seeds are highly aggregated in the seedbank and apparently this does not come a cost to *C. solstitialis*. Furthermore, *C. solstitialis* may also be able to assess risk experienced at early developmental stages and rapidly adapt through changes in its germination strategy (Hierro et al. 2009). High densities at small spatial scales with strong spatial dependence and variability may provide the ideal opportunity for *C. solstitialis* to rapidly adapt in California to changing conditions. Even under the most parsimonious interpretation of these a priori tests of alternatives, this study clearly illustrates that invasion dynamics in grasslands can be characterized using pattern detection and that at least for this invasive plant species, there is strength in numbers of seeds.

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