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Seed demographic comparisons reveal spatial and temporal niche differentiation between native and invasive species in a community of desert winter annual plants

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ABSTRACT

Question: What is the evidence for spatial and temporal niche differentiation to stabilize co-existence between invasive and native species over broad environmental conditions?

Hypothesis: Two key elements for stable co-existence via environmental niche differentiation – species-specific responses to the environment and buffered population growth – are present in an invaded plant community when the seed demography of these plants is compared over time and space.

Organisms: A community of invasive and native winter annual plants in the Sonoran Desert.

Field site: A complex landscape in the Mohawk Valley in southwestern Arizona.

Methods: We surveyed ~180 plant neighbourhood clusters and sampled the adjacent seed bank for three years over three types of habitat to obtain data on germination and seed survival. We used the data to determine both species-specific germination responses to the varying environment and buffered population growth through seed banking. We also conducted a growth-chamber experiment to assess the influence of temperature and light availability on species-specific germination responses.

Conclusions: The findings supported our hypothesis. Species-specific germination responses were observed for both spatial and temporal environmental variation in the field. Germination responses were differentiated for both temperature and light in growth chambers. The native species and one of the invasive species had persistent seed banks, an outcome of low germination and high seed survival, which strengthened their buffered population growth over time. The other invasive species had a weak seed bank in two habitats but a stronger one in the third habitat, and thus relied on spatial population structure to buffer population growth.

Keywords: *Brassica tournefortii*, desert winter annual plants, invasive species, niche differentiation, species co-existence, storage effect.

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INTRODUCTION

The potential loss of biodiversity due to biological invasions is a serious concern. Although extinctions of native species due to competition with invasive species are thus far rare (Sax and Gaines, 2008), invasive species commonly reduce local native diversity and increase the local rarity of native species, raising the potential for long-term native extinctions owing to a gradual process of competitive exclusion (Gilbert and Levine, 2013). Alternatively, mechanisms may exist that allow long-term co-existence of invasive and native species (Shea and Chesson, 2002; Melbourne *et al.*, 2007).

Whether or not species can co-exist, according to current understanding (Chesson, 2000a), involves the net outcome of average fitness differences between species and stabilizing co-existence mechanisms arising from niche differentiation. Higher average fitness promotes dominance, but stabilizing co-existence mechanisms can prevent exclusion of species of lower average fitness. Invasive species with large competitive effects on native species are often thought to be generalists that possess a competitive advantage under a broad range of limiting resources, natural enemies or physical environments (Shea and Chesson, 2002; MacDougall *et al.*, 2009). As a result, not only do such species have higher average fitness, they may also have greater niche overlap with native species that may have more specialized adaptations, weakening stabilizing mechanisms. Under such circumstances, the likely outcome is domination of average-fitness differences over stabilizing mechanisms and the exclusion of native species.

However, while such conditions might prevail on local spatial scales, a community including invasive species may often be spread over a large area. Moreover, given the observation that exclusion of native species is not rapid, it is essential to consider co-existence on long temporal scales. Due to the longer evolutionary history of native species with the broad-scale heterogeneous native environment, they may have unique fitness advantages under certain environmental conditions compared with invasive species (e.g. Kestrup and Ricciardi, 2009). These unique advantages under specific conditions amount to spatial and temporal niche differentiation via the varying environment. This spatial and temporal niche differentiation has the potential to become stabilizing mechanisms that offset any average-fitness disadvantages of native species. Moreover, these unique advantages suggest also that the average-fitness disadvantages of native species are less when the full range of conditions that a community experiences are taken into consideration.

These considerations mean that simply focusing on situations where the invasive species is having a large impact can be misleading in the wider context of the full variable environment experienced by the community. Moreover, it has recently been argued that niche differentiation along the axis of the variable physical environment on large spatial scales most likely explains the high number of species that co-exist in nature (Hart *et al.*, 2017). Assessing these ideas requires broad spatial and temporal scales to compare demographic rates such as individual growth and survival between invasive and native species under the wide range of environments in which they interact. Unfortunately, few studies of invasions have thoroughly examined demographic processes (Gurevitch *et al.*, 2011), let alone on broad scales.

We studied an invaded community of desert winter annual plants over a three-year period in a complex landscape. We measured key demographic rates between species, and studied their variation in time and space. Our goal was to assess the evidence for spatial and temporal niche differentiation to stabilize co-existence in this invaded community. We focused on the invasive Sahara mustard (*Brassica tournefortii*), Mediterranean grasses (*Schismus arabicus* or *S. barbatus*), and a suite of native winter annual plants that co-occur in the Sonoran Desert in southwestern Arizona. The focal invasive species were first recorded in the 1920s and 1930s, and thus have had a relatively short evolutionary history in the Sonoran Desert. They are also primarily self-fertilizing species, and therefore may have invaded the novel community with their pre-adapted traits instead of through genetic recombination (Winkler, 2017). Many researchers have raised concerns about the impact of these specific invasive species on native species (Van Devender *et al.*, 1997; Brooks and Berry, 2006; Barrows *et al.*, 2009; VanTassel *et al.*, 2013). It is thus important to assess whether spatial and temporal niche differentiation has the potential to reduce their long-term large-scale impact on native species.

Common to most spatial and temporal co-existence mechanisms is a requirement that species be differentiated in their responses to physical environmental conditions over the range encountered in their habitat. We refer to this condition as *species-specific responses to the environment*. In its simplest form, this means that each species has physical environmental conditions where it is more favoured than other species with regard to at least some components of fitness. At its heart, this means species have different environmental niches (Chesson *et al.*, 2001), where ‘environment’ here refers to the physical environment. By itself, however, such differentiation is not sufficient to promote co-existence; one or more other conditions are required. These other conditions have the effect of ensuring that favourable physical environmental conditions lead to density-dependent feedback through enhanced resource consumption or heightened activity of natural enemies. This feedback limits the advantages that an abundant species can accrue when experiencing favourable environmental conditions, and confers corresponding advantages to species at low density, stabilizing co-existence (Chesson, 2000a).

Key stabilizing mechanisms that stem from spatial and temporal niche differentiation include the storage effect and fitness-density covariance (Chesson, 2000b; Chesson *et al.*, 2013). A general condition called *buffered population growth* can contribute to both mechanisms. This condition limits the disadvantages experienced by a species as a result of unfavourable times and places. In the temporal form, buffered population growth can arise from a long-lived life-history stage such as dormant seeds, or persisting adult organisms. In the spatial form, it is sufficient for a population to be dispersed over an environmentally heterogeneous landscape. Finally, it is important that the competition that any species experiences varies with environmental conditions (*covariance between environment and competition*) and population densities, so the environmental niche differentiation present can stabilize co-existence (Chesson, 2000b; Chesson *et al.*, 2005, 2013).

Given these requirements for stable co-existence in a variable environment, we conducted field and growth-chamber studies in pursuit of the following objectives. First, we wished to test species-specific responses to the environment in the form of seed germination. Germination of desert winter annuals is sensitive to variation in physical environmental factors, and species can differ strongly in their preferred germination environments (Adondakis and Venable, 2004). We developed a *G*-test method to determine whether field germination fractions differed significantly between the focal species as the environment varied in space and time. This improved method remains valid in the presence of environmentally driven clumping. We also performed a growth-chamber study of the germination responses of some of the invasive and native species to determine whether they can be differentiated by their germination responses to variation in temperature and light availability.

Our second objective was to determine whether the focal species have buffered population growth over time and space. Higher seed survival combined with lower germination increases seed bank persistence and hence temporally buffered population growth (Chesson *et al.*, 2013). We used our field data to evaluate the seed bank persistence of each species. Population dispersion over heterogeneous landscapes contributes to spatial buffering (Chesson, 1990). This spatial buffering is by default present in our study system through our choice of those focal species commonly found over a heterogeneous landscape. We evaluated the spatial difference in population persistence of one of the invasive species and determined which of its local populations contribute most strongly to spatial buffering.

Our aim was to assess key elements (species-specific responses to the environment and buffered population growth) for spatial and temporal niche differentiation to stabilize coexistence. Ideally, covariance between the environment and competition should also be assessed, but drought-induced low densities during the period of study made it impossible to do so (Li, 2016).

METHODS

Field data collection

The study site was located in the Mohawk Valley of southwestern Arizona, within the Lower Colorado River Valley subdivision of the Sonoran Desert. The valley hosts a diversity of winter annual species inhabiting various types of habitat, and is heavily invaded by *Brassica tournefortii* and *Schismus arabicus*.

Three variables – the abundance of germinated seedlings, the abundance of viable seeds after germination, and the abundance of inviable seeds after germination – were used to estimate levels of germination and survival of ungerminated seeds.

To capture temporal variation in these variables, we sampled seedling emergence and the post-germination seed bank in the 2011–2012 (Year 1), 2012–2013 (Year 2), and 2013–2014 (Year 3) winter–spring growing season. To capture spatial variation, we sampled two 120 × 120 m areas situated on a sand flat and a dune respectively, approximately 0.6 km apart, centre to centre. The sand flat is characterized by open space intersected by large creosote (*Larrea tridentata*) shrubs. We sampled equally both in the open and under creosote shrubs on the sand flat (hereafter referred to as sand flat-open and sand flat-shrub habitat). There are very few shrubs on the dune. Therefore, we only sampled open space in the dune habitat. We also recorded growing-season precipitation and soil temperature in each habitat in order to assess environmental variability (www.evolutionary-ecology.com/data/3120Appendix.pdf).

For even sampling of each of the two areas we used stratified randomization, dividing each area into four 120 × 30 m sub-areas, and then further dividing each sub-area evenly into five columns. Similar numbers of clusters consisting of a group of neighbourhoods were randomly established along each column (Fig. 1). We sampled seedling emergence over the three field seasons by taking digital photographs of experimental neighbourhoods. In each neighbourhood, we digitally recorded the abundance and identity of all emerged individuals before manipulating the density of seedlings. In Year 1, the photos were taken after some individuals of *Brassica tournefortii, Chaenactis stevioides*, and *Plantago ovata* were removed from the neighbourhoods. Seedling density of those removed species in those neighbourhoods was not used in the final analysis. Neighbourhood diameter was 30 cm in

Year 1 and 20 cm in Years 2 and 3. We measured seedling abundance in one neighbourhood in each cluster in Year 1 and in two neighbourhoods per cluster in Years 2 and 3.

To infer germination fractions, we sampled the soil seed bank in locations that were a subset of all neighbourhoods where seedling emergence was recorded (Fig. 1). We sampled the seed bank using a stratified random sampling method with the aim to increase the chance of obtaining useful data. We randomly selected five neighbourhood clusters in each sub-area, one along each column, and classified them into either high or low density of seedlings. Soil samples taken adjacent to low-density clusters had a lower chance of containing seeds (results not shown). To increase the chance of finding seeds in order to gain confidence in our estimation of fractions of germination and seed survival, we then selected another 10 neighbourhood clusters in each sub-area, two in each column, which

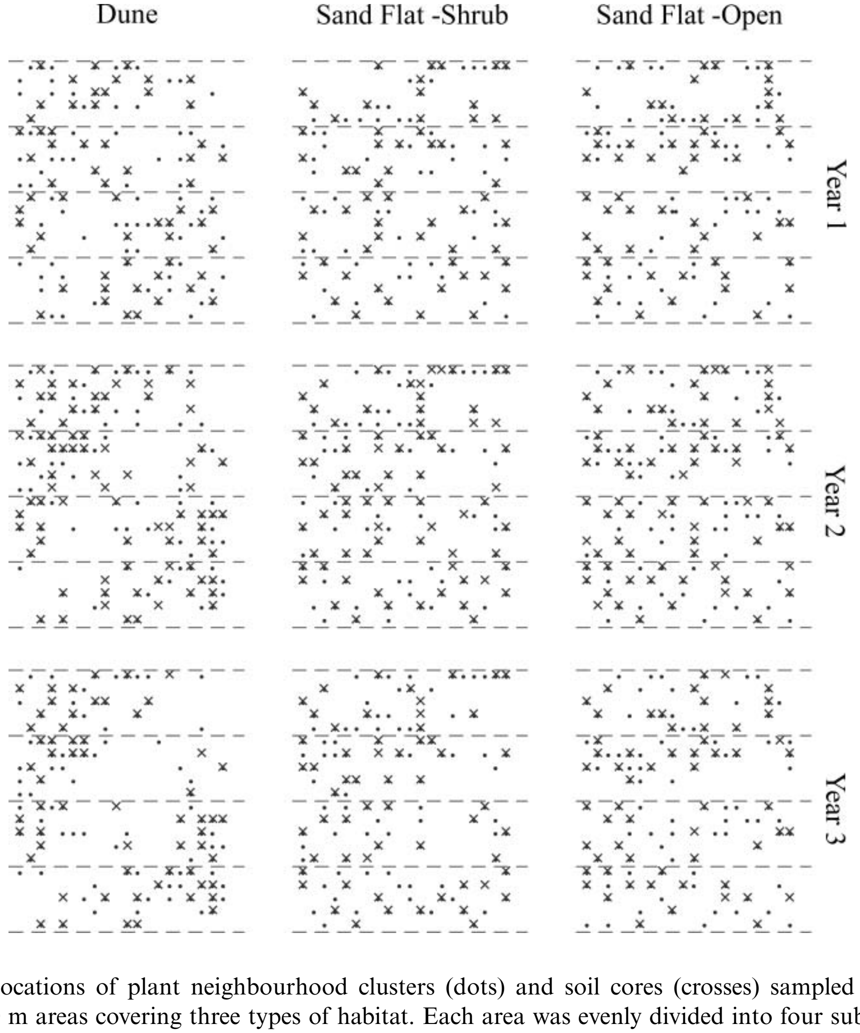

Fig. 1. Locations of plant neighbourhood clusters (dots) and soil cores (crosses) sampled in the 120 × 120 m areas covering three types of habitat. Each area was evenly divided into four sub-areas indicated by the dash lines. Density of seedlings and viable seeds sampled from paired locations were combined to estimate germination fractions. Density of viable and inviable seeds sampled from soil cores were combined to estimate seed survival fractions.

had relatively high seedling density. We also ensured that these non-randomly selected locations were evenly distributed across the site.

After all seedlings had emerged and before seed release, we took a soil core sample (5.4 cm in diameter) next to each selected cluster. We drilled to a depth of 2 cm on the sand flat, but 5 cm on the dune because the more mobile dune soil can bury seeds more deeply. Sample size was 60 soil cores in each habitat in Year 1, but deviated slightly around 60 in Years 2 and 3.

We brought soil samples back to the University of Arizona laboratory and floated them in water to coarsely separate lighter organic matter from denser inorganic matter. We examined both forms of matter under a microscope. Any seed with intact seed coat was considered to be ungerminated. The species and abundance of those seeds were recorded. To determine seed viability, we chose a seed-poking test instead of a tetrazolium chloride test because deeply dormant yet viable seeds may not pass the tetrazolium chloride test (Pake and Venable, 1996). Seeds with natural colour and robust appearance were considered viable. We broke seeds with questionable colour and rigidity and examined the freshness of the tissue inside. Seeds fresh and full inside were considered viable, whereas any that were dark or shrunken were considered inviable.

Species-specific germination responses

We developed a *G*-test to infer species-specific germination (3120Appendix B). The test remains valid in the presence of environmentally driven clumping of seedlings and seeds. Nevertheless, potential violation of this broad assumption due to other causes cannot be ruled out (3120Appendix B). The model is as follows.

Let the number of germinated seedlings of species j observed in location x be G_{xj} and the number of its viable seeds sampled in the same location be S_{xj}. Also, let a be the ratio of the sampling area of G_{xj} to that of S_{xj}. The habitat level germination fraction of species j is

$$p_j^G = \Sigma_x G_{xj} / (\Sigma_x G_{xj} + a\Sigma_x S_{xj}), \qquad (1)$$

where $\Sigma_x G_{xj}$ and $\Sigma_x S_{xj}$ are the sum of seedlings and that of viable seeds respectively over all sampled locations in a habitat.

To statistically infer species-specific germination responses, we organized $\Sigma_x G_{xj}$ and $\Sigma_x S_{xj}$ as contingency tables in five levels of species (*Brassica tournefortii, Schismus arabicus*, and the three most common native species: *Cryptantha angustifolia, Chaenactis stevioides*, and *Plantago ovata*), three levels of space (sand flat-open, sand flat-shrub, dune), and three levels of time (Years 1, 2, and 3) (3120Appendix, Table B1). A comparison of $\Sigma_x G_{xj}/\Sigma_x S_{xj}$ in a contingency table is equivalent to a comparison of the germination fraction in equation (1) (3120Appendix B). We used the *G*-test to examine: (1) whether there was a significant species × space interaction in the germination fraction in each year, indicating species-specific germination responses to the spatially variable environment; and (2) whether there was a significant species × time interaction in the germination fraction in each habitat, indicating species-specific germination responses to the temporally fluctuating environment.

To evaluate specific environmental drivers of species-specific germination responses, we also conducted a growth-chamber experiment to examine whether the germination of the invasive *Brassica tournefortii, Schismus barbatus*, and the native *Chaenactis stevioides* differ in response to variation in soil temperature and light availability. The experiment used a full factorial design that consisted of the three species, four temperature regimes, and two levels of light availability. (Details of the experimental procedures and statistical analysis can be found in 3120Appendix C.)

Buffered population growth over time

We tested the strength of temporally buffered population growth for each species by evaluating the germination fraction and survival of ungerminated seeds in the field to determine whether the species can form a persistent seed bank.

Estimation of germination fractions follows equation (1). Estimation of seed survival is based on the fractions of viable seeds among ungerminated seeds sampled in the field. Let the number of viable and inviable seeds of species j observed in the same soil core sample in location x be S_{xj} and D_{xj}, respectively. The habitat level fraction of seed survival of species j is

$$p_j^S = \Sigma_x S_{xj} / (\Sigma_x S_{xj} + \Sigma_x D_{xj}). \tag{2}$$

This estimation involves bias due to potential inclusion of seed mortality that occurred before the period of focus. Nevertheless, this bias does not affect our conclusions (3120Appendix D).

We estimated 95% confidence intervals of all fractions of germination and seed survival through 10,000 repetitions of non-parametric bootstrapping. Following the same field sampling constraint, the bootstrapping algorithm resampled pairs of G_{xj} and S_{xj} and pairs of S_{xj} and D_{xj} independently within each sub-area and then combined these resampled pairs to estimate the statistic of interest following equations (1) and (2).

RESULTS

Species-specific germination responses

The physical environment during the germination period varied strongly over years and across the landscape. There were strong annual differences in both the timing of the first major winter storm in the Mohawk Valley and the amount of precipitation (3120Appendix, Table A1). There were also strong spatial differences in the mean and variance of the soil temperature in the germination period (3120Appendix, Figs. A1 and A2). Focal winter annual species showed species-specific germination responses to this environmental variability. G-tests gave a significant species × space interaction for the germination fraction in each year, and a significant species × time interaction in each habitat (Table 1).

Moreover, germination responses to temperature, light, and their interaction differed significantly between the three species tested in the growth-chamber experiment. Mixed-model analysis of variance (ANOVA) showed that germination fraction was affected by a significant interaction between light, temperature, and species (Trial 1: $F_{2,88} = 67.28$, $P < 10^{-15}$; Trial 2: $F_{2,88} = 29.88$, $P < 10^{-10}$), between light and species (Trial 1: $F_{2,88} = 34.28$, $P < 10^{-11}$; Trial 2: $F_{2,88} = 202.17$, $P < 10^{-15}$), and between temperature and species (Trial 1: $F_{2,88} = 192.75$, $P < 10^{-15}$; Trial 2: $F_{2,88} = 36.99$, $P < 10^{-11}$). Exposure to light altered all three species' germination responses to temperature, lowering the maximum germination

Table 1. *G*-test results of the species × space and species × time interactions in seed germination fractions

	Year	Species × space	Habitat	Species × time
Native + invasive	Year 1	$\chi^2_8 = 23.21$ $P = 0.0031$	Sand flat-open	$\chi^2_8 = 69.83$ $P < 10^{-11}$
	Year 2	$\chi^2_8 = 42.85$ $P < 10^{-6}$	Sand flat-shrub	$\chi^2_8 = 133.44$ $P < 10^{-11}$
	Year 3	$\chi^2_8 = 74.60$ $P < 10^{-12}$	Dune	$\chi^2_8 = 65.55$ $P < 10^{-10}$
Native only	Year 1	$\chi^2_4 = 10.61$ $P = 0.031$	Sand flat-open	$\chi^2_4 = 25.02$ $P < 10^{-4}$
	Year 2	$\chi^2_4 = 18.40$ $P = 0.001$	Sand flat-shrub	$\chi^2_4 = 28.34$ $P < 10^{-4}$
	Year 3	$\chi^2_4 = 53.52$ $P < 10^{-10}$	Dune	$\chi^2_4 = 15.18$ $P = 0.004$

fraction and altering relative differences in germination fractions in response to temperature change (Fig. 2).

Buffered population growth

Seed survival of the focal species was generally high, with the exception of *B. tournefortii* (Fig. 3a; see also 3120Appendix, Table D1). Excluding *Brassica tournefortii*, survival of ungerminated seeds among the species ranged from 23.6% to 81.3%. Besides high seed survival, these four species also experienced low seed germination. Their germination rarely exceeded 35% over time and space (Fig. 3b; see also 3120Appendix, Table B1). This combination of high seed survival and low germination suggests strong buffered population growth over time.

Brassica tournefortii consistently had the lowest seed survival over the three years and across the three habitats (Fig. 3). No viable seeds of this species were sampled on the sand flat in Years 2 and 3. Moreover, its sand flat population had the highest germination fraction among the five species, reaching 100% in Years 2 and 3. This combination of low seed survival and high germination suggests at best weak temporally buffered population growth. An important habitat difference existed. The dune population of *B. tournefortii* had higher seed survival and substantially lower germination than its sand flat population, indicating that the dune population experienced stronger temporal buffering.

The seed bank of some focal species experienced strong spatial variation within a habitat, indicated by extremely wide 95% confidence intervals that covered 0% seed survival or 100% seed germination even though the average fractions were far from these extreme values (e.g. *B. tournefortii* germination in the dune habitat in Year 3, and *C. stevioides* seed survival and germination in the dune habitat in Year 3; Fig. 3).

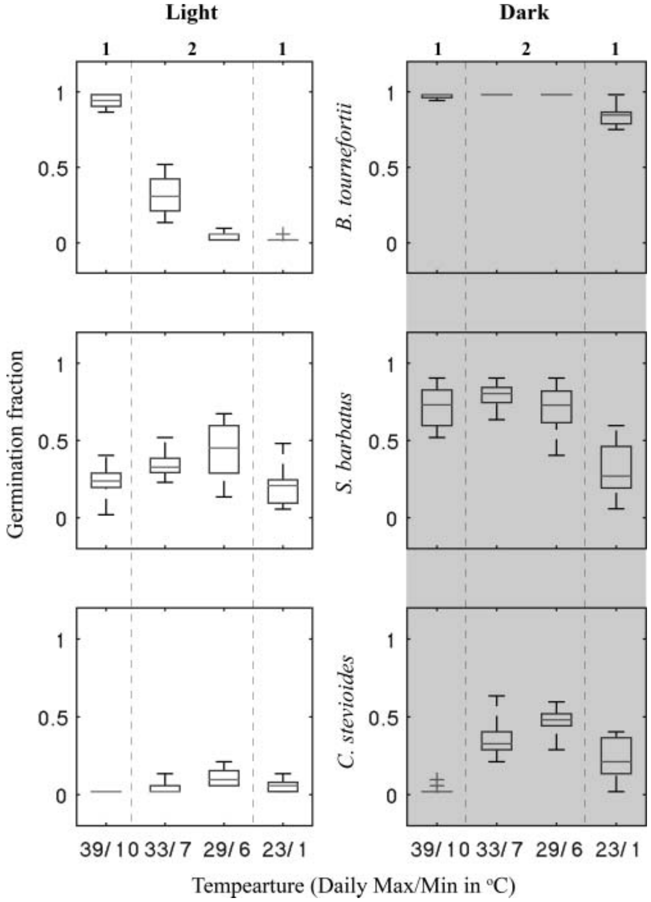

Fig. 2. Germination fraction of *Brassica tournefortii* (top panels), *Schismus barbatus* (middle panels), and *Chaenactis stevioides* (bottom panels) under different treatments of temperature and light availability (light in the left-hand panels and dark in the right-hand panels). Two separate trials of the experiment are indicated by the numbers 1 and 2 at the top of the panels. In each boxplot, the middle grey bar indicates the median; the outer two edges indicate the 1st and 3rd quartiles; and the whiskers indicate the minimum and maximum.

DISCUSSION

In this study, we assessed the evidence for spatial and temporal niche differentiation to stabilize co-existence between invasive and native desert winter annual species. We observed species-specific germination responses to the varying environment and buffered population growth, two key elements for stabilizing co-existence mechanisms arising from spatial and temporal niche differentiation. Of equal importance, we found that the invasive species studied differed in life-history characteristics that contribute to buffered population growth.

Empirical studies demonstrating species-specific responses to the environment have thus far been largely restricted to groups consisting of native species only (e.g. Ide, 1935; van den Brink *et al.*, 1995; Adler *et al.*, 2006, Zweifel *et al.*, 2009). The only studies to include both native and

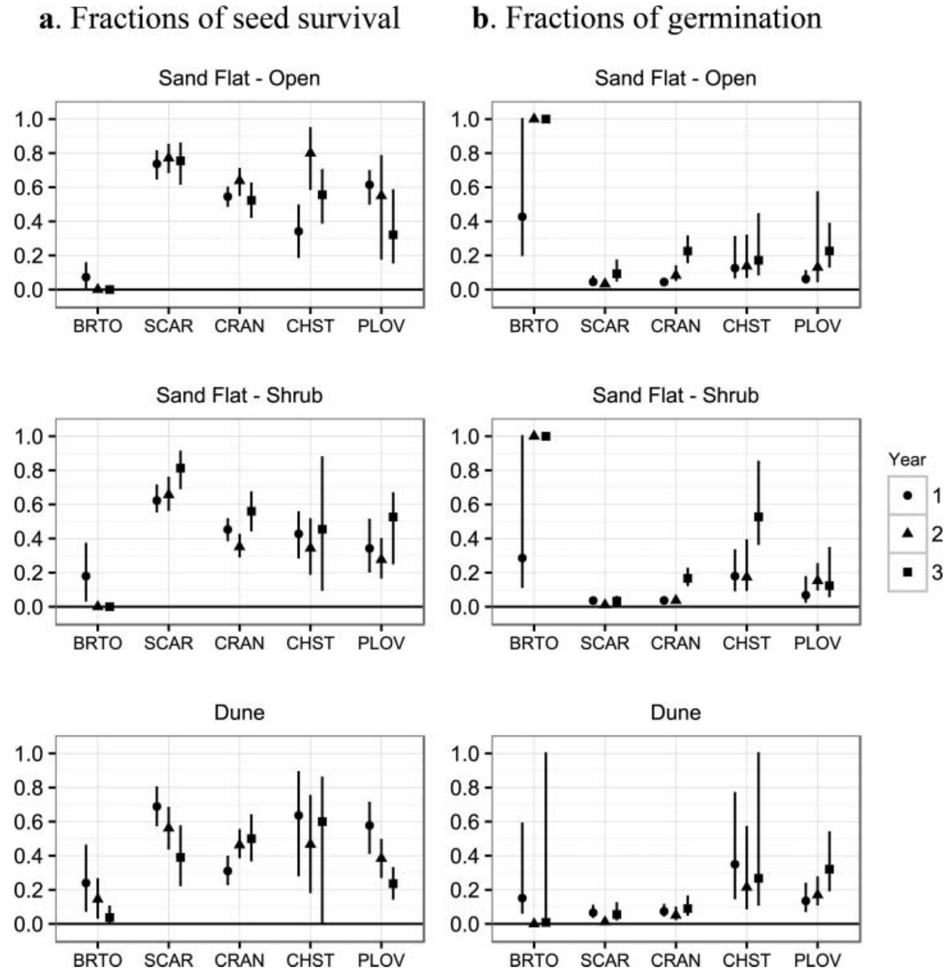

Fig. 3. Fractions of (a) seed survival and (b) germination in the three types of habitat over the three years of field study. Bars represent bootstrapped 95% confidence intervals. The focal species are *Brassica tournefortii* (BRTO), *Schismus arabicus* (SCAR), and the native *Crypthantha angustifolia* (CRAN), *Chaenactis stevioidies* (CHST), and *Plantago ovata* (PLOV).

introduced species showed interspecific differentiation in environmental responses (Levine *et al.*, 2008; Angert *et al.*, 2009), suggesting that this key element for co-existence may be common in invaded communities when environmental conditions and species responses are observed on broad scales.

Our growth-chamber experiment also suggested that soil temperature and light availability could be major environmental drivers through which the germination responses of the annual plant species studied here were differentiated. It is known that variation in environmental factors such as temperature, light availability, and soil moisture can lead to interspecific differentiation in germination fraction and speed between desert annual plants (Thanos *et al.*, 1991; Adondakis and Venable, 2004; Holt and Chesson, 2014; Huang *et al.*, 2015). Given the high dimensionality of the variable environment in nature, abundant opportunities exist for native and invasive species to be differentiated by their environmental responses.

Species-specific responses to the environment fundamentally mean that species occupy different environmental niches. The presence of this condition is essential for the operation of the storage effect and fitness-density covariance, the two major stabilizing co-existence mechanisms arising from spatial and temporal niche differentiation. However, this condition alone does not guarantee the operation of these mechanisms because it does not guarantee that the environmental responses are appropriately coupled with density-dependent processes to allow concentration of intraspecific competition relative to interspecific competition.

Buffered population growth is another key element for the operation of the storage effect. Our results suggested strong temporal buffering of native populations as well as the introduced *Schismus arabicus* given their persistent seed banks, which follow from low germination and high seed survival. Other studies have also shown that introduced species often have life-history strategies such as seed dormancy or diapause that could enhance buffered population growth over time (Rice, 1985; Mandák, 2003). Adaptation to the variable environment of its origin may explain traits strengthening the temporally buffered population growth of an introduced species such as *S. arabicus*. These traits not only facilitate its invasion of a new environment but may also contribute to the promotion of its co-existence with native species.

In contrast, the invasive *Brassica tournefortii* had a much higher germination rate than the *Schismus* species based on results from the sand-flat habitat and the growth-chamber experiment. Our field study also revealed *B. tournefortii* had lower seed survival compared with the other species. Consequently, the species had a more ephemeral seed bank and thus weaker temporal buffering. Several invasive annual plant species have been shown to have short-lived seed banks mainly as a result of high germination under broad environmental conditions (Forcella and Gill, 1986; Meyer *et al.*, 1997; Wainwright and Cleland, 2013; Jurand *et al.*, 2013; Horn *et al.*, 2015). Few studies have examined the survival of dormant seeds of these invasive annuals, but they generally indicate low rates of seed survival (Chauhan *et al.*, 2006; Jurand *et al.*, 2013). High germination coupled with low survival of dormant seeds leads to weak temporal buffering of these invasive annuals, which may explain the marked declines in their populations following years that did not favour post-germination plant growth (Young *et al.*, 1981; Hunter, 1991).

This weak temporal buffering has not been observed for native desert annuals, and suggests maladaptation of the introduced species to the new arid environment. The successful invasion of these species would require aggressive recruitment during favourable times that could adequately compensate population losses during unfavourable times provided a minimal degree of temporal buffering exists to prevent population extinction over those unfavourable periods.

More importantly, their successful invasion may be strongly attributed to spatially buffered population growth. Relatively stable local populations in places where recruitment is more reliable can compensate for population losses elsewhere. Moreover, the strength of temporal buffering of the same species can differ in space. In our study, the dune population of *B. tournefortii* experienced stronger temporal buffering than did its sand flat population. Dispersal between the dune and sand flat population could lead to spatial buffering. This spatial buffering can lead to temporal buffering because persisting local populations play the same role as a persistent life stage in creating temporal refuges for the population (Chesson, 1990).

Our findings underscore the interaction between spatial and temporal buffering in affecting long-term population persistence. Understanding this interaction can inform management actions aiming to weaken large-scale persistence of invasive species by targeting local populations with stronger temporal buffering or with more reliable recruitment. It also illustrates how an introduced species, though having traits seemingly maladapted to an unpredictable environment, can rely on other strategies to invade this novel environment.

Besides the above tested conditions, the promotion of co-existence also requires covariance between environment and competition. With this final element, the density-dependent feedback loops become more concentrated within species than between species over space and time (Chesson, 2012) and co-existence is promoted through the storage effect and fitness-density covariance (Chesson, 2000b; Chesson *et al.*, 2005, 2013). Due to practical constraints, we could not evaluate whether stronger germination responses were coupled with larger competitive effects in this system to generate this covariance. Seasonal rainfall totals recorded in our field study were below the long-term average in this region (3120Appendix A). The droughts led to technical difficulties detecting competitive effects, removing the possibility of measuring coupling of competitive effects and environmental responses over the study period (appendix C in Li, 2016).

We anticipate an increase in plant density and size, and thus a return of detectable competitive effects when precipitation returns to near or above the long-term average. It is possible that competitive effects will be coupled with species-specific germination responses detected in this study, generating covariance between environment and competition. In time, this may give rise to the temporal storage effect. In space, it may generate the spatial storage effect, as shown by a study of desert annuals in the Chihuahuan Desert (Sears and Chesson, 2007) and fitness-density covariance. Therefore, longer-term environmental variation on large spatial scales may ultimately lead to the promotion of co-existence in this invaded annual plant community. Nevertheless, the stable co-existence between these invasive and native species also depends on whether the strength of these stabilizing mechanisms can overcome average-fitness advantages of the invasive species, which requires further study.

In conclusion, we uncovered key elements in this desert winter annual plant community, through which spatial and temporal niche differentiation may potentially stabilize co-existence of invasive and native species. Our findings also suggest that the difference in evolutionary history experienced by native and introduced species may result in different life-history characteristics contributing to these key elements. Overall, it is crucial to conduct demographic studies that compare invasive and native species over the broad environmental range of their interaction in order to infer the potential for their long-term large-scale co-existence.

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