

Can spatial isolation help predict dispersal-limited sites for native species restoration?

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Abstract. When the distribution of species is limited by propagule supply, new populations may be initiated by seed addition, but identifying suitable sites for efficiently targeted seed addition remains a major challenge for restoration. In addition to the biotic or abiotic variables typically used in species distribution models, spatial isolation from conspecifics could help predict the suitability of unoccupied sites. Site suitability might be expected to increase with spatial isolation after other factors are accounted for, since isolation increases the chance that a site is unoccupied only because of propagule limitation. For two native annual forbs in Californian grasslands, we combined experimental seeding and niche modeling to ask whether suitability of unoccupied sites could be predicted by spatial variables (either distances from, or densities of, conspecific populations), either by themselves or in combination with niche models. We also asked whether experimental tests of these predictions held up not only in the short term (one year), but also in the longer term (three years). For *Lasthenia californica*, seed additions were only successful relatively near existing populations. For *Lupinus nanus*, seeding success was low and was positively related to the number of conspecifics within 1 km. For both species, a few previously unoccupied sites remained occupied three years after seeding, but this subset was not predictable based on either spatial or niche variables. Seed addition alone may be a limited means of native forb restoration if suitable unoccupied sites are either rare or unpredictable, or if they tend to be close to where the species already occurs.

Key words: California grassland (USA); community composition; dispersal limitation; *Lasthenia californica*; *Lupinus nanus*; restoration; seed addition; spatial isolation; species distribution models.

INTRODUCTION

Propagule limitation has been found to limit community diversity (Hubbell 2001, Foster and Tilman 2003), species' spatial extents (Seabloom et al. 2003a, b, Munzbergova and Herben 2004, Moore and Elmendorf 2006), and species' local abundances (Turnbull et al. 2000). Propagule availability may in some cases outweigh competition as a constraint on species' distributions (Greig-Smith 1979, Dostal 2005), suggesting that seed addition is a potential means of increasing native species persistence in landscapes that have been overtaken by highly competitive exotic species. In invaded grasslands, seed addition has often been found to increase species diversity and the density of native species (Bakker et al. 2003, Foster et al. 2007, Mitchell et al. 2008, Orrock et al. 2009, Peter et al. 2010). For example, in California grasslands, where invasions by annual exotic grasses and late-season annual forbs left many native species persisting in small, diffuse, or fragmented populations, native perennial grasses can achieve dominance over the

widespread exotics simply by the experimental addition of enough seeds (Seabloom et al. 2003a, 2006). Similarly, Foster et al. (2007) seeded 32 species into plots on a North American old-field remnant and found shifts in community composition, increased diversity, and decreased exotic plant cover over a six-year study period. Peter et al. (2010) found that seed addition of two to three competitive native grasses to a European alkali grassland promoted exclusion of exotic grasses, although other methods were needed to stimulate the return of native forbs.

While the addition of seed can often be an appropriate restoration measure (Young et al. 2005), native seeds can be expensive, high densities may be required to produce the desired effect (Jongepierova et al. 2007), and considerable effort may be wasted through seeds landing in unsuitable microsites (Gomez-Aparicio 2008). A key practical issue, therefore, is how to identify sites in which seed addition is likely to be effective. One proposed solution is to use species distribution models (SDMs), or niche models, which predict potential distributions of species based on the characteristics of occupied sites (Guisan and Thuiller 2005, Elith et al. 2006). They have been used successfully to predict the success of experimental seed additions and to identify

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dispersal-limited sites (Munzbergova and Herben 2004, Wright et al. 2006, Elmendorf and Moore 2008). However, a critical limitation is that when strongly dispersal-limited species are modeled, they should by definition yield relatively poorly fitting predictions because they are absent from many suitable sites (Moore and Elmendorf 2006). In contrast, excellent fit of SDM predictions to distributional data implies that a species is present in nearly all of its suitable sites and suggests that there is little potential to expand its distribution through transplantation (Moore and Elmendorf 2006).

An important step toward a better predictive understanding of where to add seeds in landscapes is to take dispersal limitation into account and explicitly consider the spatial scales over which it may operate. For example, to the extent that species are reasonably effective dispersers at a given scale (say, 10^2 m), it may be hypothesized that unoccupied sites within that distance from existing conspecific populations are likely to be environmentally unsuitable, while at greater distances from existing populations, there will likely be a mixture of suitable and unsuitable sites. Seeding success will therefore likely increase with distance from existing populations, at least over some range. If this is true, then the subset of distant sites that are most suitable may be most effectively targeted by combining information on the spatial locations of existing populations with other site attributes that are correlated with occupancy. Despite this possibility, links between seeding success and spatial distribution of conspecifics have rarely been made (Turnbull et al. 2000).

We combined spatially structured seed additions with species distribution models to test whether the suitability of unoccupied sites for plant establishment varied with respect to isolation from conspecifics, either with or without taking other environmental variables into account. We primarily used SDMs based on community composition data, because these have been shown to be good predictors of species distribution, abundance, and establishment success (Elith et al. 2006, Elmendorf and Moore 2008). Gradients in community composition may affect species distributions directly through competition and facilitation (e.g., Dyer and Rice 1997, Jurjavcic et al. 2002, Elmendorf and Moore 2007, Espeland and Rice 2007), or may be correlated with other important factors such as stress and productivity (e.g., Vince and Snow 1984, Wilson and Keddy 1986, Crain et al. 2004). We also considered SDMs based on environmental variables (biomass, soil chemistry, and soil moisture).

Another issue we addressed was the appropriate spatial and temporal scale of input data to use in SDMs (Guisan and Thuiller 2005). Annual grasslands are spatially and temporally variable systems in species composition (Levine and Rees 2004, Elmendorf and Harrison 2009). Distribution models might therefore be most accurate when based on data aggregated across multiple years and microsites, especially if apparent

turnover is actually caused by dormancy in a seed bank. Conversely, if site suitability for establishment is dependent on localized conditions that fluctuate in space and time, SDMs may be more accurate when based on data specific to seeding microsites and years (Guisan and Thuiller 2005, Araujo and Guisan 2006). We used SDMs based on four different spatiotemporal scales of data collection to determine whether predictions were more accurate when based on data from more or less inclusive scales of space and/or time.

Our study species were the native annual forbs *Lasthenia californica* and *Lupinus nanus*, which each show patchy spatial distributions at scales of 10^1 – 10^3 m in our study system, a heterogeneous Californian grassland landscape. We added seeds to sites that varied in isolation from existing natural populations from 0 to 950 m for *Lasthenia* and 0 to 524 m for *Lupinus*, and built species distribution models based on community composition data from a long-term study. We asked three primary questions about the resulting establishment of seedlings at previously unoccupied sites: (1) Are suitable unoccupied sites spatially predictable—does the frequency of suitable sites increase within areas that have a high density of conspecifics or decrease with distance from conspecific populations? (2) Do spatial variables provide additional information about the suitability of unoccupied sites for establishment that is not detected SDM predictions alone? (3) Is there evidence for dispersal limitation—do seeds not only establish in previously unoccupied sites in the shorter term (one year), but persist in the longer term (three years), and does spatial predictability persist in the longer term? Our study is among the first to test the effect of spatial isolation from conspecifics on the suitability of sites for seed addition in native restoration.

METHODS

Study species

Lasthenia californica (DC ex Lindley, Asteraceae) and *Lupinus nanus* (Benth., Fabaceae), henceforth *Lasthenia* and *Lupinus*, were selected because they are widespread natives that are common components of restoration seeding mixes, small-statured annuals that occur in dense, conspicuous patches; they produce abundant seed that can be readily collected before dispersal throughout the study site; and they flower concurrently in grasslands on a range of soils. *Lasthenia* is found throughout grasslands in the western United States, including on serpentine, vernal pool, and alkali soils (Ornduff 1966). Seeds are light and have a reduced pappus; dispersal is by gravity and wind, and most seeds move 5–50 cm from the maternal plant (Hobbs and Mooney 1995, Rajakaruna and Bohm 1999). Seed production is prolific compared to other co-occurring species (Hobbs and Mooney 1995). Seed banks are undocumented for this species, but are common in this system in general. *Lupinus* is native to the Northern Coast Range and Sierra Nevada foothills of California and Nevada and is

widely planted on road verges and in other restoration contexts (Harding et al. 1974, Karoly 1994). It has large, gravity-dispersed seeds that persist in the soil for 30 or more years (Dremann and Shaw 2002). At our study site we estimate that only <5% of all *Lupinus* individuals and <10% of all *Lasthenia* individuals in any given year are found outside of distinct contiguous patches. Patch margins of each species transition from >50% cover to <1% cover across a boundary of 2 m or less (K. Moore, *personal observation*). Both species are common grassland generalists of stature, fitness, and dispersal similar to a wide variety of other winter annual forbs in this system (for other examples see Hobbs and Mooney 1995). Both species have small seeds that are likely to remain in place when added to experimental plots and emerge at a measurable rate in a typical year.

Study sites and species occurrence data

Our study location was the University of California's Donald and Sylvia McLaughlin Natural Reserve and adjacent Knoxville Wildlife Area (California Department of Fish and Game), Lake and Napa counties, California, USA. Grasslands occur interspersed among chaparral and oak woodland; dominant species are exotic annual grasses and annual forbs on non-serpentine soils, and native perennial grasses, annual forbs, and perennial forbs on serpentine soils (Harrison 1999, Harrison et al. 2003). We used 69 grassland study sites on serpentine and non-serpentine soils within an ~16-km² area (see Harrison 1999 and Harrison et al. 2003 for detailed methods of study site selection). Eleven of the 80 original study sites were omitted: nine due to a fire in 2004 and two due to limited site accessibility. Study sites were comprised by a 40-m transect along which five permanently marked 1-m² plots were evenly spaced. A maximum of three study sites were located in a single meadow; sites were located at least 50 m apart. Plant occurrences (species presences/absences) were surveyed in all plots in early and late spring from 2000 to 2007.

Seeding experiment

In the fall of 2004, we added seeds of *Lasthenia* or *Lupinus* to each of two 0.25-m² plots at each site, located ~1 m from one of the existing survey plots. Seeds for addition were collected from both serpentine and non-serpentine sites throughout the reserve in 2003 and 2004; seed collections for each species were bulked. Seeds of each species were added to separate plots by scattering 1000 seeds in the central 0.09 m² of the 0.25-m² seed addition plot. We used a high seeding density to overcome seed dormancy, predation, and early seedling mortality. Addition of seed to the central portion of the plot also lowered the likelihood of dispersal beyond plot boundaries. We counted established target plants in all previously unoccupied plots in the springs of 2005 and 2007. The 2006 growing season was exceptionally short and the germination of *Lupinus* in particular was abnormally early and sparse. Seeding effects were not

analyzed for this year because of concern that most seedlings had died before the surveys were completed.

Spatial data

In the spring 2005, we mapped all natural *Lasthenia* and *Lupinus* patches >1 m² within a radius of 1000 m of each seeding site using the global positioning system (GPS). Patch locations, size, elevation, and coordinates were recorded in the Universal Transverse Mercator (UTM) system. Density was recorded in 2–4 sample 0.0625-m² plots located at random within each patch.

For each species and each focal seeding site we calculated “focal site isolation” as the distance from the seeding site to the nearest natural patch (within 1000 m) using the Nearest Features extension (version 3.8b; Jenness Enterprises, Flagstaff, Arizona, USA) in ArcView version 3.2 (Environmental Systems Research Institute, Redlands, California, USA). We estimated “surrounding conspecific abundance” for each focal site as the sum of the product of plant densities and patch areas for all patches within the transect (50 m), medium (250 m), and landscape (1000 m) scales of the focal site. The transect scale corresponded to the scale of the observational data set used in species distribution modeling. The medium scale corresponded visually with the typical size of meadows in which observational sites were located, although some meadows were considerably larger or smaller. The landscape scale generally corresponded with large-scale environmental heterogeneity; radii of 1000 m often crossed significant ecological transitions or dispersal barriers such as chaparral or oak woodland, water bodies, roads, or disturbed areas.

Species co-occurrence

We used the Beals' index of site suitability to generate SDM predictions for each target species based on their patterns of co-occurrence with other community members (Beals 1984, Munzbergova and Herben 2004). Beals' index gives site-specific probabilities of focal species occurrence. We built indices at each temporal and spatial scale using an S-Plus script (S-Plus Professional, version 6.1; Insightful Corporation, Seattle, Washington, USA), then cross-validated each set of predictions with a nominal logistic model where the response was the occurrence of the focal species at the appropriate scale and the model predictions were used as the sole effect (JMP IN version 5.1; SAS Institute, Cary, North Carolina, USA). The predictive ability of cross-validated models was ranked based on the area under the curve (AUC) metric, which represents model quality independent of classification thresholds and ranges from 0.5 (no better than random) to 1.0 (perfect fit). Models with AUC > 0.70 are considered to have reasonable to very good predictive capacity (Pearce and Ferrier 2000). We built four models for each species using input data from either the 2005 (i.e., experimental year only) or long-term (2000–2007) temporal scale and from either the transect (40 m²) or the microsite (1 m²)

spatial scale. We compared these models based on the AUC statistic and their ability to predict seeding success in the first year following seeding at previously unoccupied sites. To illustrate these models, co-occurring species showing significant Pearson product-moment correlations with *Lasthenia* or *Lupinus* are given in Appendices A and B.

We also built species distribution models based on the environmental variables available at the transect scale (aboveground plant biomass, soil chemistry, and soil moisture) using generalized additive models (GAMs; see Moore and Elmendorf 2006 for detailed methods). For both species, the models based on community composition yielded AUCs > 0.10 higher than the models based on the environmental data, so the abiotic models are not further considered.

Statistical analyses

Dispersal limitation at unoccupied sites.—For each focal species, we categorized the 69 sites as either occupied, if the species was present on that transect during at least one year in the sampling period (2000–2007), or unoccupied, meaning the species was never present ($N = 34$ unoccupied sites for *Lasthenia*, $N = 55$ for *Lupinus*). This conservative definition of absence permits strong tests for the effects of dispersal limitation. Seeding success in each year, 2005 and 2007, was the number of recruited plants per 0.25-m² seeding plot. For each year separately, we tested for dispersal limitation by using one-tailed Wilcoxon signed-rank t tests to test to determine if the number of plants in previously unoccupied seeded plots was significantly greater than zero.

Predicting suitability of unoccupied sites.—For each species, we used a three-step model selection procedure (Burnham and Anderson 2002) to determine which indicators of site suitability alone or together best predicted first-year seeding success (2005) at unoccupied sites: SDM predictions and/or the spatial distribution and abundance of conspecifics. The persistent seeding effect in 2007 did not occur at enough sites to allow for model selection. For model selection on the 2005 seeding effect, first we asked which of four combinations of spatial and temporal scales of species co-occurrence data led to the most informative Beals' index of site suitability (SDM). Second, we asked which of three spatial scales of surrounding conspecific abundance (microsite, medium scale, or large scale) best predicted seeding success at unoccupied sites. Third, we asked whether seeding success at unoccupied sites was best predicted by spatial variables by themselves or in combination with the best site suitability model by comparing the predictive capacity of (1) focal site isolation alone, (2) the best predicting surrounding conspecific abundance, (3) isolation and surrounding conspecific abundance, (4) isolation and site suitability, (5) surrounding conspecific abundance and site suitability, or (6) isolation, surrounding conspecific abundance,

and site suitability as predicted by SDMs. Individual regression models were built in SAS (PROC MIXED). We also included a null model in each step of model selection in order to consider the possibility that none of our variables were useful predictors of seeding success.

A small sample corrected version of AIC, the AIC_c statistic was used to rank the hypothesized models in terms of their ability to predict seeding effect. Computation of AIC_c from regression statistics frequently results in negative values; relative values of AIC_c are used for model comparison (Burnham and Anderson 2002). Ranking by AIC_c uses a penalty term to provide a compromise between model fit and complexity as the number of model parameters increases relative to sample size (Anderson et al. 1994). The best-fitting hypothesized model has the lowest AIC_c (Burnham and Anderson 2002). The statistic Δ_i shows the difference between each model and the model with the lowest AIC_c. Following Burnham and Anderson (2002), we considered models within two units of AIC_c of the best model (i.e., $\Delta_i < 1.00$) to be statistically important, but chose the top model for subsequent model selection steps. Akaike weights (w_i) were calculated, which denote the weight of evidence in favor of each individual model (i) in reference to all competing hypotheses. Akaike weight for a given model reflects the likelihood that it is the best solution among competing hypotheses; weights for all a priori models sum to one (Burnham and Anderson 2002).

RESULTS

Dispersal limitation

In the first year following seeding, the number of plants in previously unoccupied plots was significantly greater than zero for both species (*Lasthenia*, mean = 12.2, SE = 3.6, df = 33, $t = 3.3591$, $P = 0.0010$; *Lupinus*, mean = 0.8, SE = 0.2, df = 47, $t = 1.3029$, $P < 0.0001$). This was equivalent to averages of 48.6 *Lasthenia* plants/m² and 3.2 *Lupinus* plants/m². In 2005, seeding resulted in recruitment in 55.9% of unoccupied sites for *Lasthenia* and 36.2% of unoccupied sites for *Lupinus*.

Seeding had a weak but persistent effect for both species in 2007. In this third year since seed addition, the number of plants in seeded plots was greater than zero, although with marginal significance (*Lasthenia*, mean = 0.5, df = 32, $t = 1.30$, $P = 0.1010$; *Lupinus*, mean = 0.1, df = 44, $t = 1.4310$, $P = 0.0798$). This was equivalent to averages of 3.2 *Lasthenia* plants/m² and 0.6 *Lupinus* plants/m². In 2007, seeding resulted in persistent recruitment in 9.1% of unoccupied sites for *Lasthenia* and 6.8% of unoccupied sites for *Lupinus*. Model selection was not conducted for persistent seeding effects because of low nonzero sample size.

First-year seeding effects

Site suitability.—For *Lasthenia*, estimates of site suitability from species distribution models (SDMs) using any of the four spatiotemporal scales of input data

TABLE 1. Pearson product-moment correlations between SDM predictions and model selection for first-year seeding success in unoccupied sites for (a) *Lasthenia californica* (df = 34) and (b) *Lupinus nanus* (df = 55) in Lake and Napa counties, California, USA.

| Scale | AUC | <i>r</i> | <i>P</i> | <i>K</i> | AIC _c | Δ _i | <i>w_i</i> |
|--|-------------|--------------|---------------|----------|------------------|----------------|----------------------|
| a) <i>Lasthenia</i> hypotheses: unoccupied site suitability is best predicted by SDMs generated at the | | | | | | | |
| Transect-wide long-term scale | 0.93 | 0.46 | 0.0067 | 1 | 301.7 | 0.00 | 0.44 |
| Transect-wide 2005 scale | 0.90 | 0.38 | 0.0282 | 1 | 304.4 | 2.70 | 0.12 |
| Microsite long-term scale | 0.92 | 0.42 | 0.0121 | 1 | 302.8 | 1.10 | 0.26 |
| Microsite 2005 scale | 0.88 | 0.39 | 0.0210 | 1 | 303.8 | 2.10 | 0.16 |
| No scale | | | | 0 | 307.2 | 5.50 | 0.03 |
| b) <i>Lupinus</i> hypotheses: unoccupied site suitability is best predicted by SDMs generated at the | | | | | | | |
| Transect-wide long-term scale | 0.78 | -0.23 | 0.1226 | 1 | 163.2 | 0.50 | 0.26 |
| Transect-wide 2005 scale | 0.76 | -0.25 | 0.8132 | 1 | 162.7 | 0.00 | 0.33 |
| Microsite long-term scale | 0.79 | -0.25 | 0.0932 | 1 | 165.7 | 3.00 | 0.07 |
| Microsite 2005 scale | 0.76 | -0.02 | 0.8966 | 1 | 165.1 | 2.40 | 0.10 |
| No scale | | | | 0 | 163.4 | 0.70 | 0.23 |

Notes: For *Lasthenia* and *Lupinus*, SDMs and a null model were compared in their ability to predict first-year seeding success (the number of plants in seeded plots in 2005) at previously unoccupied sites. More plausible models are indicated by smaller values of AIC_c and Δ_i. Akaike weight, *w_i*, denotes the weight of evidence in support of the model at hand given the set of proposed models. Models with the lowest AIC_c and those within two units of AIC_c from this model are shown in boldface type.

had excellent predictive ability (cross-validation AUCs 0.88–0.93) and showed significant positive relationships with first-year seeding success (2005) in unoccupied sites (Table 1a). Transect-wide long-term scale predictions had the highest AUC, indicating best model fit, and the highest and most significant correlation with first-year seeding success. All scales of model predictions had high AUCs, were similar in model fit, and were significant predictors of first-year seeding success.

Model selection based on AIC_c also demonstrated that the transect-wide long-term scale was the best predictor of *Lasthenia* first-year seeding success; however, the microsite long-term scale was a very close second with Δ_i = 1.10 (Table 1). The considerably higher AIC_c values of both predictions based on 2005 alone suggest although each scale of model was able to identify successful seeding sites for *Lasthenia*, there is some benefit to a temporally wider data set. There was no support for the null model.

In contrast, for *Lupinus*, site suitability estimates based on the four spatiotemporal scales of input data had only moderate predictive abilities (cross-validation AUCs 0.76–0.79) and in fact showed negative relationships to first-year seeding success (2005) in unoccupied sites (Table 1b). Model selection based on AIC_c also demonstrated the poor ability of SDMs to predict *Lupinus* first-year seeding success. The best-predicting SDM, based on transect-wide data in 2005, was similar in its predictive capacity to a null model when compared in terms of AIC_c (Table 1b). Because of their failure to positively predict seeding success, no SDMs were included in subsequent analyses for *Lupinus*.

Spatial isolation from conspecifics.—On average, *Lasthenia* seeding sites were 206.7 ± 37.2 m (mean ± SE) from the nearest conspecific patch and located within 1000 m of 7.9 patches (SE = 0.8). *Lupinus* seeding sites were on average 172.8 ± 21.3 m from the nearest conspecific patch and located within 1000 m of 9.7 patches (SE = 0.9).

Surrounding species abundance was a significant positive predictor of first-year seeding success for both species at each measured scale (Fig. 1a, c). *Lasthenia* first-year seeding success was best predicted by abundance at the medium scale (250 m; *w_i* = 0.94; β = 3.0 × 10⁻⁴, *F*_{1,34} = 12.1842, *P* = 0.0014; Table 2a, Fig. 1a). Abundance at the large scale was a similarly excellent predictor, although with a substantially reduced *w_i* (Table 2a). Although conspecific abundance at the 50- and 250-m scales were highly correlated (*r* = 0.90, *P* < 0.0001) for *Lasthenia*, the local scale of conspecific abundance had much lower predictive ability (Δ_i = 6.4) and was more similar to the null model. *Lupinus* first-year seeding success was best predicted by abundance at the large scale (1000 m; *w_i* = 0.57; β = 4.6 × 10⁻⁶, *F*_{1,56} = 5.2779, *P* = 0.0263; Table 2b, Fig. 1c). This effect was driven by three seeding locations in which *Lupinus* had both very high abundance at this scale and relatively high seeding success (Fig. 1c). Similarly, conspecific abundance at the 50- and 250-m scales were correlated (*r* = 0.42, *P* = 0.0028), but the local scale of conspecific abundance had much lower predictive ability (Δ_i = 5.0). There were no other correlations between scales of conspecific abundance for either species.

Models combining site suitability and spatial variables.—For *Lasthenia*, first-year seeding success was best predicted by surrounding conspecific abundance (*w_i* = 0.46; Table 3) when ranked against isolation alone and/or predicted site suitability. In contrast to our hypothesis, seeding success was lower at more distant sites (isolation: β = -2.1 × 10⁻², *F*_{1,33} = 3.8290, *P* = 0.0591). The second best predicting model included both isolation and surrounding conspecific abundance and had equivalent predictive ability; in this model isolation was not a significant predictor (isolation and surrounding conspecific abundance: isolation β = -7.2 × 10⁻³, *P* = 0.5189; conspecific abundance β = 3.3 × 10⁻⁴, *P* = 0.0091; Table 3, Fig. 1a, b). Isolation alone was also a poor negative predictor of first-year seeding success.

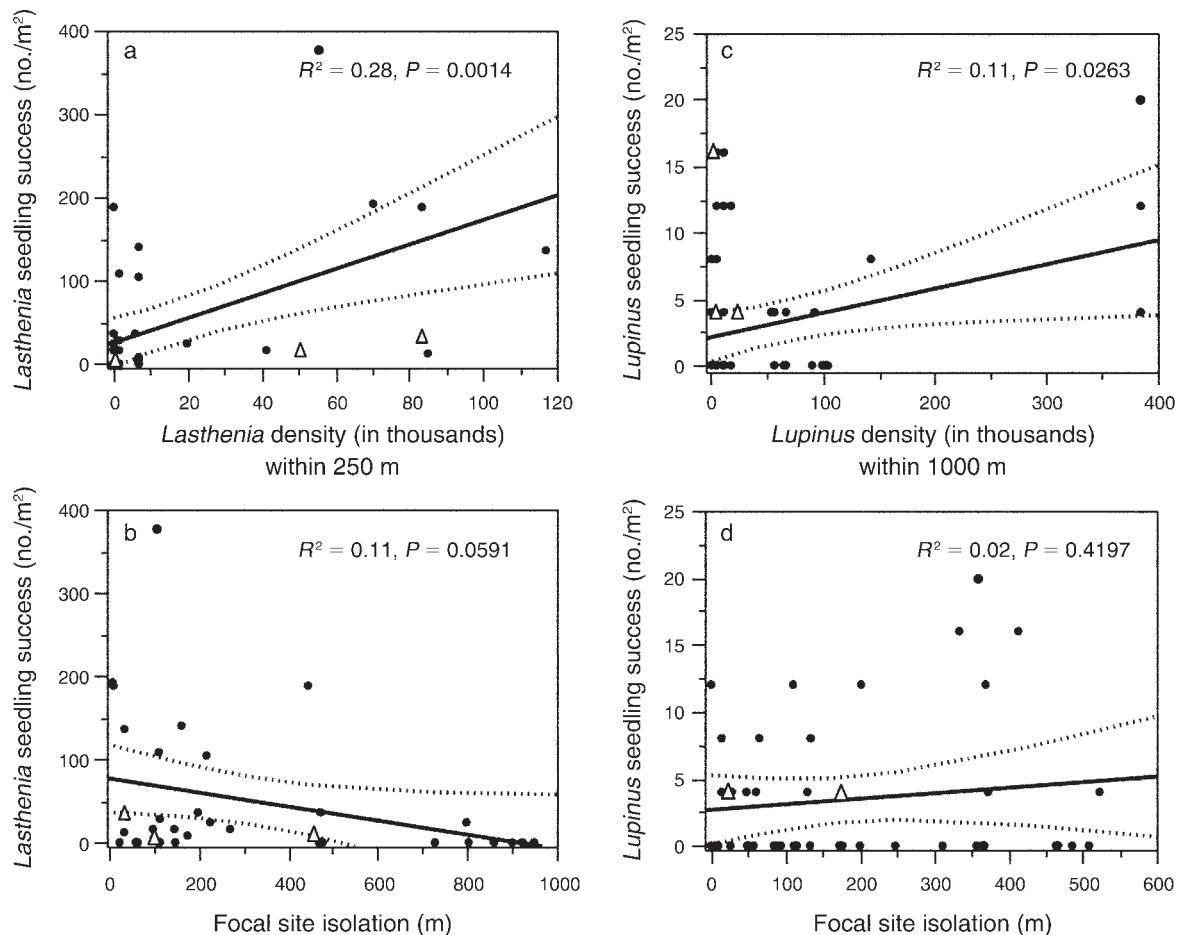


FIG. 1. First-year seeding success at unoccupied sites for each seeded species (*Lupinus nanus* and *Lasthenia californica*) as predicted by focal site isolation and surrounding conspecific density, the estimated number of conspecifics in patches within a given radius in Lake and Napa counties, California, USA. First-year seeding success is the number of plants in 2005 within 0.25-m² plots. Seeding success had the strongest relationship with density for *Lasthenia* at the 250-m scale ($w_i = 0.46$), and the combination of isolation and density at the 1000-m scale for *Lupinus* ($w_i = 0.69$). Persistent seeding effects, represented as triangles, were observed at three sites for each species in 2007; these data points were not included in calculating the depicted regressions of 2005 seeding effect but are shown for comparison.

Although SDMs were significant positive predictors of *Lasthenia* seeding success, they did not improve our ability to detect successful seeding sites when compared to spatial predictors (Table 3).

Lupinus seeding success at unoccupied sites was strongly positively predicted by surrounding conspecific abundance at the 1000-m scale ($w_i = 0.69$; conspecific abundance: $\beta = -4.6 \times 10^{-6}$, $F_{1,46} = 5.2779$, $P = 0.0263$; Table 3, Fig. 1c). There was no relationship between *Lupinus* seeding success and isolation ($\beta = -1.0 \times 10^{-3}$, $F_{1,43} = 0.6642$, $P = 0.4197$; Fig. 1d).

Persistent seeding effect

For both seeded species, previously unoccupied sites that exhibited a persistent seeding effect in 2007 were an apparent random subset of those in which plants established in 2005; they were unrelated to SDM predictions, isolation, or surrounding conspecific abun-

dance (Fig. 1). For *Lasthenia*, persistently occupied sites occurred at predicted values of the best SDM (long-term transect-wide scale) that ranged from 0.39 to 0.61. They ranged from very close to conspecific patches (10.1 m) to relatively far (444.4 m; Fig. 1a) and had very widely ranging abundances of conspecifics within a 250 m radius (0–55 768 individuals; Fig. 1b). For *Lupinus*, persistently occupied sites occurred at relatively low predicted values of the best SDM (transect-wide 2005 scale) that ranged from 0.06 to 0.21; the lack of correspondence with site suitability to seeding is in this case consistent with the low predictive capacity of these models. Sites with a persistent seeding effect for *Lupinus* ranged from adjacent to conspecific patches to a moderate range (1–133.2 m; Fig. 1c) and had very widely ranging abundances of conspecifics within a 1000 m radius (0–24 550 individuals; Fig. 1d).

TABLE 2. Comparison of surrounding conspecific abundance data, collected at different spatial scales, in their ability to predict seeding success for (a) *Lasthenia californica*, $N = 34$ sites, and (b) *Lupinus nanus*, $N = 55$ sites, in unoccupied sites.

| Scale | K | AIC_c | Δ_i | w_i |
|--|----------|--------------|------------|-------------|
| a) <i>Lasthenia</i> hypotheses: unoccupied site suitability is best predicted by SDMs generated at the | | | | |
| Transect scale, 50 m | 1 | 305.0 | 6.4 | 0.04 |
| Medium scale, 250 m | 1 | 298.6 | 0.0 | 0.94 |
| Maximum scale, 1000 m | 1 | 309.4 | 10.8 | 0.00 |
| No scale | 0 | 307.2 | 8.6 | 0.01 |
| b) <i>Lupinus</i> hypotheses: unoccupied site suitability is best predicted by SDMs generated at the | | | | |
| Transect scale, 50 m | 1 | 165.5 | 5.0 | 0.05 |
| Medium scale, 250 m | 1 | 162.1 | 1.6 | 0.25 |
| Maximum scale, 1000 m | 1 | 160.5 | 0.0 | 0.57 |
| No scale | 0 | 163.4 | 2.9 | 0.13 |

Notes: Seeding success was calculated as the number of plants in seeded plots in 2005. Models at the three scales were compared separately for each species. More plausible models are indicated by smaller values of AIC_c and Δ_i . For each model, i , K is the number of parameters. Akaike weight, w_i , denotes the weight of evidence in support of the model at hand, given the set of proposed models. Models with the lowest AIC_c and those within two units of AIC_c from this model are shown in boldface type.

DISCUSSION

Contrary to our predictions, spatial isolation from conspecifics was never a positive predictor of establishment success; in fact for both species it was a negative predictor. In the first year following seeding, suitable sites for *Lasthenia* were best predicted by local conspecific abundance and were similarly well predicted by an index of site suitability based on plant community data (Tables 2 and 3, Fig. 1). Good sites for establishment existed where *Lasthenia* was profuse

within 250 m, a common size of meadows in our study system. The excellent predictive ability of all four spatiotemporal scales of plant community-based models suggested that these suitable unoccupied sites for *Lasthenia* were actually uncommon because the predictive power of species distribution models that include many suitable unoccupied sites was relatively low (Moore and Elmendorf 2006). For *Lupinus*, good sites for seeding establishment existed where the species was abundant within 1000 m (Table 2, Fig. 1d), a distance

TABLE 3. Comparison of spatial variables with respect to their ability to predict first-year seeding success for (a) *Lasthenia californica*, $N = 34$, and (b) *Lupinus nanus*, $N = 55$, in unoccupied sites.

| Scale | k | AIC_c | Δ_i | w_i |
|--|----------|--------------|------------|-------------|
| a) <i>Lasthenia</i> hypotheses: unoccupied site suitability is best predicted by | | | | |
| Best spatial variables: | | | | |
| Focal site isolation | 1 | 305.7 | 7.1 | 0.01 |
| Surrounding conspecific abundance, medium scale (250 m) | 1 | 298.6 | 0.0 | 0.46 |
| Both spatial variables | 2 | 300.7 | 2.1 | 0.16 |
| Best SDM predictions: | | | | |
| Transect-wide long-term scale SDM predictions | 1 | 301.7 | 3.1 | 0.10 |
| Combinations of spatial variables and best SDM predictions: | | | | |
| Focal site isolation and transect-wide long-term SDM predictions | 2 | 302.1 | 3.5 | 0.08 |
| Surrounding conspecific abundance (250 m) and transect-wide long-term SDM | 2 | 301.0 | 2.4 | 0.14 |
| Both spatial variables and transect-wide long-term SDM predictions | 3 | 303.2 | 4.6 | 0.05 |
| No variables: | | | | |
| No predictors | 0 | 307.2 | 8.6 | 0.01 |
| b) <i>Lupinus</i> hypotheses: unoccupied site suitability is best predicted by | | | | |
| Best spatial variables: | | | | |
| Focal site isolation | 1 | 156.6 | 1.9 | 0.27 |
| Surrounding conspecific abundance, medium scale, 1000 m | 1 | 160.5 | 5.8 | 0.04 |
| Combinations of spatial variables: | | | | |
| Focal site isolation and surrounding conspecific density | 2 | 154.7 | 0.0 | 0.69 |
| No variables: | | | | |
| No predictors | 0 | 163.4 | 8.7 | 0.01 |

Notes: Seeding success was calculated as the number of plants in seeded plots in 2005. Surrounding conspecific abundance was the estimated number of conspecifics in patches within a given radius. Focal site isolation was the distance of seeding locations from the nearest conspecific patch. Scales of surrounding conspecific abundance and species distribution model (SDM) predictions were included based on earlier model comparisons. All models comparisons were species specific. For *Lupinus*, SDM predictions were not significantly correlated with seeding success (see Table 1). More plausible models are indicated by smaller values of AIC_c . For each model, i , K is the number of parameters. Akaike weight, w_i , denotes the weight of evidence in support of the model at hand, given the set of proposed models. Models with the lowest AIC_c and those within two units of AIC_c from this model are shown in bold.

that coincides with the typical scale of significant cover and land type changes in our research site. Isolation from conspecific patches and predictions based on plant community composition completely failed to identify successful seeding sites for *Lupinus*. Thus, suitable sites for *Lupinus* establishment existed, but were difficult to pinpoint within broad landscapes. Dispersal limitation and/or fine-scale establishment requirements are likely to limit the distribution of *Lupinus*, a finding that is in accordance with previous work at the site (Moore and Elmendorf 2006, Moore 2009).

Dispersal limitation operated relatively close to existing populations for *Lasthenia* and in microsites within broadly occupied landscapes for *Lupinus* (Fig. 1). This suggests that favorable environmental conditions were spatially autocorrelated to a finer degree than even good model predictions can represent. Gram et al. (2004) similarly found that seeding success of some native species in restored invaded grasslands increased with proximity to source habitat, in their case uninvaded serpentine hummocks. They attributed their findings to patterns in soil quality, whereas we found that for *Lasthenia*, even very good niche models did not improve our ability to pinpoint dispersal limited sites over spatial variables alone. Our findings are in some ways unfortunate because it would be valuable to find distant yet highly predictable suitable sites in which restoration could greatly expand the distribution of the species of concern. In contrast to Seabloom et al. (2003a), our results suggest that restoration via simple seed addition is very challenging in this annual grassland system.

The ability of SDMs to predict first-year seeding success in *Lasthenia* was greater when models were built on observations from larger scales of space and time. All scales of SDM predictions positively predicted *Lasthenia* first-year seeding success, but the best model was the one based on the most inclusive data: the transect-wide, long-term scale (Table 3). The second best model was generated at the microsite long-term scale. These models considerably outperformed those generated based on a single year of data collection, by ~ 2.0 units of AIC_c . Higher performance of models based on larger and longer scales of observation may reflect the well-known importance of seed banks in annual grasslands (e.g., Levine and Rees 2004). Seed dormancy is an important determinant of annual species abundance and both *Lasthenia* and *Lupinus* populations fluctuate dramatically in response to annual rainfall (Hobbs and Mooney 1995, Moore 2009, Levine et al. 2010). When previously occupied sites are seemingly "vacant" in any given year, therefore, they may in fact be inhabited by viable dormant seeds, and the same may be true of vacant sites that lie very close to occupied ones. Models thus may be more predictive when they use input data that averages over this source of small-scale noise in apparent occupancy. We suggest that whenever possible use of multiple years of survey data should be considered for generation of SDM predictions in annual systems or

those with significant interannual variation in demography.

We found considerable evidence for dispersal limitation for both species in the first year, and substantial power to predict these successful sites using environmental data, particularly for *Lasthenia*. In 2005, seeding was successful in 55.9% of sites for *Lasthenia* and 36.2% of sites for *Lupinus*. *Lasthenia* densities within plots were within the range found commonly in *Lasthenia* patches; *Lupinus* densities were lower than those observed in natural patches. In the third year, a few persistently occupied sites for each species occurred at a wide range of spatial isolation and conspecific abundance (Fig. 1), and for *Lasthenia*, whose seeding effect was well predicted by SDMs, they had a wide range of predicted levels of site suitability. It is possible that the persistent effect in the third year of our study underestimates the longer-term impact of our seeding treatments. In a similar grassland system, Seabloom et al. (2005) found that added annual forbs decreased dramatically to near zero cover from 2 to 4 years after seeding, but had a strong increase in cover in the fifth year.

Two factors that may have limited our ability to detect persistent seeding effects are the numbers of seeds we added and differential seed emergence in response to local environmental conditions. Although our seeding rate was high, greater quantities of seed might have helped overcome the seed dormancy, low emergence, and interannual demographic variability common in these annual grasslands. Consumer pressure on added seeds and their progeny may have contributed to low establishment success for our target species and has been observed to influence establishment patterns in other seed addition studies (e.g., Orrock et al. 2009). Lupines in particular are commonly the target of granivory (Maron 1997, Maron and Simms 1997, Maron and Gardner 2000). If seed predation is spatially density dependent, restoration far from established populations could be advantageous (Janzen 1970, Connell 1971). In previous work on *Lupinus nanus*, however, we found no evidence for such an effect (Moore 2009). We expect that preemergence seed dispersal from plots contributed minimally, if at all, to the low observed emergence rates; characteristics of our species' seeds (i.e., small, no seed coat modifications for dispersal) and lack of increase in target species density in control plots suggest that seeds were likely to have stayed in place.

Conclusion

The spatial distributions of many or most species are dispersal-limited at some scale, offering opportunities for restoration through simple seed addition. Approaches that target the establishment of novel populations in known suitable unoccupied locations or supplement the demography of depauperate populations may conserve economic resources while buffering populations from Allee effects and demographic stochasticity. However, precisely determining the locations

of suitable and unoccupied sites in which seeding is likely to have a strong persistent effect remains a major challenge. Our study points to the clear need to incorporate dispersal limitation and habitat suitability into predictive models of restoration success. We found a striking role for closeness to conspecifics in predicting seed addition success, involving either near proximity (<250 m isolation) in the case of *Lasthenia*, or broader co-occurrence (within the same 1000 m landscape) in the case of *Lupinus*. These results suggest that at scales of 10^1 – 10^3 m, first, both of these species are relatively poor dispersers, incapable of saturating their available habitats, and second, environmental suitability for these species is strongly spatially autocorrelated in ways that cannot be captured by plant community (or abiotic) data alone. Based on our results, increasing the density of such species near to where they already occur appears to be the most efficient use of limited monetary and temporal restoration resources. While perhaps not heartening for large-scale restoration, this result minimizes conflicts between genetic and ecological restoration goals.

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APPENDIX A

List of species that co-occur with *Lasthenia californica* (*Ecological Archives* A021-095-A1).

APPENDIX B

List of species that co-occur with *Lupinus nanus* (*Ecological Archives* A021-095-A2).