Using models and field experiments to define niche versus dispersal limitation in California grassland annuals

By

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ABSTRACT

A vital component of understanding community structure, species invasions, and the potential for ecosystem restoration is the ability to distinguish between the roles of environmental constraints versus dispersal limitation in controlling species distributions. Three main concerns are: (1) how to identify dispersal-limited species, (2) the degree to which the distributions of individual species are influenced by particular environmental constraints versus seed availability, and (3) how to locate suitable, but unoccupied sites. To address these concerns, species distribution models and experimental and observational field methods were applied in a series of three studies on annual plants in California grasslands. First, species distribution models were paired with a seeding experiment to test a novel technique for identifying dispersal-limited species. Species that distribution models suggested were niche-limited had lower fitness when planted in unoccupied sites, while species that models suggested were dispersal-limited had equivalent fitness when planted in occupied and unoccupied sites. Thus, species distribution models based on observation data successfully identified dispersal-limited species. Second, a multi-year study of the shifting distributional patterns of a single annual forb, *Lupinus nanus,* revealed that patch locations and extents were determined by temporal variation in environmental constraints rather than by seed availability. Third, species distribution models created on multiple spatial and temporal scales, spatial data on existing species' patches, and a seeding experiment were used to identify the location of suitable unoccupied sites for *Lasthenia californica* and *Lupinus nanus*. Dispersal-limited sites for *Lupinus* were rare and poorly predicted by environmental and/or spatial variables. Dispersal-limited sites for *Lasthenia* were more abundant, but generally occurred near existing patches (within 500 m). These results indicated that dispersal-limited sites may have limited use in a restoration context, since seeding of either species was found to be unlikely to establish new populations distant from existing ones. Collectively, findings from these three studies suggest that although dispersal-limited sites exist for some species, they may have only a weak influence on observed species distributions. Furthermore, in the context of ecosystem management, dispersal limitation may be of limited practical significance to restoration, emphasizing the paramount need for conservation of intact populations and ecosystems.

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INTRODUCTION

A recent debate in ecology has contrasted the degree to which the availability of suitable sites versus propagules controls species distributions, and thus community composition. A recent influential work by Hubbell (2001) proposed that species distributions could be the results of random dispersal and subsequent demographic stochasticity, rather than abiotic and biotic niche constraints. Indeed, empirical studies have found that diversity and abundance of plants can be increased through propagule addition (Turnbull et al. 2000, Seabloom et al. 2003, Foster et al. 2004, Ehrlen et al. 2006).

The current focus on propagule availability stands in contrast to the work of foundational by ecologists such as Whittaker (1975), Hutchinson (1958), and Grubb (1977), who outlined the mechanisms that lead to species distributions in an environmentally focused context. For example, Whittaker used meticulous documentation of how the distribution of species coincides with large scale environmental gradients as evidence that environmental factors drive community composition (e.g. Whittaker and Niering 1975). At smaller scales, the strong role of microsite availability in delineating species distributions has been widely recognized, and "niche limitation" has been consistently considered the primary constraint on species' distributions (see review by Silvertown 2004). In fact, the majority of conservation and restoration efforts have been geared towards ensuring that appropriate environmental conditions (be they soil, water availability, nutrients) exist for species of concern.

In the following three chapters, I have sought to clarify the relative importance of niche and dispersal limitation on the distribution of annual plant species in grasslands in the North Coast Range of California. I delineated two areas in need of focused study. First, recent work by Seabloom et al. (2005) and others has suggested that alleviation of dispersal limitation through seed addition is a potential means of grassland restoration. In order for seeding to be an efficient and effective restoration strategy, improved understanding of both which species are indeed dispersal limited and the location of suitable unoccupied sites is necessary. Second, dispersal limitation is unlikely to be the single constraint on a species' distribution. Focused study of multiple constraints on species with distributions that appear likely to be limited by seed availability, such as those that occur in temporally variable patches, would increase our ecological understanding of the importance of dispersal limitation relative to other constraints.

With coauthors Susan Harrison and Sarah Elmendorf, I contrasted the influences of niche limitation (in terms of specific environmental constraints) and dispersal limitation on a suite of native and non-native annual plants through three studies that each included experimental and observational components. First, in a study on six annual species, we asked if it was possible to apply species distribution models to identify propagule-limited versus niche-limited species. Second, I conducted an in-depth study of a single species, *Lupinus nanus*, in which I determined the relative contributions of environmental constraints versus seed availability to its distributional pattern at the fine-scale. Third, we explored the utility of propagule limitation in a restoration context, by applying species distribution models and spatial data together to identify propagule-limited sites for two native annuals, sky lupine, *Lupinus nanus,* and common goldfields, *Lasthenia californica*. The later two studies focused on species with patchy distributions, since aggregation of species into well-defined patches provides the opportunity to contrast conditions and interactions at their borders, where distributional constraints, be they resources, demographic stochasticity, or dispersal, are presumably most significant.

The first chapter of this dissertation was also the first in a series of continuing work in collaboration with Sarah Elmendorf, spanning both of our dissertations. Through combining a seeding experiment with species distribution modeling, we determined that propagule limitation does exist and developed a new method for the differentiation of propagule versus niche constraints. We found that the majority of the examined species were limited by microsite availability, since fitness in occupied sites was greater than in unoccupied sites. We suggest that species distribution models can be applied to predict which species are more likely to be limited by propagule than microsite, or niche, availability. This research is particularly novel because it integrates empirical and analytical methods to address a prominent restoration issue.

In the second chapter, I queried the roles of abiotic and biotic niche constraints, seed availability, and annual weather variation on the patchy occurrence and demography of *Lupinus nanus* through a fine-scale seed addition experiment that perturbed the boundaries of naturally occurring patches. Environmental factors presented specific niche constraints for this species, and were the most important drivers of *Lupinus* distribution, though they varied over space and time. Seed availability was influential in patch margins in some years, but played a minor role relative to environmental constraints.

In the third chapter, Susan Harrison, Sarah Elmendorf, and I combined a seeding experiment with spatial and temporal data on the distribution of two annual plant species in order to predict the distribution of suitable unoccupied sites, with respect to existing populations. Although suitable unoccupied sites existed for both species, we concluded that they were unlikely to be useful in a restoration context since they were either, rare and difficult to predict, or occurred predominately adjacent to occupied patches.

The most significant conclusion from these three studies is that although dispersal limited sites occur for some species, we found dispersal limitation to have limited influence on the species and sites examined. In no case did our findings suggest that dispersal limitation is a dominant mechanism for species distributions in these grasslands. When we examined dispersal versus niche limitation through species distribution models, we found that the majority of species had distributions well-explained by site attributes. I found that dispersal limitation has only weak influence in the shifting distributional patterns of *Lupinus nanus*, despite the fact that spatio-temporal variation in species distributions is a product of variation in propagule availability in several prominent ecological models. Finally, when we examined the spatial distribution of suitable unoccupied sites for two native forbs, we found that dispersal limited sites were rare, and were located near existing populations.

Our findings suggest some critical directions for future study on species distributions. First, there is a strong need for clarification of the concepts of niche and propagule limitation. In particular, rather than simply stating that a species is niche limited, it is more valuable to know the specific environmental constraints that are significant, and on what life stage these constraints act. Second, it is important to recognize that only rarely are species limited by single constraints alone, rather the majority of species are likely to all on a continuum between niche and propagule limitation (Gravel et al. 2006). Rather than continuing to debate whether propagule or niche constraints dominate, more interesting avenues for future research will identify conditions under which we find the balance to swing in favor of one or another. Third, there is an increasing need to determine how each of these constraints on species distributions can be applied in the context of species conservation and ecosystem restoration. Our findings that dispersal limited sites and species are not common stresses that restoration is universally a difficult process, and highlights the pressing need for conservation of species and intact ecosystems.

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CHAPTER 1

Propagule versus niche limitation:

Untangling the mechanisms behind plant species' distributions

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ABSTRACT

Distinguishing the roles of propagule limitation and niche requirements in controlling plant species distributions is important for understanding community structure, invasion, and restoration. We used species distribution models based on plant and environmental survey data to assess the strength of species' affinities for particular environmental conditions. We hypothesized that species with statistically detectable environmental requirements were primarily niche-limited, while species with weak habitat affinities were primarily propagule-limited. We tested this hypothesis via a seeding experiment in which we compared species' reproductive fitness in occupied and unoccupied sites. Species that appeared niche-limited based on distribution models had lower fitness when planted in unoccupied sites, while species that models suggested were propagule-limited had equivalent fitness when planted in occupied and unoccupied sites. Our results demonstrate that within a single community, both species limited primarily by niche availability or primarily by propagule availability can be identified using observational data.

INTRODUCTION

Plant distribution patterns are primarily determined by two constraints: the availability of environmentally suitable sites, and the likelihood of seeds reaching those sites. These two processes are not mutually exclusive, but rather characterize extremes of a continuum (Munzbergova & Herben 2005). At one extreme, species disperse to all sites within a landscape, but only persist where niche requirements are met, leading to highly predictable and stable communities in space and time (Grubb 1977; Pulliam 2000). This paradigm is the basis of species distribution models, which predict occurrence patterns from environmental data (Guisan & Thuiller 2005). At the other end of the continuum, distributions are strongly influenced by propagule availability such that plants occupy only a subset of environmentally suitable sites. (Levine & Murrell 2003).

Foundational works in community ecology emphasized the role of abiotic niche requirements in species' distributions (de Candolle 1859; Grinnell 1917; Whittaker & Niering 1975; Ellenberg 1988). Since then, the niche concept has grown in sophistication to encompass biotic as well as abiotic influences on species' distributions. For example, competitors, facilitators, predators, and parasites can also be influential on species occurrence patterns (Callaway & Walker 1997; Shea & Chesson 2002; Bruno *et al.* 2003). Here, we refer to species whose distributions are largely a product of ecological sorting, driven by site-specific differences in both biotic interactions and abiotic conditions, as niche-limited.

A recent surge of interest in the role of propagule supply in structuring communities has resulted in a re-evaluation of the importance of niche differentiation for community structure (Levine & Murrell 2003; Munzbergova & Herben 2005). Individual species could be limited by propagule availability for several reasons: low reproductive fitness in some years, invasion of new habitat, lack of persistent seed banks, or inadequate dispersal. We refer to propagule-limited species as those whose landscape distribution is more strongly influenced by seed availability than habitat availability.

Seed addition experiments have provided empirical support for *community-level* seed limitation (Burke & Grime 1996; Tilman 1997; Zobel *et al.* 2000; Foster & Tilman 2003), but they do not reveal how the relative strength of distributional constraints varies among different species within the same community. By adding propagules of multiple species to same plots, community studies evaluate propagule limitation as an emergent property of communities, assaying which characteristics of communities make them open to immigration. Diversity may sometimes be enhanced through seed addition, but most species seeded into previously unoccupied habitats do not survive to maturity (Turnbull *et al.* 2000), suggesting that the majority of individual species are niche-limited. Notably, some single species seed addition experiments have identified significant propagule limitation (Primack & Miao 1992; Miller & Duncan 2003; Seabloom *et al.* 2003a; Szentesi & Jermy 2003). Yet it remains unclear how the relative importance of niche versus propagule limitation varies among constituent species in a community.

Two aspects of most existing seed addition studies limit the population-level inferences that can be made. First, in order to increase the likelihood that some individuals will survive, seeds are often added at much higher densities than would naturally occur during colonization events (Turnbull *et al.* 2000) High seeding rates ensure that a small fraction of colonizing individuals will survive in the short-term, but only long-term monitoring can reveal whether the individuals will form a persistent population. Second, many studies on propagule limitation have focused on perennial species, which often do not reproduce within the time frame of observation (Miller & Duncan 2003; Seabloom *et al.* 2003b; Makana & Thomas 2004, but see Werner 1977 and Primack & Miao 1992). In order for a species to be propagule-limited within a landscape, empty regeneration niches must exist in which individuals can successfully germinate, survive, and reproduce (Grubb 1977).

Experimental comparisons of lifetime reproductive fitness in occupied versus unoccupied sites provide the most robust test of niche versus propagule limitation. This relatively straightforward experiment has not yet, to our knowledge, been conducted. Another way to test for niche versus propagule limitation relies on observational data. Species distribution models (SDMs) were originally developed to determine the environmental gradients that define a species' niche (Austin *et al.* 1990). We propose that SDMs can also be used to investigate the relative importance of niche versus propagule limitation in species' distributions. SDMs correlate species occurrence data with environmental factors to delineate niche space. Predictors can be measures of the environment (e.g., soil chemistry, landscape attributes, or presence of interacting species), or proxies for environmental conditions such as distribution patterns of coexisting species. For a species whose distribution is in equilibrium, these models can be very powerful and generate accurate predictions of occurrence over large areas (Lehmann *et al.* 2002a). Conversely, for species that do not inhabit the majority of suitable sites, these models may lead to highly inaccurate predictive maps, because absences will reflect both habitat unsuitability and propagule limitation (Collingham *et al.* 2000; Guisan & Thuiller 2005). Such models are missing a critical factor influencing species occurrence and may therefore lead to erroneous predictions about habitat suitability, resulting in poor model predictive ability. Thus, a well-parameterized SDM that is unable to distinguish between occupied and unoccupied sites may be indicative of a species that is propagule- rather than niche-limited.

We used both SDMs and a seed addition experiment to determine whether each of six species' distributions was affected predominantly by niche or propagule limitation within a heterogeneous grassland landscape. Using three years of plant occurrence data and a wide range of environmental parameters, we developed two different types of SDMs: one parameterized from measured environmental conditions, and the other based on the distributional patterns of coexisting species. We hypothesized that species whose distributions were strongly predictable by SDMs were niche-limited, whereas those whose distributions were not strongly predictable with respect to environmental and plant community data, i.e., did not have a statistically defined niche by either SDM method, were propagule-limited. To test this hypothesis, we conducted a seeding experiment at approximately half of the sites used in the SDMs. We compared the reproductive fitness of each of six species grown in sites that were previously occupied versus unoccupied by that species. We predicted that the niche-limited species as determined by the SDMs would have significantly higher fitness in sites they occupied than in sites where they were absent, while the propagule-limited species would not, since the latter species' absences are expected to be uninformative about site suitability.

METHODS

Study site

Our grassland study area was located in Napa County at the McLaughlin Natural Reserve in the Coast Range of northern California, USA. We selected a study area with dramatic fine-scale heterogeneity in multiple abiotic resources. The area is a patchy mosaic of soil types ranging from harsh serpentine to more neutral sandstone-derived soils. Serpentine soils are derived from ultramafic rock and are high in magnesium and iron and macro-nutrient poor, conditions that present hostile growth conditions to many plant species. The close proximity of very different environmental conditions in the study area allowed us to create niche models that included a wide range of environmental factors within a spatial extent that was practical for experimentation.

The study area contained a grid of 132 evenly spaced sampling sites placed 50-m apart covering a 0.33-km^2 area. We excluded 29 sites located in dense chaparral; our final data set had 103 grassland sites. At each point soil samples were taken in 2001 and analyzed for soil chemistry at A & L Western Laboratories (Modesto, California, USA). Soil water was measured gravimetrically in April of 2003. Slope, aspect, and soil depth were also recorded. We made a visual estimate of shading at each site, categorizing each as beneath tree canopy, receiving indirect shade or in full sun. Aboveground plant biomass samples were taken at each site after both the 2001 and 2002 growing seasons as an estimate of annual site productivity. Four 1-m quadrats were sampled from 2001-2003 for plant species presence/absence at each site. Observational data on plant community composition and soil chemistry measurements were obtained from a previous study (Davies *et al.* 2005).

Species distribution modeling

Generalized additive models

We built generalized additive models (GAMs) based on factors that influence plant fitness for all herbaceous plant species at the study area. GAMs are related to generalized linear models, but relax the assumption of linearity between predictor and response variables. By using a non-parametric smoothing function to estimate the relationship between the dependent and independent variables, GAMs fit variable shapes of species responses to environmental gradients (Lehmann *et al.* 2002b). Out of the 191 species present out our study site, we modeled the distributions of the 36 species that occurred in at least 25% and no more than 75% of the sampling sites, using each species' presence/absence as a binomial response variable. Presence at a site was defined as occurrence in any of the four sampling quadrats between 2001 and 2003. We averaged productivity from the two years when it was measured. We used the ratio of Ca:Mg because previous work suggests this ratio controls plant responses to serpentine soils (Kruckeberg 1984; Harrison 1999). We used an estimate of solar radiation derived from slope and aspect (McCune & Keon 2002). Prior to conducting analyses we checked for correlation among variables and discarded one variable from each pair with $r^2 > 0.50$. Our final list of predictor variables included NO_3, P, K, Ca:Mg, S, Na, Ni, organic matter, pH, % clay, soil water content, solar radiation, soil depth, and productivity.

All GAM model fitting and cross-validation was implemented in S-plus (version 6.0) using the GRASP platform (version 3.2, Lehmann *et al.* 2002b). We estimated nonparametric functions simultaneously using a spline smoother with two degrees of freedom. We used a forwards-backwards stepwise procedure based on the AIC (Akaike

Information Criterion) to parameterize models. For cross-validation, the program built five separate models per species, parameterizing each with 80% of the original data, and testing model predictions on the remaining 20%. We used the area under curve (AUC) statistic calculated from the ROC (Receiver Operating Characteristic) curve for the cross-validated models to assess model quality for each species. This is an unbiased method for evaluating fit of models to presence-absence data (Metz 1986; Fielding & Bell 1997). The AUC for a given model can range from 0.5-1.0; models with AUC=0.5 predict distribution no better than randomly, whereas models with AUC = 1.0 perfectly predict distribution. Using AUC thresholds defined by Pearce and Ferrier (2000), we evaluated each species' model according to its ability to predict site occupancy in the cross-validation data. Models with $AUC \leq 0.70$ are considered to have poor predictive capability, whereas those with $AUC > 0.70$ are considered to have reasonable to very good predictive capability (Pearce & Ferrier 2000).

Beals' plant community index

We used plant survey data from 2001-2003 to predict site suitability for each species based on patterns of plant co-occurrence. We based our predictions on the Beals' index (Beals 1984; Munzbergova & Herben 2004), which is calculated according to the formula:

$$p_{ij}=(1/S_i)\Sigma_k N_{jk}/N_k$$

where p_{ij} is the probability of finding species j at site i, S_i is the species richness of site i (minus one if species j is present), N_{jk} is number of joint occurrences of species j and k in the predictor sites, N_k is number of occurrences of species k in the predictor sites. In order to make results broadly comparable to the GAM results, we calculated site suitability for the Beals' index models using a similar cross-validation approach: we randomly subset the data into five groups and built models for each species using 80% of the data as the predictor sites. From these models, we generated predictions for the remaining 20% of the sites, and calculated AUC values for each species from the resulting predictions. We developed an S-Plus script to calculate Beals' predictions; AUC statistics were calculated in JMP (version 5.1).

Seed addition experiment

From the 36 species modeled, we selected six for an experimental test of our hypothesis that species whose distributions could not be reliably predicted based on SDMs were propagule-limited, while species that could be well predicted were niche-limited. We selected both species that we anticipated were niche-limited (i.e., those with relatively high model AUCs) and species that we anticipated were propagule-limited (i.e., those with relatively low model AUCs). A functionally diverse group of annual species were included in the experiment: a native annual forb (*Amsinckia menziesii* Lehm.), an exotic annual grass (*Bromus madritensis* L.), an exotic annual forb (*Geranium dissectum* L.), a native annual legume (*Lupinus nanus* Benth.), an exotic annual legume (*Melilotus indica* L.), and a native annual grass (*Vulpia microstachys* Nutt.).

We used 47 of the 103 grassland sites for experimentation. We determined this subset by calculating the Gower distance among all of our points based on the environmental variables used in the above models and selecting the most dissimilar sites in order to capture the full range of environmental gradients (Gower 1971). For each species, we treated sites as "occupied" where it was present in any of the four sampling quadrats between 2001 and 2003. These sites included at least 12 occupied and 26 unoccupied sites for each of the experimental species. At each experimental point we established a 1-m^2 experimental plot within 2-m of the original survey quadrats. We divided this plot into nine, 0.3 x 0.3-m subplots and seeded one species into each of six randomly selected subplots. Seeds of the experimental species were collected locally within the study area. For each experimental point we added seed collected from the nearest possible sources (generally <200-m from planting sites). In fall 2004, we planted multiple seeds in each plot, aiming to achieve at least five individuals per species per site. Based on seed availability, we added 20 seeds of *Lupinus*, 25 seeds of the other forbs, and 25 spikelets of the annual grasses to each plot in five, equally spaced, planting holes. Planted seeds were marked with a colored toothpick in order to distinguish between experimental plants and natural recruits. In cases where multiple plants emerged in a single hole, we randomly removed extra emergents, leaving a maximum of five individuals per subplot. This plant density was within the range of natural variation observed at the site.

We surveyed the experimental plots throughout the 2005 growing season. Surveys commenced during emergence (December) and continued at least monthly until senescence. During fruit set (March-June) surveys occurred biweekly. In each survey we counted and collected all green-ripe reproductive units to determine fitness. Reproductive units were the smallest unit that we could accurately count prior to dispersal and were fruits for forbs and spikelets for grasses. Since number of seeds per reproductive unit varied among species, they are a relative measure of fitness within species only.

Statistical analysis

Based on the SDM results, we classified species into one of two "model classes": those with high model AUCs (potentially niche-limited species) and those with low model AUCs (potentially propagule-limited species). We used a nested ANOVA to test whether fitness differences in occupied and unoccupied sites varied between these two classes (PROC GLM procedure, SAS version 9.1). AUC class, site occupancy (conspecifics present or absent at the site based on three years of survey data), and AUC*occupancy were treated as fixed effects, while species nested within AUC class and species nested within AUC class*occupancy were treated as random effects. Reproductive units were used as a measure of reproductive fitness. Prior to analysis, fitness data were transformed using the Box-Cox procedure in order to meet assumptions of ANOVA.

RESULTS

Species distribution models

Four of our experimental species (*Bromus, Geranium, Lupinus,* and *Vulpia*) had reasonable to very good models (AUC >0.70, Table 1.1, Pearce & Ferrier 2000) based on GAM cross validation. The predictability of their distributions by environmental data suggests that these species are niche-limited. In contrast, two species (*Amsinckia* and *Melilotus*) had poor models (AUC ≤0.70, Table 1.1). The distributions of these species were not well explained by the environmental variables, suggesting that they may be determined by propagule availability. Overall, 78% of the 36 species that we modeled had predictable distributions based on environmental variables whereas 22% did not. Of the species the species with poorly predicted distributions there were no obvious trends in seed size, dispersal mechanism, or in plant families or functional groups.

The Beals' index approach, based on community composition data, generated AUC statistics that were correlated with those from the environmentally-based GAM models (r^2=0.48, n=36, *P*<0.0001). For our six experimental species, overall model discrimination ability was the same with both methods (Table 1.1), indicating consistent predictive ability of models based on either environmental parameters or plant co-occurrence patterns.

Comparing models with experimental data

On average, species had higher fitness in sites occupied by conspecifics than in sites outside of their observed distribution. However, this effect differed between groups of species based on model class (significant model class*Presence_Absence interaction, Table 1.2). Species with high model AUCs had lower fitness when planted outside their natural distribution whereas species with low model AUCs performed equally well in all sites regardless of occupancy (Fig. 1.1). Because the AUC statistic for *Lupinus* was in the low range of the reasonable to very good category for model predictive capacity, we also conducted the same analysis without *Lupinus* as a conservative test. With this subset of species, the model class by presence/absence interaction remained significant (*F*=9.01, *P*=0.05).

DISCUSSION

In both our environmentally-based and our species-based distributional models, *Bromus*, *Geranium, Lupinus,* and *Vulpia* had patterns of occurrence that were well described by model parameters, leading us to hypothesize these species were niche-limited. In contrast, these models found weak relationships between *Amsinckia* and *Melilotus* distributions and measured environmental variables suggesting they were propagule-limited. Our experimental results supported these expectations. The four well-predicted species (*Bromus, Geranium, Lupinus,* and *Vulpia)* had lower fitness when planted outside their current distributions, while the two poorly predicted species (*Amsinckia* and *Melilotus*) had statistically equivalent reproductive fitness regardless of site occupancy. Thus, both experimental and modeling approaches identified the same groups of niche- and propagule-limited species.

Corroboration of our modeling results by field experimentation demonstrates clearly that at our study site and in our experimental year, *Amsinckia* and *Melilotus* were propagule-limited. But notably, propagule limitation is only one of a number of possible causes for poor model discrimination ability. Though propagule limitation may be an important source of omission errors (i.e., unexplained absences) from SDMs, these errors can also be algorithmic or result from failure to include all relevant parameters (Guisan & Thuiller 2005). There are several reasons to expect that the latter explanations were unlikely in our system. First, we included an extensive list of environmental parameters known to affect plant fitness. Second, the explanatory variables that we used were sufficient to build accurate predictive models for the majority of species within our community. Third, although we did not directly parameterize site-specific differences in biotic interactions, those that covaried with measured environmental variables included in our models would be included indirectly. For example, productivity serves as a proxy for the magnitude of diffuse competitive interactions. In our system, measured correlates appear to have been sufficient to account for site-specific variation in biotic effects; if competitors or generalist herbivores or parasites were responsible for the poor fit of species distribution models, we would not have found that the distribution of these plants could be altered through seed addition.

The same experimental species were identified as either niche- or propagule-limited based on both environmentally based GAM models and plant occurrence based Beals' index models. This congruity strengthens our conclusion that differences between classes of model predictive ability were unlikely to be caused by lack of appropriate environmental parameters but reflect actual biological processes. Furthermore, agreement between SDM methods suggests that on average plant composition within our study system varied predictably along environmental axes. Predictability of community composition implies that most of the component species are acting as reliable phytometers of underlying environmental conditions, and are thus niche-limited. However, even in this predominantly deterministic system, both types of SDMs identified the presence of some propagule-limited species.

To our knowledge, this is one of the few experimental validations of contrasting distributional constraints acting on species within the same community. Several authors have discriminated between niche- and propagule-limited species at the emergence and establishment stages (Miller & Duncan 2003; Makana & Thomas 2004; Munzbergova 2004; van Eck *et al.* 2005), but unless reproductive fitness is considered it is impossible to predict whether putatively propagule-limited species could form persistent populations in seeded locales. Two controlled studies (Werner 1977; Primack and Miao 1992), as well as of thousands accidental introductions of invasive species, have demonstrated that persistent populations can sometimes result from seed additions. Our work demonstrates by both modeling and empirical methods that propagule limitation is a potentially important cause of landscape distribution patterns, rather than a constraint in a limited subset of sites. This was an explicit objective of our experimental design, which compared the reproductive fitness of each species in occupied and unoccupied sites, rather than solely examining performance in unoccupied sites as is more commonly done.

Propagule limitation might reasonably be expected to depend on species traits, but the evidence thus far is mixed. An observational study of sites throughout the Netherlands found that the degree of propagule limitation was negatively correlated with long-distance dispersal ability, adult longevity and seed bank persistence (Ozinga *et al.* 2005). However, another large-scale experimental study found no relation between dispersal ability and degree of propagule-limitation (Munzbergova 2004). Similarly, we found no obvious trends in dispersal mechanism or life history traits for species that models indicated were likely to be either niche- or propagule-limited. None of the species we selected are adaptated for long-distance wind dispersal. Nor was there any apparent relationship between propagule limitation and seed weight. Additionally, grasses are generally thought to have the least persistent seed-banks (Levine & Rees 2004), but the two grass species we studied experimentally both appeared to be niche-limited.

In our grassland system, species' distributions may be in disequilibrium due to dynamic site characteristics, rather than life-history traits of the species themselves. Cattle grazed the area prior to 2001. It is possible that some plant species have not yet colonized sites that have become favorable since grazing pressure has been eliminated. Other potential causes of non-equilibrium distributions include cyclic interactions with host-specific natural enemies. Observational tallies of damage on our experimental plants revealed that rates of herbivory and pre-dispersal seed predation were too low to permit formal analysis (Moore & Elmendorf, unpubl. data). It is possible that build-up of inconspicuous herbivores or pathogens might eventually extirpate species from some environmentally suitable sites (Schops 2002) or induce metapopulation fluctuations (Thrall & Antonovics 1995; Holyoak & Lawler 1996).

Our results provide strong evidence that some species are primarily niche-limited whereas others are more strongly propagule-limited. However, care must be taken in extending these results to other systems. The likelihood of propagule limitation is highly dependent on both the pool of immigrant species and the spatial and temporal scales of abiotic and biotic constraints. As an extreme example, terrestrial plants are niche-limited in that they cannot persist in aquatic ecosystems (Munzbergova 2004). Likewise, many plant species are propagule-limited with respect to large landscape barriers. Indeed, the large number of introduced and invasive species suggests that many species are propagule limited on an inter-continental scale, although the same species may be niche-limited within their native range.

Scaling up results from a single study, such as ours, to a larger landscape requires a more detailed understanding of the mechanisms behind propagule limitation than provided by these simple statistical tests. Using sites with relatively uniform characteristics Munzbergova (2004) found that the relative importance of seed addition tended to increase with increasing spatial scale. In contrast, where variation in site characteristics is highly spatially autocorrelated, increasing the spatial extent of investigation may actually increase the likelihood of finding niche-limitation. Site specific study and experimentation may be necessary in many cases. There is no inherent reason to believe that in another landscape either *Melilotus* or *Amsinckia* would be relevantly propagule-limited. Rather, distributional constraints are a species attribute specific to a given landscape, scale, and time.

With these caveats, we believe that this novel SDM-based approach can be beneficially applied to distinguish constraints on species distributions in other systems. We anticipate that application of this technique to multiple species in other ecosystems will have many practical implications. For example, it presents a valuable conservation tool for identification of species most likely to be in non-equilibrium distributions. The use of SDMs to test for propagule limitation could identify native species as candidates for restoration by seed addition. Conversely, it could also be used to identify which exotic species are currently niche-limited and have completed their invasion. Ability to make these distinctions may assist managers in expedient allocation of resources for species restoration and eradication (Seabloom *et al.* 2003a; Nel *et al.* 2004). Since parameterization of models requires at least a moderate abundance of individuals on the landscape, it is unlikely to be an appropriate technique for species whose distributions are currently extremely restricted, such as most critically endangered species, or very recent invaders. Last, in this study we deliberately selected species that were likely to be either predominantly niche- or propagule-limited, but both niche and propagule limitation may act simultaneously on species to influence their distributions (Karst *et al.* 2005). Our results do not imply that restoration of important species that are niche-limited should not be attempted, but rather that careful site selection will be critical for successful restoration programs for these species.

We stress that the condition of propagule limitation is unique to the combination of species and location in question. When precisely communities are invasible will depend jointly on the suite of potential immigrants, the community, and underlying abiotic characteristics. From a management perspective, the most important question is not whether a community is open to immigration by *any* species, but *which* species are potential colonists. Our methods and findings demonstrate that both niche and propagule limitation can exist within the same landscape, and that SDM approaches may be applied to efficiently identify the distributional constraints acting on specific native and non-native species.

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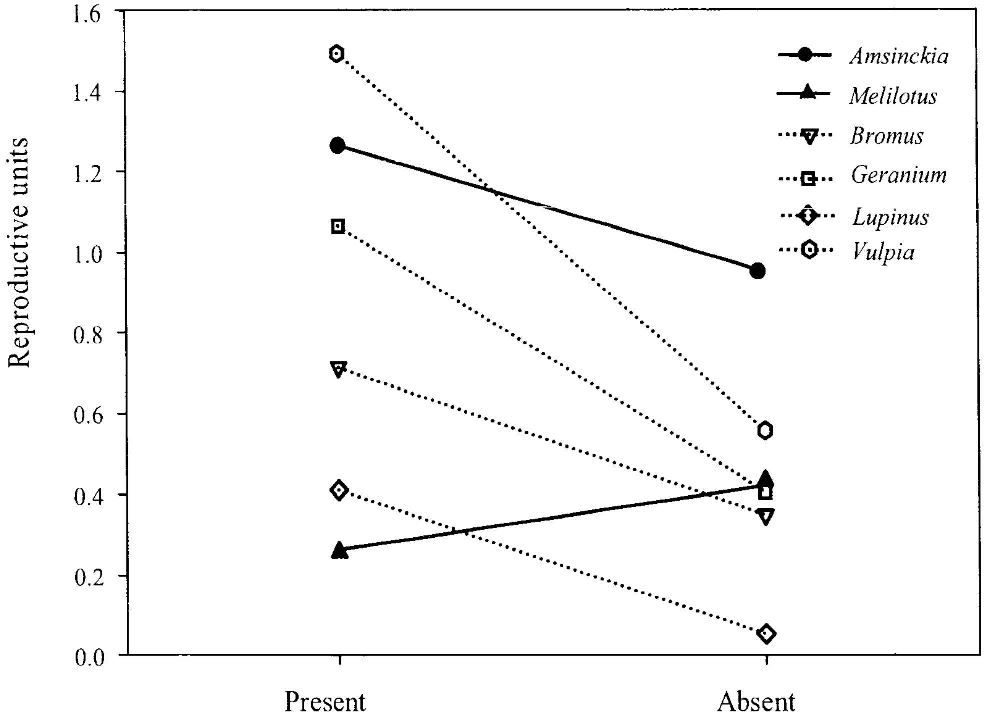
Table 1.1 Life history types, prevalence, and model performance for each of the six experimental species. For life history types, A refers to annual, N and E refer to native and exotic, L, F, and G refer to legume, forb, and grass. Prevalence is percentage of 103 survey sites occupied by a species. AUC values are from cross-validation procedures. AUCs for the models with low predictive ability (AUC <0.70) are in bold.

Species	Life history	Prevalence	GAM AUC	Beal's index AUC
Amsinckia	A, N, F	29%	**0.63**	**0.60**
Melilotus	A, E, L	32%	**0.65**	**0.66**
Bromus	A, E, G	72%	0.85	0.79
Geranium	A, E, F	30%	0.92	0.87
Lupine	A, N, L	37%	0.75	0.76
Vulpia	A, N, G	50%	0.89	0.91

Table 1.2 Analysis of variance of plant reproductive fitness at 47 planting sites. Presence_Absence is occurrence in observational data between 2001-2003. Presence_Absence and Model_Class (AUC) were treated as fixed effects; species was included as a random nested factor. A significant interaction between Model_Class and Presence_Absence indicates that species with distributions poorly predicted by SDMs responded differently than species with well-described niches when planted outside their natural distribution.

Source	d.f.	SS	MS	SSE	MSE	*F*	*P*
Species (Model_Class)	4, 4.0	64.47	16.12	3.32	0.83	19.42	**0.007**
Presence_Absence	1, 4.5	12.31	12.31	3.83	0.85	14.42	**0.015**
Model_Class	1, 4.0	1.26	1.26	62.82	15.59	0.08	0.791
Spp(Model_Class)*Presence_Absence	4, 268.0	3.32	0.83	431.78	1.61	0.52	0.725
Model_Class*Presence_Absence	1, 4.6	11.39	11.39	3.95	0.86	13.26	**0.017**

Figure 1.1 Per capita reproductive output (fruits or spikelets) by species in sites where conspecifics were present or absent. Species that SDMs identified as propagule-limited have solid lines; species that SDMs identified as niche-limited have dotted lines. Data are back-transformed least-squared means from a nested ANOVA. Significance levels reflect planned contrasts for each species in occupied and unoccupied sites; ° $P = 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$.



CHAPTER 2

Fluctuating patch boundaries of a charismatic annual forb result from niche, not dispersal, limitation

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ABSTRACT

Patchy spatial distributions of plants are often assumed to be caused either by heterogeneity in the environment, i.e. niche constraints, or by stochastic forces such as local extinction or dispersal. However, relatively few empirical studies have asked how niche and dispersal constraints interact to control spatial distributions, and even fewer have examined how these forces may vary over time to create shifting spatial distributions. For three years, I used experimental and observational methods to investigate limits on the local distribution of *Lupinus nanus*, a native annual legume that grows in dense discrete patches within California grasslands. For all three years of the study, patch cores were consistently occupied, whereas patch peripheries were occupied only during the first and third years that had above average rainfall. Exteriors were sparsely and variably occupied. Core, periphery, and exterior soils differed in soil moisture, P and NO_3. Mean fitness in these areas differed in response to competition and year. In the dry year, competition reduced fitness in patch peripheries; no other biotic limitations were observed. Seed additions showed that fitness was (R_0) > 1.0 during all years in core sites and in wet years in periphery sites. Exterior population fitness was < 1.0 in a wet year and $<< 1.0$ in a dry year regardless of the presence of competitors. Patch limits appeared to be set by soil moisture and competition in the dry year and by soil moisture and seed availability in the wet years. These findings suggest that apparently complex and dynamic spatial distribution of *L. nanus* is more a product of temporally variable, environmental heterogeneity than of dispersal limitation.

INTRODUCTION

Strongly aggregated, or 'patchy,' distributions are common for numerous taxa (e.g. Omori and Hamner 1982, Daniels 1992), even within seemingly continuous habitats (Seabloom et al. 2005). Although the study of species' distributions is fundamental to the discipline of ecology, empirical understanding of the relative roles of abiotic tolerances, species interactions, and dispersal in producing spatially or temporally patchy distributions remains weak. Populations that aggregate into patches provide the opportunity to contrast at the local scale the relative importance of constraints at patch margins, where variations in resources, demographic stochasticity, or dispersal, are most influential and determine patch size/distribution. In a few cases, a single factor appears to have dominant effects in delineating patch edges (e.g. Maron and Harrison 1997, Bossuyt et al. 2004). Where multiple factors are influential (e.g. Werner and Platt 1976, Seabloom et al. 2005), simultaneous investigation of interactions between spatial heterogeneity, propagule availability, and species' interactions may be necessary to identify the precise mechanisms that lead to patchy distributions.

Patchy distributions provide an excellent opportunity to contrast the degree to which both the constraints that define a species' niche and those that limit propagule availability ultimately determine a species' realized distributional pattern. Although frequently referred to in the literature, "niche limitation" has been defined in many different ways, or more frequently, remained a vague undefined term to be contrasted with neutral processes. Here, I define niche limitation as a broad term that encompasses all constraints on a species' fitness, including multiple abiotic and biotic dimensions, but excluding propagule availability. In the case of plants, the most significant niche constraints are often linked to spatial heterogeneity in soil resources and resource limitation by competitors. Grubb (1977), and subsequently Young et al. (2005), defined what they term the "regeneration" and "recruitment" niches respectively, pointing out that the environmental space in which a species can emerge and grow, is often more strongly constrained by environmental factors than the "adult" or "reproductive" niches in which we observe mature individuals and reproduction. Specific constraints on both the regeneration and fitness stages will ultimately contribute to the resulting spatial patterns in mature individuals and seed availability.

Both negative and positive interactions with other species can be influential on species distributional boundaries (Bertness and Leonard 1997, Silvertown 2004) and on spatial or temporal patchiness in specific (Keitt et al. 2001). Competitors can restrict occurrence of tolerator species to patches of suboptimal habitat (Harrison 1999, Veblen and Young *In review*). Biotic feedbacks that foster patchiness can be the result of positive interactions between plants and soil microbes (Klironomos 2002) or from the satiation of specialist natural enemies (Maron and Harrison 1997). Mate limitation can limit the reproduction of isolated individuals (Karoly 1992, Groom 1998), thus reinforcing aggregation. Non-competitive biotic feedbacks can also interact with both dispersal (Muller-Landau et al. 2003, Adler and Muller-Landau 2005) and competition (Maron 2001, Casper and Castelli 2007, Eppstein and Molofsky 2007) in ways that foster aggregation.

Propagule availability has been shown to be an additional constraint on the spatial distributions of many plant species (Turnbull et al. 2000, Ehrlen et al. 2006) and is a feature of several important ecological models of species distributional mechanisms including metapopulations and neutral theory. For example, a metapopulation model of a grassland perennial plant by Milden et al. (2006) found that rare, long distance dispersal was more important than short distance dispersal to patch occupancy. Propagule arrival outweighed the importance of environmental constraints on this species' distribution in the short term (Milden et al. 2006). Dispersal has also been found to have consistent long-term effects on species' distributions (Ehrlen et al. 2006). In some cases, distributions of species could be the results of random dispersal and subsequent trait-based demographic stochasticity, rather than abiotic and biotic niche constraints (Hubbell 2001).

Patches of some species shift spatially over time, suggesting that the suitability of their habitats is the result of dynamic temporally variable processes. Annual weather variation alters abiotic and biotic constraints on fitness and abundance of multiple species, effectively temporally shifting their niches from year to year (Goldberg and Turner 1986, Debinski et al. 2006). Propagule availability can also vary temporally, based on fluctuations in fecundity, dispersal, and the life cycles and demographic stochasticity of natural enemies (Maron and Gardner 2000, Muller-Landau et al. 2003). However, despite wide recognition that competition and its effects vary temporally, ecologists rarely examine changes in competitive intensity over time (Goldberg and Barton 1992), let alone how temporal variation in competitive intensity may affect species distributions (Thompson and Grime 1979, Rice 1987). Vaughn and Young (*In prep*) found that less than 5% (17 of 366) of published manipulative studies of competition conducted experiments in multiple years that allowed for between-year comparisons. When shifts in patch locations occur over time, the question arises whether environmental fluctuations alone are responsible, or if a change may have taken place in the relative importance of site suitability versus propagule availability.

I investigated the causes of spatio-temporal patchiness in *Lupinus nanus*, an annual, within its native California grassland habitat. Though observational and experimental study, I compared the influences of dispersal limitation versus multiple potential niche constraints, including temporal and spatial environmental heterogeneity, competition, and herbivory, on patch distribution. I transplanted the species across the bounds of its current distributional limits, yet within apparently suitable habitat, and assessed its demographic success in plots with and without competitor removal. To assess the influence of temporal variability, I repeated this experiment in multiple years that varied in key environmental conditions. If the spatial distribution of *L. nanus* is primarily limited by environmental heterogeneity, I predicted that fitness of both sown plants and natural recruits would be higher in locations where the species always occurs when compared to peripheral or unoccupied habitats. If competition plays a key role in the spatial distribution of *L. nanus*, I predicted that removal of competitors from peripheral or unoccupied habitats would increase its fitness enough to permit expansion of the spatial niche. If conspecific aggregation provides protection from natural enemies, I predicted that rates of herbivory would be higher in peripheral or unoccupied habitats compared with those in core occupied habitats. Finally, if the spatial distribution of *L. nanus* is largely dispersal limited, I predicted that addition of propagules to peripheral or unoccupied sites should cause expansion of the spatial niche.

METHODS

Study species

Lupinus nanus (Benth., Fabaceae), sky lupine, is a showy native annual that is common to grasslands and oak woodlands of the northern Coast Range of California. For brevity, I will refer to the focal species by its genus, but note that there are other species of *Lupinus* present at the field site. It is characterized by relatively large seeds (random sample, N = 340, mean = 141.8 mg, s.d. = 33.2 mg), and has no specialized adaptations for fruit or seed dispersal. After seed hardening, dormancy is physically enforced (Hyde 1954) until broken by subtle abrasion due to fluctuation in temperature (Quinlivan 1966). *Lupinus* occurs largely in patches; by visual estimate, < 5% of all *Lupinus* individuals at the study site were found outside patches in any given year. Patches exhibit sharp spatial boundaries with the surrounding plant community, with changes from > 50% cover to < 5% cover in 2 m or less (K. Moore, unpublished data). Patches vary in size, position, and spatial extent among years and are found in a wide range of habitats that vary in both abiotic conditions and productivity (e.g., serpentine and non-serpentine soils, short/sparse and tall/lush grasslands). In 2003, I selected sixteen *Lupinus* patches based on their size (e.g., large enough to contain multiple sample and experimental points) and accessibility, across an approximately 8 km^2 landscape. These patches were located in grasslands at the University of California, Donald and Silvia McLaughlin Natural Reserve, located in Lake and Napa Counties in the Coast Range of northern California, USA.

Field methods

Temporal patch shifts

To determine how patches varied in location and size over the study years, I used the global positioning system to map the boundaries of selected patches each spring from 2003-2005 (GPS Pathfinder Office 2.90). Patch locations, size, elevation, and coordinates were taken using the Universal Transverse Mercator (UTM) system, which provides *x, y* coordinates based on a regional reference point. Daily and monthly weather data were collected from the Knoxville Creek weather station (United States Bureau of Land Management), located on the reserve. For each observational or experimental year (2003-2005), precipitation, temperature, and percent humidity were collected on a monthly basis. I created a composite map of patches for 2003-2005, which I used to determine the area of each patch in each year, and the spatial overlap ("nestedness") of the patches across years (Arc/InfoGIS v9.2, ESRI, Redlands, CA, USA), which was calculated as percent of areal overlap among years.

Plot locations and environmental heterogeneity

In 2003, I established 240 observational plots, such that half of the plots were in high density locations within the sixteen selected patches (> 70% *Lupinus* cover) and the half other were in adjacent zero density areas (no *Lupinus* for at least 2 m, generally over 10 m). All plots were clearly inside and outside of the patches in this initial year and were 0.09 m^2. Subsequently, as patch boundaries shifted from year to year from 2003-2005, three "area types" were categorized by the frequency at which they fell inside a *Lupinus* patch. Areas inside patches in all three years were termed "core," areas inside patches in one or two years were termed "periphery." Locations never in patches were termed "exterior." Patch area type categories referred to temporal occurrence rather than spatial position, such that periphery and core sites were not necessarily spatially adjacent (Fig. 2.1). The number of *Lupinus* individuals in each observational plot was tallied in each year at peak flowering as an estimate of local density. A few scattered individuals occurred in some parts of the exterior in each year, but at very low density.

Soil samples were collected from each observational plot and were analyzed for organic content, Ca, Mg, K, Ni, P (Bray method), NO_3, and texture (A & L Laboratory, Modesto, CA). In 2004 and 2005, soil moisture was determined gravimetrically for all experimental plots in mid-March. A sub-sample of aboveground biomass harvested directly adjacent to each experimental plot in August of 2004 and 2005 provided an estimate of local productivity.

Dispersal and competition limitation

Immediately adjacent to each observational plot, I established an additional 0.0625 m^2 experimental plot. In these plots I established an experiment with two crossed treatments: (1) neighbor removal or undisturbed and (2) sown seed or natural recruits. I tracked two resulting categories of plants, those from seed addition ("sown") and those that naturally emerged from the seed bank ("recruits"), each in separate neighbor removal and undisturbed plots. Seeds were collected in dense areas within each patch in the previous spring and were sown patch-specifically in July of 2003 and 2004. All plots were surveyed across the 2004 and 2005 growing seasons (January to June). To distinguish sown seeds from natural recruits, seeds were affixed to wooden toothpicks prior to planting using water-soluble glue (2 seeds/toothpick in 2004 and 5 seeds/toothpick in 2005; 10 toothpicks planted per plot). This method of marking annual seeds has been shown not to interfere with emergence in other experiments in this system (Hobbs and Mooney 1995). In plots without sown seed, I randomly selected and marked ten natural recruits in each plot/subplot at emergence, which I followed analogously to sown seed plants throughout the growing season.

The neighbor removal treatment was established by removing ~95% of the aboveground biomass before seed addition, and was maintained by weeding non-target plants (including non-target *Lupinus*) monthly during the growing season. Seeds were sown in ~2 x 2 x 4 mm holes spaced at 5 cm. For the 2005 growing season, I adjusted plot configuration slightly to facilitate field measurements. I established blocks of four 0.0625 m^2 experimental plots next to a random subset of 80 of the observational plots (for a total of 320 plots) such that each new block had all four treatments (control, sown, neighbor removal, and sown with neighbor removal).

In sown plots, emergence rates were calculated as the percentage of toothpicks that had one or more emergent seedlings. I did not include data on subsequent emergents at the same toothpick, since the propensity for germination inhibition is not known for this species. In cases where a second plant germinated at the same toothpick, it was promptly removed and was not included in fitness calculations. Emergence was not recorded in non-seeded plots since the number of seeds in the seed bank was unknown. Over the course of the experiment, I visually tallied the percentage of leaf area and reproductive structures damaged by herbivory on each target plant. I then calculated a plot-wide average of the running total of herbivore damage for each treatment.

Two independent metrics for fitness were calculated: one that included the probability of emergence and one that was based on the fitness of emergent plants only.

First, in sown plots, "fitness of seeds" was determined as the plot-wide average of the number of seeds produced at each toothpick. Toothpicks where no plant emerged were scored as zero. Second, in both sown and non-sown plots, "fitness of emergents" was calculated as the plot-wide average number of seeds produced per emerged individual. For natural recruits, fitness of emergents was based on the final seed output of the subsample of marked plants; where there were fewer than five natural recruits in a plot, I used seed output from all available plants. In each plot, I also noted plants that did not flower and calculated and additional fitness metric including only plants that flowered in order to contrast reproduction of flower plants among area types.

Seed bank, dormancy, and germination

In April 2005 (after 2005 emergence), a soil sample (approx 200 mL from the top 3 cm) was collected at each experimental plot and sieved to extract all *Lupinus* seeds as an estimate of seed bank density. I used buried pouches of seed to estimate spatio-temporal differences in germination rates. In 2003, I made 120 replicates of pouches in which 20 seeds were sealed in individual chambers of fiberglass screening. Pouches were buried 2 cm below the soil surface next to experimental plots. Following emergence in each year (2004-2006), I excavated the pouches, tallied the remaining seeds, and then reburied them. Seeds missing from pouches presumably had germinated and decayed (E. Simms, personal communication).

Analyses

To test for limitation by extrinsic environmental factors, I compared abiotic and biotic site characteristics among the three patch area types (core, periphery, and exteriors). In particular, I looked for differences in P, NO_3, and pH that may denote common biotic feedbacks for legumes. To test for competition limitation, the fitness of seeds in sown plots was compared between plots where neighbors were and were not removed. I compared rates of herbivore damage among patch area types to assess the likelihood that natural enemies reinforce patch spatial structure. To test for dispersal limitation, I tested if fitness of sown emergents in patch exteriors was greater than the replacement rate, one.

Variation among patch area types for 11 environmental site characteristics was characterized by multivariate analysis of variance (MANOVA), using site characteristics as the dependent variables and patch area types as the independent variable in JMP (version 5.1 SAS Institute 2004). Response variables were transformed prior to analysis to meet the assumptions of parametric models. Univariate ANOVA tests were then performed and contrasts were used to assess differences between patch area types on each response.

I used separate general linear mixed models (GLMMs) to determine (1) if emergence and fitness varied in response to treatments and patch area types and (2) if herbivory rates, seed bank densities, or germination rates varied among patch area types. In the first case, the treatment, patch area type, and their interaction were fixed effects, whereas in the latter analyses patch area type was the sole fixed effect. I used the maximum-likelihood method in SAS PROC MIXED (version 9.1, SAS Institute 2002), and applied Satterthwaite's approximation to calculate degrees of freedom. In all GLMM analyses, analyses were blocked based on patch. Patch and its second degree interactions with the fixed effects were designated as random to account for unequal sample sizes among treatments. Response variables were transformed to approximate the assumptions of parametric models. Due to unequal variances among patch area types, I weighted samples by their estimated reciprocal variance within area type. Each year was evaluated by a separate GLMM since plot locations changed over the two experimental years. For each year, I conducted a one-tailed non-parametric Wilcoxon signed rank tests to determine if mean fitness of emergence and fitness of added seeds, my best estimate of λ, were greater than one in exterior plots. If plots in exteriors had mean fitness > 1 only when seed was added, than these sites would be dispersal limited.

RESULTS

Environmental variation and *Lupinus* patches

The observational year, 2003, was very moderate, with favorable growing conditions for *Lupinus*. Peak precipitation occurred during March and April (1.63 and 1.57 in/mo). The following two experimental years differed considerably in weather characteristics that affect moisture availability. In 2004, rainfall declined early in the season, dropping off very steeply after February (February 2.20 in, thereafter < 1 in/mo, Fig. 2.2). In comparison, 2005 was characterized by frequent precipitation, including late precipitation that extended the growing season for many species (precipitation over 1.20 in/mo in January, March, and May). The spring of 2004 was slightly warmer than 2005, and was marked by a series of unseasonably hot days in early March that caused high mortality in many plants at the emergence stage, including *Lupinus*.

Abiotic factors differed among patch area types in both dry (2004) and wet (2005) years. Patch area types varied significantly with respect to soil moisture, soil chemistry, and aboveground biomass (Table 2.1). Core and periphery plots had lower soil moisture in both years, and higher P and NO_3 concentrations, compared with exterior plots. The effects of differences in precipitation strongly affected resource availability during the growing season in *Lupinus* patches. In 2004, mean soil moisture was nearly half that in 2005 in patch core and periphery locations (Table 2.2).

The aboveground spatial extent of *Lupinus* patches, both individually and totally, differed greatly among years, including a > 10-fold difference between the total patch area in 2004 (5,370 m^2) and 2005 (67,853 m^2). Patches in both 2003 and 2004 were minor spatial subsets of those in 2005 (e.g. Fig. 2.1). A striking 80% of the 2005 patch area occurred in areas not occupied in either 2003 or 2004. Patches were thus centered on core spatial locations, with boundaries shifting from year to year, sometimes radically. The majority of area varied in occupancy among years, such that only 35% of area ever inside patches was stably occupied (i.e., patch cores).

Population level fitness of sown seed was consistently greatest in core subpopulations and lowest in exteriors (difference in each year significant to the $P <$ 0.0001 level; Table 2.2). Core subpopulations had higher mean fitness than periphery subpopulations in both years (2004 $t = 2.61$, d.f. = 150, $P = 0.0100$; 2005 $t = 2.69$, d.f. = 155, $P = 0.0079$). Similarly, the periphery subpopulations had greater fitness than those in the exterior, though in 2005 this difference was only marginally significant (2004 $t =$ 2.49, d.f. = 143, $P = 0.0139$; 2005 $t = 1.62$, d.f. = 146, $P = 0.1082$).

Temporal variation in naturally occurring recruits

Differences between years had dramatic effects on potential population growth rate of natural recruits. In the dry year (2004), fitness of recruits was only above one when neighbors were removed in the core (range among plots: 0 - 1.7 seeds produced/seed sown), whereas in the favorable year (2005), mean reproductive fitness of recruits was > 1 in all patch area types and treatments (range 1.4 - 12.8 seeds produced/seed sown). Although a few plants occurred in exterior locations in each year, fitness was significantly below replacement, even in 2005 (undisturbed: mean = 1.4 seeds produced/emergent, st. dev. = 5.10, $z = 1.03$, d.f. = 30, $P = 0.981$, neighbor removal: mean = 7.1 seeds produced/emergent, st. dev. = 22.4, $z = 1.47$, d.f. = 28, $P = 0.973$). Only 3 of 30 undisturbed plots and 5 of 28 neighbor removal plots had non-zero fitness in 2005, whereas in 2004 all undisturbed plots had zero fitness and 3 of 28 neighbor removal plots had non-zero fitness (mean = 0.94 seeds produced/emergent, st. dev. = 1.96, $z = -0.16$, d.f. = 28, $P = 0.97$).

Spatio-temporal variation in competition limitation

Competition effects on *Lupinus* fitness varied among area types in 2004, but had no significant effect in 2005 (Table 2.2, Fig. 2.3). In 2004, competition reduced both emergence and fitness of emergents, and interacted with area type (Table 2.2). Emergence was not affected by neighbor removal in the core or exteriors, but periphery subpopulations had higher emergence when competition was reduced ($t = 3.99$, d.f. = 59.4, $P = 0.0002$). In fact, in 2004, neighbor removal improved fitness of emergents in the periphery subpopulations (plot mean fitness 0.7 seeds produced/seed sown) to levels statistically indistinguishable from undisturbed plots in the core (plot mean 0.2 seeds produced/seed sown; $t = 0.66$, d.f. = 43.8, $P = 0.9482$). This suggests that competition was responsible for differences between core and periphery fitness and may limit patches to core locations in dry years. Note that there was no main effect of patch area type on emergence in 2004 (Table 2.2). Rather, a post-emergence fitness bottleneck dependent on both patch area type and competition limited at the reproductive stage.

In 2005, there were no statistically significant effects of competition on either emergence or fitness (Table 2.2). There was a non-significant trend such that fitness was higher in the neighbor removal plots in the periphery (11.2 seeds produced/seed sown) than in undisturbed plots in the periphery (3.6 seeds produced/seed sown) or even undisturbed plots in the core (6.1 seeds produced/seed sown). Thus, competition constrained the spatial extent of *Lupinus* patches, by limiting fitness in periphery subpopulations in the unfavorable (dry) year.

Herbivory

There was no variation in herbivore damage among area types in 2004 ($F_{2, 28.4} = 0.35$, $P = 0.7810$). In 2005, herbivory varied among area types ($F_{2, 31.4} = 6.39$, $P = 0.0047$): it was significantly greater in both the core ($t = 2.95$, d.f = 35.4, $P = 0.0055$) and the periphery ($t = 3.38$, d.f = 42.3, $P = 0.0016$), than in the exterior.

Spatial variation in seed availability and germination

Seeds were present belowground in all three area types, though at varying density (area type: $F_{6,67} = 6.44$, $P = 0.0028$). The core and periphery did not differ in seed bank density ($t = 1.13$, d.f. = 70.3, $P = 0.2605$), but were both denser than the exterior (core and exterior $t = 3.22$, d.f = 68.9, $P = 0.0020$; periphery and exterior $F = 2.73$, d.f. = 62.8, $P = 0.0083$). Germination of buried seed differed between years ($F_{1, 143} = 17.29$, $P < 0.0001$), but was consistent among patch area types (area types $F_{2, 143} = 1.68$, $P = 0.1895$; interaction $F_{2, 143} = 1.69$, $P = 0.1893$). These tests together suggest that seeds are present even in areas exterior to *Lupinus* patches, albeit at low densities, and that conditions in those sites are suitable for germination. In fact, Pearson product-moment correlations plots showed no relationship between the density of the seed bank and the density of above ground *Lupinus* in either 2004 or 2005 (2004: $r = 0.02$, d.f. = 77, $P = 0.8446$; 2005: $r = -0.06$, d.f. = 78, $P = 0.6271$).

Dispersal limitation

Exterior sites were not dispersal limited in 2004, since fitness was zero even with seed addition and was not significantly different from zero even with neighbor removal (mean = 0.95 seeds produced/seed sown, st. dev.=2.0, $z = -0.16$, $P = 0.94$). In 2005, seed addition in the exterior yielded some reproductive plants, however, variance in seed production was very high and the mean fitness of seeds was significantly below the replacement rate, one (mean = 6.32 seeds produced/seed sown, st. dev. = 24.11 seeds produced per seed added, d.f. = 31, $z = -73.5$, $P = 0.940$). Even with seed addition, neighbor removal and favorable conditions, exterior sites remained unsuitable for *Lupinus* (neighbor removal plots mean = 6.0 seeds produced/seed added, st. dev. = 17.2, $z = 1.59$, $P = 0.558$).

DISCUSSION

The shifting patchiness of *Lupinus nanus* populations results from spatio-temporal variation in abiotic constraints and competitive exclusion. Suitable microsites for seed addition occurred only stochastically beyond patch margins and did not amount to dispersal limitation. Although the landscape appeared superficially to be relatively homogeneous, the consistently occupied core areas occurred on relatively dry soils. Fitness of *Lupinus* was below replacement in the rarely occupied exteriors of patches, even when seed was added and/or when competition was removed (Table 2, Fig. 3). *Lupinus* patches are the result of spatio-temporal variation in both abiotic and biotic constraints, which delineate a shifting niche within which the species occurs, reproduces, and adds to the local seed bank.

Fluctuations in environmental conditions that affected soil moisture led directly to variation in the size of *L. nanus* patches via both resource limitation and competition. *Lupinus* fitness was lower in all area types in the dry year, compared to the favorable year. However, *Lupinus* was able to tolerate very low soil water availability, such that soil water was lowest in the core in both years; this tolerance may be a key mechanism that allows *Lupinus* to coexist among its competitors. When soil water conditions were favorable (2005), competition had no effect on *Lupinus* fitness in any location. But in the dry year (2004), competition limited *Lupinus* in periphery subpopulations only by reducing emergence, survival to flowering, and resulting reproductive rates, presumably because sufficient water availability in these locations allowed neighboring species to gain the competitive edge. In even drier core locations, no competition was observed, likely because *Lupinus* was a superior tolerator of low moisture conditions.

Notably, limitation of *Lupinus* by both resource availability and competition occurred primarily at early life stages. Germination rates were the same in all patch area types and a nearly constant minimum of approximately 15% emergence was maintained in all undisturbed locations. In the dry year, emergence rates were statistically the same in all area types (range: 13-19%). In the favorable year, emergence in the exterior was 18%; higher emergence rates were observed in the drier (i.e. more suitable) periphery and core sites (24% and 40%). A survival bottleneck caused by soil moisture levels and competition occurred between emergence and flowering and was responsible for most observed differences between treatments and area types on fitness. There were no differences between area types and treatments in the seed production of plants that reached flowering. For *Lupinus*, this demonstrates distinct differences between the regeneration niche and the reproductive niche and that regeneration niche limitation (by resource levels and competition) is a strong determinant of *Lupinus* distributions.

In addition to differences in soil water availability, soil P and NO_3 concentrations also varied among patch area types. However, these differences are more likely to be products, rather than causes, of variation in *Lupinus* patch occurrence. Due to nitrogen-fixing root associates, *Lupinus* species have been found to enrich mineral nitrogen availability, particularly in dry habitats (Gill et al. 2006). Legumes are generally more limited by P availability than by N. In a nutrient addition study on *Lupinus* stands (Kamh et al. 1999, Massonneau et al. 2001) found that *Lupinus lepidus* density was increased by P addition, but experienced a competition-mediated decrease upon N addition. Other researchers have found that elevated soil P levels can be caused by *Lupinus* root structure and/or associated soil biota and nodule-forming symbiotes (Karoly 1992, Massonneau et al. 2001). If this is also the case for *Lupinus nanus*, positive feedbacks mediated by mutualists could reinforce patch spatial structure. However, in another experiment, when I added both P and seed to plots within *Lupinus* patches I found no effect of P enrichment on either emergence or fitness over two years (K. Moore, unpublished data). Positive feedbacks with herbivores were also not observed, though belowground and cryptic herbivory cannot be ruled out without further study.

Lupinus patches have attributes that fit both niche and source/sink distributional models, rather than models based on propagule supply such as metapopulations and neutral theory. Although dispersal can affect occurrence of *Lupinus* in suitable microsites in patch exteriors, lack of an explicit dispersal mechanism (e.g., a pappus or other active transport) suggests that dispersal between patches (approximately 80 m on average) is minimal, and dispersal was not found to limit fitness in unoccupied locations. Environmental conditions, including competition, drive *Lupinus* fitness and patch occurrence. However, the presence of a dormant seed bank makes *Lupinus* occurrence patterns difficult to fit into a standard niche framework, since populations exist below ground in many locations, whether or not they are evident aboveground or have positive fitness at that time. For this reason, a modified version of the source-sink model that incorporates seed dormancy may be the most appropriate formal distributional model for this annual plant species (Pulliam 2000). In dry years, the aboveground periphery subpopulations act as sinks, since plants emerge and reproduce, but fitness is too low for replacement. The result is that seeds are removed from the seed bank and not returned, a net fitness loss. However, "remnant populations" in the form of a seed bank persist in peripheries in all years. Seeds in the seed bank may originate from local individuals or by occasional short distance dispersal from nearby core areas (Freckleton and Watkinson 2002). In contrast, in wet years, fitness in periphery subpopulations is high and they act as sources, adding seed to the seed bank for future generations. Core subpopulations remain sources in all years, adding to the seed bank continuously and dispersing seed to suitable locations at low rates. Note that high emergence rates in core areas also act as a constant draw on the seed bank, whereas temporally variable emergence in periphery areas may moderate seed bank density over time. Seed availability limits reproduction in the exterior zone, and only very rarely, in stochastically suitable microsites. In general, exterior locations remain sinks, occupied predominately by a low density seed bank with extremely low prospects for future fitness. Limitation by specific niche constraints, in the form of resource availability and competition, determines spatio-temporal suitability of source and sink locations over time.

The clear and highly visible patches of *Lupinus nanus* in flowering, coupled with empirically derived information on specific constraints on fitness and seed availability allow for a rare comprehensive example of a species' niche. Niche limitation broadly suggests that a species' distribution is driven by factors other than propagule availability. I found that this *Lupinus* was indeed niche limited, but I was also able to determine more specifically how a combination of abiotic and biotic factors that shift over space and time influence its distribution in the seed bank, at emergence, at flowering, and at reproduction. Soil water availability influenced emergence rates. However, the regeneration niche of this species was considerably broader than its reproductive niche, which was further restricted by both soil water availability and competition. Each of these effects varied spatially and temporally, based on inter-annual weather. Although stochastically suitable sites occasionally existed beyond visible population boundaries, dispersal limitation did not influence the species' distribution, because it was outweighed by strong effects of environmental heterogeneity.

In conclusion, my findings point to the need for long term studies of local species distributions and to the importance of interacting constraints on distribution patterns. The shifting niche of *Lupinus nanus* was observed in two radically different years that demonstrated the fluctuating presence of competition and dispersal limitation along patch margins. Evidence from multiple years was necessary to determine how constraints vary in their spatial influence on the species' fitness. *Lupinus nanus* is an example of a species that appears spatially patchy and dynamic, although spatial dispersal dynamics are not the key reasons for its persistence. Instead, persistence in a dormant seed bank provides spatial stability for the population through time, while specific environmental constraints shift with annual weather. Rather than shifting due to stochastic propagule availability, *L. nanus* patches are an example of how specific environmental constraints, when played out in a landscape with high temporal variation in major niche axes, can produce a spatiotemporally complex pattern of distribution and abundance.

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Table 2.1 Mean site conditions for three types of patch areas. Overall variation among area types was significant in a MANOVA (Wilks χ22,130=4.36, $P<0.0001$). Rows in bold highlight factors showing significant variation ($P<0.01$) in univariate ANOVA models comparing core, periphery, and exterior patch areas. For significant models, significant pair-wise differences between patch area types are indicated by different letters.

			Mean per area type		
Dependent variables	$F_{2,75}$	P	Core n=60	Periphery n=132	Exterior n=120
Productivity 2004 (g/m^2)	1.052	0.3542	288.1	320.6	313.3
Productivity 2005 (g/m^2)	1.464	0.2377	577.7	702.1	796.1
Soil Moisture 2004 (%)	**6.202**	**0.0032**	**5.7 a**	**6.6 a**	**10.6 b**
Soil Moisture 2005 (%)	**4.413**	**0.0154**	**12.0 a**	**14.7 b**	**15.6 b**
Organic matter (g/m^2)	2.241	0.1134	4.2	3.8	3.6
NO_3 (ppm)	**4.433**	**0.0151**	**93.3 a**	**68.8 b**	**65.7 b**
P (ppm)	**20.774**	**<0.0001**	**22.2 a**	**11.9 b**	**8.2 c**
pH	2.264	0.1110	5.9	5.9	5.7
K (ppm)	2.166	0.1217	169.2	180.4	192.5
Ca:Mg	0.166	0.8473	4.3	4.1	4.3
% Sand	1.453	0.2403	56.4	55.1	52.2

Table 2.2 Percent emergence and fitness of *Lupinus nanus* in undisturbed and neighbor removal and patch area types, from four weighted GLMMs. Fitness is the number of seeds produced per experimentally added seed. In each analysis, neighbor treatment and area type were fixed effects; site and its interaction with neighbor removal were random effects.

Response	**Effect**	**Num d.f.**	**Den d.f.**	***F***	***P***
% Emergence 2004	Area type	2	24.4	1.22	0.3126
	Neighbor removal	1	127.0	3.00	0.0859
	Neighbor removal*Area type	2	124.0	3.95	0.0218
% Emergence 2005	Area type	2	156.0	4.48	0.0128
	Neighbor removal	1	156.0	0.08	0.7739
	Neighbor removal*Area type	2	156.0	0.12	0.8874
Fitness 2004	Area type	2	29.6	4.25	0.0239
	Neighbor removal	1	149.0	51.62	<0.0001
	Neighbor removal*Area type	2	149.0	6.47	0.0020
Fitness 2005	Area type	2	29.0	25.23	<0.0001
	Neighbor removal	1	124.0	0.50	0.4817
	Neighbor removal*Area type	2	125.0	2.09	0.1274

Figure 2.1 An example of the spatial extent of a single *Lupinus nanus* patch based on GPS data from 2003-2005. Observational plots (240) were located inside of and outside of 16 such patches in 2003; experimental plots were established in adjacent locations. For analyses, plot locations were designated as core (sites inside *Lupinus* patches in all years; solid gray) area), peripheral (locations inside patches for one or two years; cumulative hatched areas), or exterior, locations never in patches (white area).

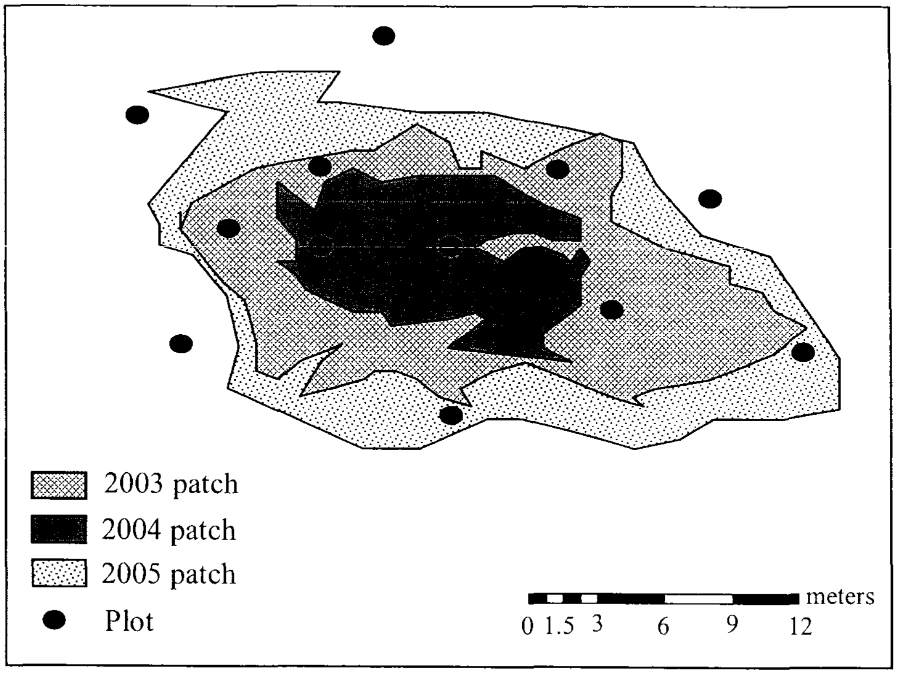


Figure 2.2 Monthly precipitation two years in which seed transplantation experiments were conducted. Monthly averages and standard deviations were generated from daily measurements.

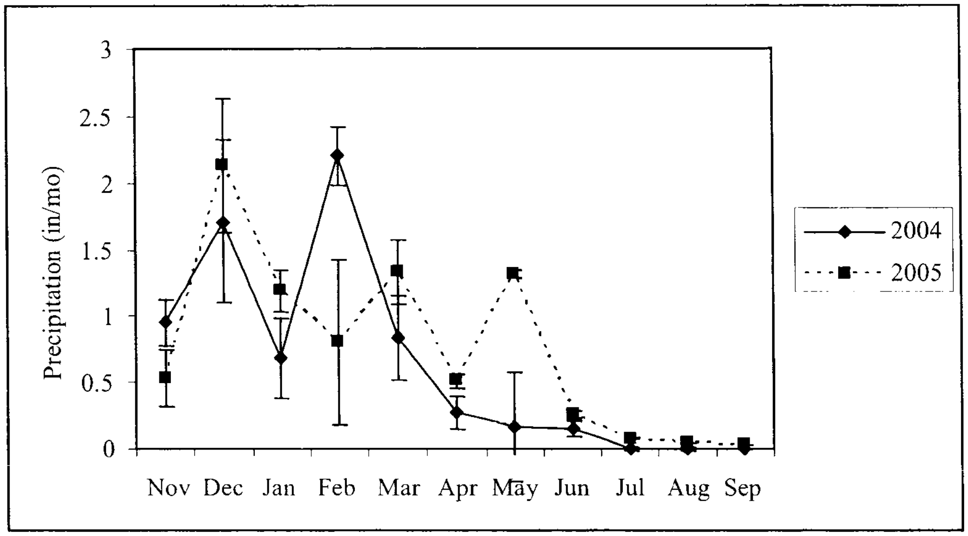
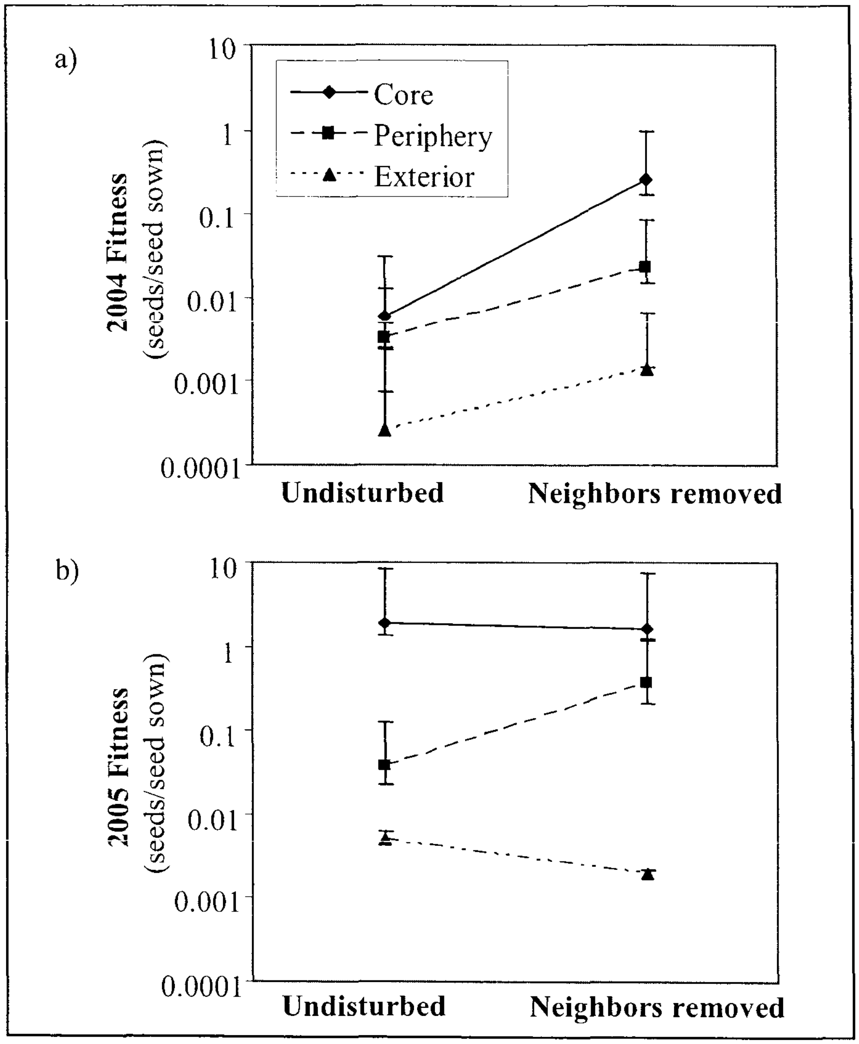


Figure 2.3 Fitness of *Lupinus nanus* seeds sown into patch areas of different types, in either undisturbed or neighbor removal plots, in a) 2004 and b) 2005. Fitness was calculated as the plotwide mean of seeds produced per seed own. Data are back-transformed LSMEANS and plot-based standard errors. For 2004, N ranged from 12-34; for 2005 N ranged from 15-33. Y-axes are Log scaled.



CHAPTER 3

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

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ABSTRACT

While the limited abundance and distribution of native grassland species is commonly attributed to either competitive exclusion by exotic species or abiotic conditions, recent studies have pointed to restricted seed availability as an alternative constraint. If this mechanism is indeed responsible for native species decline, restoration may sometimes be achieved just by adding enough seeds to sites that are suitable, but dispersal-limited. Identifying these sites remains a major challenge. One possible hypothesis is that the farther a vacant site is from existing occupied sites, the more likely it is to be dispersal-limited and thus to be suitable for restoration via seed addition, provided that the underlying environmental conditions are appropriate. For two native annual forbs in Californian grasslands, we used experimental seeding, spatial analyses, and species distribution models to ask: (1) Is there strong evidence for dispersal limitation in unoccupied sites? (2) Can spatial and environmental variables successfully predict which sites are dispersal-limited? (3) Is there evidence that the suitability of unoccupied sites is positively correlated with distance from occupied sites? For *Lasthenia californica*, we found that, while environmental constraints on establishment were stronger than dispersal limitation, both spatial variables and site characteristics were highly successful at identifying dispersal-limited (i.e., suitable unoccupied) sites; however, these sites were found only near existing patches. For *Lupinus nanus*, suitable unoccupied sites were rare, and had no relationship to distance from existing patches or the site characteristics we measured; site suitability was positively correlated only with the number of conspecifics within 1 km. Seed addition alone may be a limited means of restoration if suitable sites are either rare, unpredictable, or close to where the species already occurs.

INTRODUCTION

Like many other ecosystems, grasslands have been heavily invaded by a wide range of non-native plants over the last 300 years (Hamilton 1997). In California, this invasion has resulted in radical ecosystem transformation, from dominance by native perennial grasses and early-season annual forbs to dominance by annual exotic grasses and late-season annual forbs, and has had considerable impacts on the distribution and abundance of many native species (Heady 1958, Seabloom et al. 2006). Although competitive exclusion from suitable habitat has clearly had strong impacts on native species, availability of propagules may also present a serious limitation on native species distributions in invaded landscapes. Recent studies have found dispersal limitation to restrict community diversity (Hubbell 2001, Foster and Tilman 2003), species' spatial extents (Munzbergova and Herben 2004), and species' local abundances (Turnbull et al. 2000). Seed addition has been found to increase some native species' spatial distributions, even without manipulation of establishment conditions or competitor densities (e.g. Seabloom et al. 2003a, Seabloom et al. 2003b, Moore and Elmendorf 2006), and some studies have concluded that propagule availability outweighs competition as a constraint on species' distributions (Greig-Smith 1979, Dostal 2005).

A key practical issue in applying these ideas to restoration is whether dispersal-limited sites occur close to or far from existing occurrences of the species. If suitable unoccupied sites are predominantly very close to currently occupied sites, as might be expected simply based on spatial autocorrelation in environmental conditions, then seed addition would have relatively limited potential to expand the distribution of the species. However, a more promising possibility is that dispersal-limited sites tend to occur at relatively large distances from occupied sites, simply because the probability of the species arriving by natural dispersal is likely to decrease with distance from a source. For example, Harrison (Harrison et al. 1988, 1989) found that unoccupied sites for the checkerspot butterfly within 4.5 km of a large population were all unsuitable for the species, while those > 4.5 km away were a mixture of suitable and unsuitable; a species distribution model based on environmental parameters successfully predicted the suitability of the more distant sites. In cases such as this, propagule addition has considerable potential to expand a species' spatial distribution, as long as suitable recipient sites can be accurately identified *a priori*.

Species distribution models (SDMs) are an increasingly popular tool for predicting the suitability of sites for species. SDMs are built by analyzing the spatial distribution of a species, with respect to environmental attributes (Guisan and Thuiller 2005, Elith et al. 2006), and several experimental studies have shown that such models can successfully predict the results of transplants to unoccupied sites (Munzbergova and Herben 2004, Elmendorf and Moore *in review*). However, one important limitation of using SDMs in restoration is that strongly dispersal-limited species should show relatively poor fits of models to data, so that while many suitable unoccupied sites for the species may exist, they cannot be identified accurately (Moore and Elmendorf 2006). Conversely, excellent fit of an SDM to distributional data implies that a species is present in nearly all of its suitable sites, and so there is little potential to expand its distribution through transplantation. For these reasons, it is important to develop additional tools that enable the role of habitat quality to be distinguished from the role of dispersal limitation in determining a species' distribution. One promising approach recognizes that focal sites that are spatially isolated from potential sources of propagules are more likely to be dispersal limited and less likely to be occupied. In the present study we predict site suitability based on the combination of SDM predictions and spatial isolation, and we test these predictions using transplant experiments.

One challenge posed by applying SDMs to the identification of potential restoration sites is that we may not know *a priori* which spatial and temporal scales and types of data will yield the most accurate predictions. Many SDMs are done opportunistically using data that were collected for other purposes, but in the present study we were able to compare multiple approaches, using data that included species distributions and environmental variables collected over an 8-year period and at several spatial scales. In our previous work (Moore and Elmendorf 2006, Elmendorf and Moore *In press*, *in review*), we obtained more successful SDM predictions using plant community data than using abiotic variables. SDM approaches that incorporated at least some community data were also found to be superior to those based solely on abiotic variables in a comprehensive review by Elith et al. (2006). Thus, we opted to use a community-based SDM.

Due to both spatial and temporal heterogeneity in conditions that affect annual plant emergence and fitness, grassland species composition varies considerably in space (Harrison 1999, Harrison et al 2003) and in time (Hobbs and Mooney 1995, Seabloom et al. 2003a). We therefore compared the predictive ability of SDMs based on spatially larger versus smaller scales, and single versus multiple years of data collection.

Our primary goal was to test the hypothesis that suitable unoccupied sites for two native annual plants within a grassland landscape should occur further away from existing occupied sites than expected by chance, since propagule supply should diminish with distance from established patches. Our secondary objective was to determine the best independent predictors of site suitability for each species among an array of spatial variables and a series of SDMs based on data collected over different temporal and spatial scales. We compared the predictive ability of SDMs based on four spatio-temporal scales of data collection in order to determine the scale that best, and most efficiently, predicted annual plant occurrences. We used the abundance of plants seeded into experimental sites as our measure of site suitability, and used SDMs based on community composition to predict the suitability of transplant sites. We applied spatial analyses of the species' natural distributions in the study landscape to ask whether any of several measures of isolation from conspecifics was a positive predictor of transplant success, either before or after accounting for spatial variation in other environmental parameters.

METHODS

Study site

Sixty-nine study sites were located throughout grasslands at the Donald and Sylvia McLaughlin Natural Reserve and adjacent California State Fish and Game lands, in Lake and Napa Counties in the Coast Range of northern California, USA. These sites occurred across an approximately 16 km^2 landscape, and were chosen to encompass serpentine and non-serpentine grasslands with a variety of slopes and aspects; see (Harrison 1999, Harrison et al. 2003) for detailed methods on site establishment. Eleven of the 80 original sites were omitted from the present study due to a recent fire. At each site, five permanently marked 1 m^2 plots are evenly spaced along a 40 m transect. The presence of all plant species was surveyed in all plots from 2000-2007, once each spring (at peak flowering time for early season annual forbs, including *Lupinus* and *Lasthenia*).

We chose two focal species for our study, both of which are small-stature annual plants that occur in dense, conspicuous patches throughout the study site. *Lasthenia californica* (DC ex Lindley, Asteraceae: Helenieae), or common goldfields, has a very wide ecological range and is found in grasslands throughout the California Floristic Province (Ornduff 1966). The majority of seeds have been found to disperse within 5-50 cm of the maternal plant (Hobbs and Mooney 1995, Rajakaruna and Bohm 1999). *Lupinus nanus* (Benth., Fabaceae) is native to the oak-savannah grasslands in the Northern coast range and Sierra Nevada foothills of California (Harding et al. 1974, Karoly 1994). It has large, gravity-dispersed seeds that persist in a seed bank, possibly for 30 or more years (Dremann and Shaw 2002). At the study area, both target species occurred predominantly in distinct patches within the surrounding plant community (changing from > 50% cover to < 1% cover in 2 m or less, K. Moore, personal observation). We estimate that < 5% of all *Lupinus* individuals and <10% of all *Lasthenia* individuals at the reserve are found outside of such patches in any given year.

Spatial data

To determine the distribution and abundance of patches of the focal species in our study landscape, in the spring of 2005, we searched all grasslands within a radius of 1000 m of each study site and mapped all patches using a global positioning system (GPS). Patch locations, size, elevation, and coordinates were taken using the Universal Transverse Mercator (UTM) system, which provides *x, y* coordinates based on a regional reference point. Within each mapped patch, the number of individuals of the target species was recorded in 2 - 4 sample 0.0625 m^2 plots, located at random.

For each species, distance from each randomly located study site to the nearest patch ("focal site isolation") was calculated assessed using the Nearest Features extension (v.3.8b Jenness Enterprises, Flagstaff, AZ, USA) in ArcView v3.2. We calculated the cumulative number of plants in patches within three radii of the study site ("surrounding species abundance"): the transect scale (50 m), medium scale (250 m), and the largest scale surveyed (1000 m). We estimated the number of plants in each patch as the area of the patch multiplied by the mean number of plants in the sample plots. The Nearest Features extension was used to calculate the estimated number of plants in all patches within each radius ("surrounding species abundance").

Seeding experiment

In the fall of 2004, we added seed of *Lasthenia* or *Lupinus* to each of two 0.25 m^2 plots at each site, located approximately 1 m from one of the existing survey plots. Seeds were added from a bulked sample collected in 2003-2004 for *Lupinus*, and collected in 2004 for *Lasthenia* in patches of the species across the reserve (in both serpentine and non-serpentine sites). For each species, 1000 seeds were scattered into the central 0.09 m^2 of one plot per site.

Statistical analyses

Dispersal limitation at unoccupied sites

For each focal species, we categorized sites as either "occupied," meaning that the species was present in at least one year in the transect over the sampling period (2000-2007), or "unoccupied" meaning that the species was never present. We made our estimate of unoccupied sites conservative by including all transect plots and years so that we could most stringently test for the utility of dispersal limitation in the context of finding new restoration sites. From our 69 original sites, this categorization resulted in 34 unoccupied sites for *Lasthenia* and 55 for *Lupinus*. We calculated "seeding success" as ln(number of plants in seeded plots + 1). We tested for dispersal limitation in unoccupied sites by using one-tailed Wilcoxon signed rank *t* tests to test to determine if the number of plants in the seeded plots was significantly greater than zero.

Species distribution modeling

We used Beals' index of site suitability based on species co-occurrences to generate SDM predictions for each species at all sites. This index yields the probability of finding the target species, given the frequency of joint occurrences of the target species and the species present at that site and the total number of species at the site (Beals 1984, Munzbergova and Herben 2004). For each species, we built four SDMs, including all combinations of two spatial scales and two temporal scales, so that we could compare the efficacy of different datasets for predicting seeding success. For each site at each scale, we built models using species co-occurence patterns at all other sites, at the relevant scale. Transect-wide presence meant that the species was present in at least one of the five plots on a given transect, whereas microsite presence denoted a species' presence only in the sampling plot adjacent to the seeding experiment. Presence over the long-term temporal scale was defined as a species' presence in any of the eight sampling years (2000-2007), whereas experimental year presence was from 2005 only. Thus the four SDMs were: (1) *transect-wide long-term*, the most spatially and temporally inclusive possible, (2) *transect-wide 2005,* the widest spatial scope but specific in time, (3) *microsite long-term,* specific in space but with the widest temporal scope, and (4) *microsite 2005,* the most temporally and spatially specific dataset possible.

We generated the Beals' indices via an S-plus script (S-PLUS 6.1, Insightful Corporation). Then, to evaluate the predictive ability of the resulting SDM predictions, we cross-validated each model by building a nominal logistic model, where the response was the occurrence of the target species at the appropriate scale and the model predictions were used as the sole effect (JMP IN version 5.1, SAS Institute, Cary NC). The predictive ability of cross-validated SDMs can be ranked based on the area under the curve (AUC) metric, which ranges from 0.5 to 1.0. This metric represents model quality independent of classification thresholds. Pearce and Ferrier (2000) defined AUCs of 0.5 to predict no better than a random draw, whereas models with AUC > 0.70 are considered to have reasonable to very good predictive capacity. Models with AUC = 1.0 represent perfect fit. We compared models constructed at the four spatio-temporal scales using AUC, then used the model with the highest AUC (the "best" SDM), in all additional analyses for each species.

Based on previous studies, we predicted that the most informative models would be those based on plant species co-occurrence data. To test this working hypothesis, in preliminary analyses we built species distribution models that were based solely on environmental variables (soil chemistry attributes, above-ground plant biomass, and soil moisture) to predict the presence of our focal species at the transect-wide scale. We followed the methods for generalized additive models (GAMs) in Moore and Elmendorf (2006). For both species, the community composition-based SDMs yielded models with AUCs > 0.10 higher than environmentally based GAMs.

Predicting suitability of unoccupied sites

For each species, we determined the direction of the relationship between each of the SDM predictions and seeding success at unoccupied sites for each species through univariate GLMs. We then used a two-step model selection approach to compare the degree to which seeding success was explained by the spatial variables at unoccupied sites. First, we used a model selection process to determine the spatial scale of surrounding species abundance that best explained seeding success. We then conducted a second model selection to determine the degree to which seeding success of each target species was explained by: (1) focal site isolation alone, (2) the best surrounding species abundance model alone, or (3) both isolation and surrounding species abundance. Where SDM predictions were positively correlated with seeding success, we also included models that combined spatial variables and predicted site suitability: (4) focal site isolation and the best SDM predictions, (5) the best surrounding species abundance model and the best SDM predictions, or (6) isolation, the best surrounding species abundance, and the best SDM predictions.

For both steps (determination of the best surrounding species abundance predictor and the best combination of all spatial and SDM models), individual regression models were built in SAS (PROC REG). For each selection step and species, the AIC_c statistic was used to rank models in terms of their predictive ability. Based on AIC_c, we calculated Akaike weights (W_i), which denote the weight of evidence in favor of each model in reference to all competing hypotheses. Akaike weights for all *a priori* models sum to one (Burnham and Anderson 2002).

RESULTS

Dispersal limitation

Both species exhibited some degree of dispersal limitation in unoccupied sites. Seeding increased the number of plants in plots such that it was significantly different from zero (*Lasthenia*: mean = 3.1, s.e. = 0.3, d.f = 55, $t = 4.52$, $P < 0.0001$; *Lupinus*: mean = 0.6, s.e. = 0.1 d.f. = 34, $t = 3.376$, $P = 0.0019$; means and s.e. are back-transformed). This was analogous to 9.6 *Lupinus* and 51.2 *Lasthenia* plants if seed addition had been conducted at the square meter scale. At unoccupied sites, seeding was 54.6% successful for *Lasthenia* and 36.2% successful for *Lupinus*.

Species distribution models

All four spatio-temporal scales of SDM models had excellent predictive ability for *Lasthenia* (cross-validation AUCs ranged 0.93 - 0.88), and all SDM predictions had significant positive relationships with *Lasthenia* seeding success (Table 3.1). Predictions of *Lupinus* occurrence from SDMs at different scales were also of nearly identical, but much reduced, predictive power. For *Lupinus*, AUCs ranged 0.76-0.78, indicating moderate predictive ability, but SDM predictions were not significantly correlated with seeding success (Table 3.1), and were therefore not included in subsequent analyses.

Spatial predictors of suitable unoccupied sites

Surrounding species abundance

For each species and scale, surrounding species abundance was a positive predictor of seeding success. However, the two focal species differed in the scale of surrounding species abundance that best predicted seeding success (Table 3.2a; Figure 3.1). Abundance within the medium scale (250 m) radius was the best predictor of

Lasthenia seeding success ($W_i = 0.92$, ; $\beta = 3.0 \times 10^5$, $F_{1,34} = 11.44$, $P = 0.0019$), whereas abundance within the largest scale (1000 m) radius best predicted *Lupinus* seeding effect ($W_i = 0.86$; $\beta = 2.0 \times 10^6$, $F_{1,54} = 1.83$, $P = 0.0193$). For both species, abundance within a 50 m radius was the poorest predictor of seeding success at unoccupied sites, suggesting that sites near to occupied locations are limited by factors other than seed availability.

Best predictors of seeding success

When the both spatial variables (best scale of surrounding species abundance and isolation) and best SDMs were considered together, three models garnered nearly equal support as predictors of seeding success in unoccupied sites for *Lasthenia* (Table 3a). Two of these models included focal site isolation and either the transect-wide long-term SDM predictions ($W_i = 0.26$) or surrounding species abundance at 250 m ($W_i = 0.25$). Either by itself, ($W_i = 0.04$; isolation only: $\beta = -2.0 \times 10^3$, $F_{1,33} = 7.28$, $P = 0.0110$, Figure 3.2a), or together with SDM predictions (isolation $\beta = -2.0 \times 10^3$, $F_{1,33} = 4.81$, $P = 0.0358$, SDM $\beta = 7.555$, $F_{1,33} = 6.17$, $P = 0.0186$) focal site isolation had a negative relationship with seeding success. Recall that Akaike weights (W_i) denote the proportion of evidence in favor of each model in reference to all competing models. In other words, experimentally introduced seeds were more likely to succeed in empty sites that were closer to existing populations of *Lasthenia*. When paired with surrounding species abundance, isolation had a non-significant relationship to seeding success (isolation $\beta = -1.1 \times 10^3$, $F_{1,33} = 2.21$, $P = 0.1471$, abundance $\beta = 2.0 \times 10^5$, $F_{1,33} = 5.73$, $P = 0.0229$), though its inclusion did yield improvement over the model based solely on surrounding species abundance ($W_i = 0.20$). In all cases, both SDM predictions and surrounding species abundance had positive relationships with seeding success. The two top model results for *Lasthenia* together emphasize an important point: that SDM predictions and surrounding species abundance each explain additional variation in the suitability of unoccupied sites not explained by isolation alone. The global model including isolation, surrounding species abundance, and SDM predictions received relatively little support ($W_i = 0.10$), demonstrating that surrounding species abundance and SDM predictions do not explain unique portions of the variation in unoccupied site suitability.

When compared to and in combination with site isolation, surrounding species abundance at the 1000 m scale was by far the best predictor of *Lupinus* seeding success at unoccupied sites. Nearly all of the evidence supported this model ($W_i = 0.97$; Table 3.3), which had a significant positive relationship to seeding success (Fig 3.1b). There was no relationship between *Lupinus* seeding success and isolation ($\beta = -1.1 \times 10^4$, $F_{1,54} = 0.09$, $P = 0.7615$, Figure 3.2b).

DISCUSSION

Our results demonstrate both that suitable unoccupied sites exist for the species we examined, and that their locations are predicted by measurable spatial and environmental variables. However, contrary to our predictions, dispersal-limited sites tended to be close to, rather than far from, existing occupied sites for both species (Figure 3.1). For *Lasthenia*, the suitability of unoccupied sites was well-predicted by site isolation and either the plant community (SDM predictions) or conspecific abundance at a moderate distance (250 m). Local abundance (50 m) or very large scale abundance (1000 m) were not strong indicators of *Lasthenia* site suitability. Identification of suitable unoccupied sites for *Lupinus* was even less specific and may be difficult to achieve *a priori*. By far the best predictor of unoccupied site suitability was abundance within a 1000 m radius of the seeded location. Isolation was a comparatively weak predictor, and SDM predictions based on plant community composition completely failed to predict seeding success. We conclude that good sites for *Lasthenia* restoration exist in areas where *Lasthenia* patches not immediately adjacent, but are spatially clustered in areas where the species is abundant within approximately 250 m. In contrast, successful prediction of suitable unoccupied *Lupinus* sites by the abundance of conspecifics within 1000 m indicates that ideal sites for restoration may be hard to locate more specifically within generally suitable grasslands (Table 3.2, Figure 3.2b).

In the case of *Lasthenia*, the excellent predictive ability of the community-based SDM hinted that suitable yet unoccupied sites are not common. High cross-validation AUC scores suggest that *Lasthenia* occurs consistently within the same plant communities (Moore and Elmendorf 2006). For this species, SDMs based on species co-occurrence patterns were able to predict the suitability of sites for seeding, even when site isolation was accounted for. This demonstrates their utility in locating dispersal-limited sites in landscapes where such sites are not abundant. Another possibility, yet to be tested, is that the excellent SDM predictions from this dataset could be applied to another location where *Lasthenia* is less common, but in which similar species occur, and there used to identify suitable sites for seeding. In contrast, the lower predictive capacity of *Lupinus* SDMs could either be the result of an abundance of dispersal-limited sites or more stringent emergence or growth conditions. In fact, results from a concurrent study have found that microsite conditions for *Lupinus nanus* are highly specific, and dependent on both competition and weather variation (K. Moore *in prep*). In cases such as these, the utility of general spatial characteristics such as site isolation and surrounding species abundance may provide the best estimates, albeit rough ones, of potential site suitability.

To our knowledge, no other research program has explicitly addressed how the spatial and temporal scales at which data are collected may influence the accuracy of species distribution models at predicting suitable unoccupied sites. We confirmed that SDMs based on cumulative data collected over a number of years and over broader spatial scales can yield superior predictions to those built on shorter-term, finer-scale datasets. We conclude that efforts to identify suitable sites for restoration seeding based on SDMs should use the largest dataset possible to create model predictions, and that highly localized sampling may not be needed to make accurate predictions, especially when other spatial variables, such as isolation, are available.

Despite the negative relationship between site suitability and isolation, it is interesting to note that for both species, a few highly suitable unoccupied sites did occur at a considerable distance from occupied sites (Figure 3.1). In fact, in the case of *Lupinus*, suitable sites occurred with some frequency at all distances from focal sites, likely weakening the overall relationship between suitability and isolation (Figure 3.1b). Within generally suitable landscapes, as indicated by large-scale *Lupinus* abundance (1000 m surrounding species abundance), suitable sites are apparently scattered, with some clustering of sites near occupied locations. Both of these species are not likely to be truly "dispersal-limited" at the landscape scale. Rather, we infer that unoccupied sites are occasionally suitable due to environmental stochasticity, not because otherwise amenable locations are continually being located at isolated locations from seed sources.

While we found that suitable unoccupied sites existed for our target species, they were either adjacent to occupied sites (*Lasthenia*) or relatively spatially unpredictable (*Lupinus*). In terms of restoration goals, it would be much more valuable to find distant, yet suitable sites, since such locations may allow managers to extend the range of species of concern or allow restoration sites to be selected in management locales without existing populations of the focal species. However, our results suggest that spatial autocorrelation in important environmental conditions is a powerful force influencing plant distributions.

We found that one-time seeding is very unlikely to significantly increase the spatial distribution of *Lasthenia*, since the suitability of unoccupied sites declined with distance from occupied patches. For *Lupinus*, our inability to identify suitable unoccupied using either SDMs or spatial variables suggests that restoration efforts based on seed supplementation are likely to have limited success. These findings are particularly significant, since both species are common components of restoration seeding mixes. In particular, *Lupinus nanus* is commonly planted by the California Department of Transportation and is promoted by prominent California native seed producers as being easily established. *Lasthenia californica* is a member of several threatened plant communities in California grasslands, including vernal pool, serpentine, and alkali seep communities, which are popular targets of restoration efforts. Other studies have suggested that other native annual forbs and perennial grasses also suffer from dispersal limitation in California grassland communities (Seabloom et al. 2003a, Seabloom et al. 2003b). In a rare corroborating study, Gram et al. (2004) found that the success of seeding for some native species was correlated with proximity to serpentine hummocks, likely due to autocorrelation in environmental factors. In contrast, we found that distance was a significant predictor of site suitability for *Lasthenia*, even when site suitability was accounted for by SDM models. This suggests that proximity is correlated with site suitability to a finer degree than even excellent model predictions can represent. It will be crucial to determine if the establishment success of other native species seeded into other natural landscapes is generally correlated with distance from existing populations, or with other measurable site characteristics, be they physical or spatial, in a way that would facilitate that identification of potential restoration sites.

We found that dispersal-limited sites existed for two charismatic native annual forbs, but that seeding alone is unlikely to be an effective method for grassland restorations with either species. We found that a combination of spatial variables and species distribution models could successfully applied to locate suitable unoccupied sites for the seeding of *Lasthenia,* although only near existing populations, and to rule out efficient restoration of *Lupinus* through seed addition. Our results support the position that conservation of intact ecosystems is essential to grassland conservation, since suitable unoccupied sites were clustered near existing populations. Moreover, even with the use of spatial and plant community data, it can be difficult to identify those rare, more distant sites in which the restoration of populations through seeding is likely to be successful.

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Table 3.1 Predictive ability of species distribution models at each of four spatio-temporal scales and Pearson product moment correlations between SDM predictions and seeding success, ln(number of plants in seeded plots + 1) in unoccupied sites for a) *Lasthenia californica* (d.f. = 34) and b) *Lupinus nanus* (d.f. = 55). Values shown in bold indicate significant relationships to the $P < 0.05$ level.

	a) ***Lasthenia***					b) ***Lupinus***				
	AUC	r^2	β	F	P	AUC	r^2	β	F	P
SDM prections:										
Transect-wide long-term scale	0.93	0.46	9.22	8.77	**0.0057**	0.78	-0.14	-1.53	1.09	0.3012
Transect-wide 2005 scale	0.90	0.39	6.37	5.88	**0.0212**	0.76	-0.02	-0.21	0.03	0.8717
Microsite long-term scale	0.92	0.40	7.23	5.95	**0.0204**	0.89	-0.14	-1.03	0.53	0.4686
Microsite 2005 scale	0.88	0.36	7.86	4.80	**0.0359**	0.76	0.06	0.80	0.17	0.6857

Table 3.2 Comparison of surrounding species density data, collected at different spatial scales, in their ability to predict seeding success for a) *Lasthenia californica*, $n = 34$, and b) *Lupinus nanus*, $n = 55$, in unoccupied sites. Seeding success was calculated as ln(number of plants in seeded plots + 1). Models at the three scales were compared separately for each species. Akaike weights (W*i*) denote the weight of evidence in favor of each model in reference to all competing hypotheses. Weights shown in bold indicate the models with the best predictive ability for that species.

a) *Lasthenia*	k	AIC$_C$	Δ_i	W$_i$
Hypotheses:				
Unoccupied site suitability is best predicted by surrounding species density when collected at the				
a. Transect scale, 50 m	1	26.22	5.02	0.07
b. Medium scale, 250 m	1	21.20	0.00	**0.92**
c. Maximum scale, 1000 m	1	31.31	10.11	0.01
b) *Lupinus*	k	AIC$_C$	Δ_i	W$_i$
Hypotheses:				
Unoccupied site suitability is best predicted by surrounding species density when collected at the				
a. Transect scale, 50 m	1	-56.33	5.40	0.06
b. Medium scale, 250 m	1	-57.07	4.66	0.08
c. Maximum scale, 1000 m	1	-61.73	0.00	**0.86**

Table 3.3 Comparison of spatial variables with respect to their ability to predict seeding success for a) *Lasthenia californica, n* = 34, and b) *Lupinus nanus*, *n* = 55, in unoccupied sites. Seeding success was calculated as ln(number of plants in seeded plots + 1). The scale of surrounding species density models included was selected based on comparison with surrounding species density models at the transect and maximum scales. Models were compared separately for each species. For *Lupinus*, SDM predictions were not significantly correlated with seeding success (see Table 3.1). Akaike weights (W*i*) denote the weight of evidence in favor of each model in reference to all competing hypotheses. Weights shown in bold indicate the models with the best predictive ability for that species.

a) *Lasthenia*	k	AIC_C	Δ_i	W_i
Hypotheses: Unoccupied site suitability is best predicted by				
Best spatial variables:				
a. Focal site isolation	1	24.6	0.14	0.04
b. Surrounding species density, medium scale (250 m)	1	21.2	0.79	**0.20**
c. Both spatial variables	2	20.7	0.99	**0.25**
Best SDM predictions:				
d. Transect-wide long-term scale SDM predictions	1	23.4	0.27	0.07
Combinations of spatial variables and best SDM predictions:				
e. Focal site isolation and transect-wide long-term SDM predictions	2	20.7	1.00	**0.26**
f. Surrounding species density (250 m) and transect-wide long-term SDM	2	23.0	0.31	0.08
g. Both spatial variables and transect-wide long-term SDM predictions	3	22.5	0.41	0.10
b) *Lupinus*	k	AIC_C	Δ_i	W_i
Hypotheses: Unoccupied site suitability is best predicted by				
Best spatial variables:				
a. Focal site isolation	1	-52.15	0.01	0.01
b. Surrounding species density, medium scale, 1000 m	1	-61.73	1.00	**0.97**
Combinations of spatial variables:				
c. Focal site isolation and surrounding species density	1	-53.93	0.02	0.02

Figure 3.1 Seeding success at unoccupied sites, as predicted by surrounding species density for a) *Lasthenia california* and b) *Lupinus nanus*. Seeding success is ln(number of plants in seeded plots + 1) within 0.0625 m^2 plots. For *Lasthenia*, this relationship was strongest at the 250 m scale ($W_i = 0.92$), whereas for *Lupinus* this relationship was strongest at the 1000 m scale ($W_i = 0.86$).

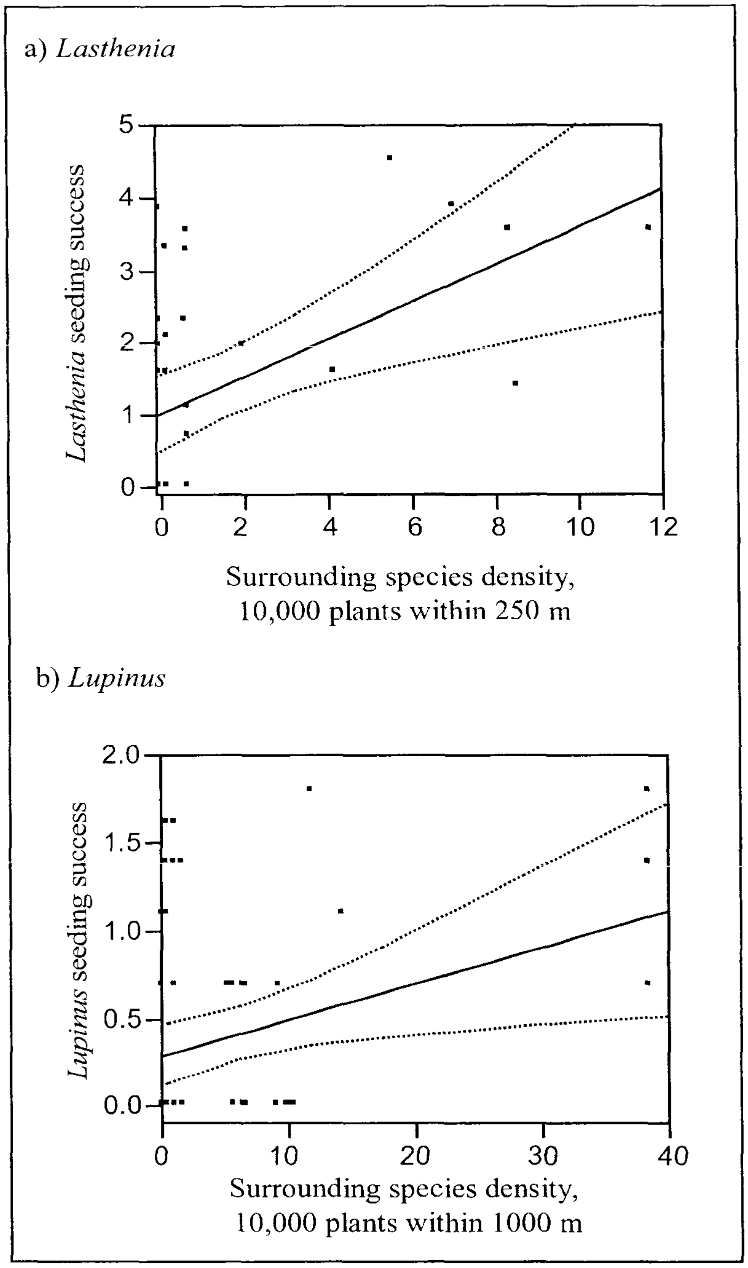
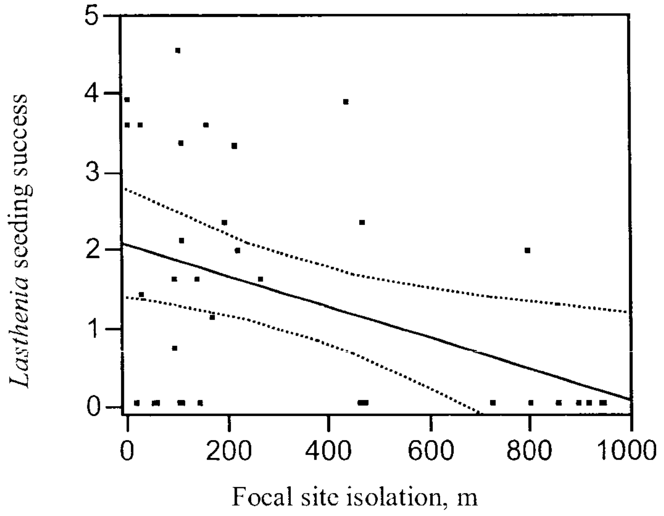


Figure 3.2 Seeding success at unoccupied sites is negatively correlated with focal site isolation for a) *Lasthenia californica* and b) *Lupinus nanus*. Seeding success is ln(number of plants in seeded plots + 1) in 0.0625 m^2 plots.

a) *Lasthenia*



b) *Lupinus*