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Authors
Hufford, Kristina M
Mazer, Susan J
Schimel, Joshua P

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Soil heterogeneity and the distribution of native grasses in California: Can soil properties inform restoration plans?

KRISTINA M. HUFFORD,1,‡ SUSAN J. MAZER, AND JOSHUA P. SCHIMEL

Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA

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Abstract. When historical vegetation patterns are unknown and local environments are highly degraded, the relationship between plant species distributions and environmental properties may provide a means to determine which species are suitable for individual restoration sites. We investigated the role of edaphic variation in explaining the distributions of three native bunchgrass species (Bromus carinatus, Elymus glaucus and Nassella pulchra) among central California mainland and island grasslands. The relative contribution of soil properties and spatial variation to native grass species abundance was estimated using canonical redundancy analysis, with subsequent testing of individual variables identified in ordination. Soil variables predicted a significant proportion (22–27%) of the variation in species distributions. Abiotic soil properties that drive species distributions included serpentine substrates and soil texture. Biotic properties that correlated with species distributions were ammonium and nitrogen mineralization rates. Spatial autocorrelation also contributed to species presence or absence at each site, and the significant negative autocorrelation suggested that species interactions and niche differentiation may play a role in species distributions in central California mainland and island grasslands. We explored the application of plant-environment relationships to ecological restoration for species selection at locations where degradation levels are high and historical communities are unclear.

Key words: Bromus carinatus; California Channel Islands; ecological restoration; Elymus glaucus; grasslands; Nassella pulchra; soil heterogeneity; spatial autocorrelation.

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1 Present address: Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming 82071 USA.
‡ E-mail: khufford@uwyo.edu

INTRODUCTION

In the face of widespread habitat destruction and biological invasion, land management often requires active restoration of native plant communities. Reintroduction of target species is common practice with the goal of restoring ecosystem composition and, consequently, structure and function (Falk et al. 1996, Chapin et al. 1997). However, reestablishing suites of species—and even single species—can be challenging if site conditions have been greatly altered. Many revegetation efforts fail, and restoration practitioners recognize that success rates can be improved with remediation of physical and biotic environments (Fahselt 2007, Drayton and Primack 2012). Nevertheless, landscape remediation is often inadequate because reference sites are either difficult to identify or nonexistent (Halle and Fattorini 2004), and many sources of...
disturbance, such as exotic species, represent permanent changes to ecosystem properties (Vitousek 1990).

If we aim to increase the likelihood of plant establishment at restoration sites, we need a better understanding of the factors that drive species distributions in existing environments (Hobbs and Harris 2001). Plant-environment associations are well-documented, and while species distributions are primarily controlled by climate at the continental scale, edaphic factors frequently determine species and plant communities at regional or local scales (Cramer and Leemans 1992, Prentice et al. 1992). Thus, soil properties may serve to predict which species are suitable for reintroduction in cases where historical reference vegetation is unknown, and local environments are highly degraded (Allen and Wilson 1991).

Species distributions reflect spatial processes as well as adaptation to heterogeneous environments (Kramer et al. 2011). Species with limited dispersal show strong relationships with geographic distance, and their distribution declines rapidly with declining environmental similarity. Species with wide dispersal have stronger relationships with ecological distance, and will persist at sites with similar plant communities and environmental conditions at larger geographic scales (Soininen et al. 2007). Much of the current research investigates the contribution of spatial and environmental variation to species range limits and niche availability (e.g., Fan et al. 1998, McCrea et al. 2001, Zhang et al. 2011). Fewer studies have applied plant-environment and spatial relationships to ecological restoration with the goal of predicting suitable sites for revegetation using selected plant taxa (Allen and Wilson 1991, Corry and McEachern 2000, Volis et al. 2011). These studies offer the potential to improve restoration outcomes via a better understanding of the factors that drive species’ distributions.

Dispersal limitations and landscape heterogeneity in soil properties may be important considerations for restoring California grasslands (Harrison et al. 2003, Grman and Suding 2010, Seabloom 2011). Since the period of European colonization, introductions of exotic species have resulted in the invasion of annual Mediterranean grasses and forbs across the state (Bartolome et al. 1986). Native perennial bunchgrass species remain relatively widespread, but historical grassland communities no longer exist and their original composition is unclear (Hamilton 1997, Holstein 2001). Weed control and restoration efforts are underway, but non-native plants dominate contemporary grasslands, and evidence suggests that ongoing anthropogenic disturbance promotes their persistence (HilleRisLambers et al. 2010, Vallano et al. 2012).

We investigated the role of edaphic variation and spatial processes in explaining the distributions of native bunchgrass species among central California mainland and island grasslands. Our study focused on three perennial bunchgrasses: *Bromus carinatus* Hook & Arn. (California brome), *Elymus glaucus* Buckeye (blue wild rye), and *Nassella pulchra* (A. Hitchc.) Barkworth (purple needlegrass) (Hickman 1993). These species are the targets of numerous restoration programs and evidence suggests that they were historically common in coastal woodlands and grasslands (Holstein 2001, Bartolome et al. 2004, Rein et al. 2007). The contribution of spatial and environmental components to bunchgrass species abundance was estimated using canonical analysis and variation partitioning, with subsequent testing of individual variables identified in ordination. Our objectives were to: (1) test the relative importance of spatial structure and soil variables for species distributions, and (2) determine whether soil biotic and abiotic properties predict the potential for target species to reestablish at restoration sites.

**METHODS**

**Site characteristics and study species**

We studied the distributions of three native perennial bunchgrass species relative to soil factors among two central California mainland sites and five Channel Islands (Fig. 1). Mainland sites included the 2358-ha University of California Sedgwick Reserve in Santa Ynez, California and Vandenberg Air Force Base near Lompoc, California. Island sites included four northern
Channel Islands (Anacapa, Santa Cruz, Santa Rosa and San Miguel) in Channel Islands National Park, and one southern Channel Island (Santa Catalina) where we collected samples within the Catalina Island Conservancy. Soils across the region have a diverse volcanic and sedimentary origin (Norris 2003) and serpentine rock outcrops occur at mainland sites and Santa Catalina Island. Serpentine soils are low-nutrient substrates, and have a high ratio of magnesium to calcium as well as elevated levels of nickel and chromium (Whittaker 1954, Schechter and Bruns 2008). The regional climate is Mediterranean with hot, dry summers and cool, wet winters (Schoenherr et al. 1999).

Following more than two centuries of exotic plant and animal introductions, the Channel Islands have been the subject of intense efforts to remove non-native herbivores such as sheep, pigs, goats and cattle (Donlan et al. 2003). However, introduced plant species are widespread and continue to present challenges for island restoration (Halvorson 1994). On the mainland, livestock have been removed from Sedgwick Reserve, but are still present at VAFB. Mainland grasslands are also targets for restoration and are heavily impacted by exotic plant species. Native bunchgrass communities throughout the region grow in a matrix of introduced, European annual grasses that include *Avena* spp., *B. diandrus*, *B. hordeaceus*, *Hordeum murinum*, *Lolium multiflorum*, and *Vulpia myuros* (Jackson 1985). Other common, introduced species include yellow starthistle (*Centaurea solstitialis*), fennel (*Foeniculum vulgare*) and iceplant (e.g., *Carpobrotus edulis*) (D’Antonio 1993, Bell et al. 2008, Knapp et al. 2009). *Bromus carinatus*, *E. glaucus*, and *N. pulchra* are wind-pollinated, non-rhizomatous bunchgrasses. All three species have awned seeds that are dispersed passively by wind, with some potential for dispersal by animals. Investigation of the
factors influencing the persistence of native species in California grasslands has indicated these three bunchgrass species are propagule limited, and seedling success is affected by spatial heterogeneity (Seabloom et al. 2003). Each of the three species occurs at the focal mainland locations, as well as on Santa Cruz, Santa Rosa and Santa Catalina Islands. Only two of the three species, *B. carinatus* and *N. pulchra*, occur on Anacapa and San Miguel Islands (Junak et al. 1997). Anacapa Island is a chain of three islets; we sampled East Anacapa, which is most accessible. Habitats vary among these locations (Heady 1977). Native grasses are commonly located in patchy populations in coastal prairies and riparian areas of the Channel Islands and Vandenberg Air Force Base (VAFB), and in oak woodland savannahs at Sedgwick Reserve (Sedgwick).

**Field collections**

We located and georeferenced populations of each bunchgrass species during spring and summer of 2002 and 2003 with the goal of representing the geographic range of the three species across the islands and within the mainland study region (Fig. 1). Sampling was restricted to sites where one or more of the three species was present in order to sample species-associated soil properties. At each site, three soil cores (7 cm × 20 cm) located between 10 and 20 m apart within the sampled population were collected using an AMS slide hammer (AMS, American Falls, Idaho, USA). Cores were bagged separately and transported to the University of California at Santa Barbara (UCSB) for subsequent analyses. We sampled a total of 118 sites, including twelve sites where two of three species overlapped (Table 1).

**Soil sampling and analyses**

Soil cores were sieved to 4 mm shortly after collection and stored at 4°C until the initiation of rewetting treatments approximately 60 days later. Water holding capacity (WHC) was determined by weighing a sample of 30 g of soil saturated with distilled water, and then drying the sample overnight at 75°C prior to measuring dry weight. Soils were subsequently adjusted to 50% WHC for nitrogen mineralization analysis, which was conducted for duplicate samples of 10 g of soil after the first day and also after a 14-day incubation period at 20°C (Weintraub and Schimel 2003). We analyzed extractable ammonium (NH₄⁺) with the diffusion method, and nitrate (NO₃⁻) using the Griess-Ilosvay reaction after reduction with cadmium (Lachat Instruments, Milwaukee, Wisconsin, USA; Lachat Methods 12-107-04-1-B and 31-107-06-5-A). Net nitrogen mineralization rates were calculated by subtracting the initial soil nitrogen (NH₄⁺ plus NO₃⁻) content from the sum of values for NH₄⁺ and NO₃⁻ measured in incubated soil.

Soil pH was measured for a 1:2 soil and water suspension that was shaken for 30 minutes and allowed to settle for five minutes. Samples were also analyzed for cation exchange capacity (CEC) including exchangeable calcium, magnesium, sodium and potassium (measured in milliequivalents per 100 g soil) using the NH₄-OAc method buffered at pH 7.0 (Lavkulich 1981). Total carbon and nitrogen content (mg/L) was determined by analysis of dried samples on an elemental analyzer (Fissons Instruments, Milan, Italy) using an acetanilide standard. Duplicates were run every 10 samples to check accuracy of analysis (difference of 1–3%). Particle size analyses were performed at the Division of Agriculture and Natural Resources Analytical (DANR) Laboratory at the University of California Cooperative Extension in Davis, California following Sheldrick and Wang (1993).

We analyzed each of the three cores per site separately and subsequently averaged results for

| Location  | *Bromus carinatus* | *Elymus glaucus* | *Nassella pulchra* |
|-----------|-------------------|-----------------|-------------------|
| Island    |                   |                 |                   |
| Anacapa   | 3                 | ...             | 4                 |
| San Miguel| 5                 | ...             | 5                 |
| Santa Catalina | 5       | 5              | 6                 |
| Santa Cruz| 12                | 7              | 13                |
| Santa Rosa| 10                | 5              | 10                |
| Mainland  |                   |                 |                   |
| Sedgwick  | 10                | 6              | 10                |
| VAFB      | 5                 | 4              | 5                 |
| Total     | 50                | 27             | 53                |

Note: *E. glaucus* does not occur on Anacapa and San Miguel Islands.
all variables with the exception of exchangeable cations and particle size. For those two variables, we combined equal portions of 100–200 g of each subsample to create a single sample for each site prior to analyses. Average soil pH was calculated as the mean of H\(^+\) concentration (pH = -log [H\(^+\)]). Altogether, 15 soil variables were measured for use in subsequent data analyses. These variables included soil pH; WHC; total carbon and nitrogen; exchangeable calcium (X-Ca), potassium (X-K), magnesium (X-Mg) and sodium (X-Na); CEC; percent clay, sand and silt; initial NH\(_4^+\) and NO\(_3^-\); and net nitrogen mineralization (or delta N).

**Data analysis**

Soil variables were compared to species presence-absence data using canonical redundancy analysis (RDA) and variation partitioning (Legendre and Legendre 1998). Prior to RDA, species values were Hellinger transformed to account for the large number of zeros in the dataset (Legendre and Gallagher 2001). To improve symmetry of the environmental data and meet expectations of statistical tests, the ratio of carbon and nitrogen, cations including the ratio of magnesium to calcium, and nitrogen mineralization values were ln(x + 1) transformed. Particle size data were arcsine square-root transformed. Ordination methods were performed with R software version 2.15.1 (R Development Core Team 2009).

RDA was first conducted for the full dataset (island and mainland) using a matrix of spatial data created by recoding the five islands and two mainland locations as binary “dummy” variables to indicate the presence or absence of a sampled population at each island or mainland site (Legendre and Legendre 1998, Borcard et al. 2011). We chose this method due to the irregular sampling scheme required as a result of the variable geographic distances among the five islands and two mainland locations. Environmental data were altered to include standardized soil variables as well their second and third order polynomials to model nonlinear relationships in the dataset (Makarenkov and Legendre 2002). To reduce variance inflation, we selected among soil variables by forward selection with randomization tests (9,999 permutations) using the “pack-for” R package (http://r-forge.r-project.org/R/?group_id=195) based on methods described by Blanchet et al. (2008). Exchangeable sodium was not included in RDA analysis of the full dataset due to multiple missing values for Sedgwick samples.

Once we determined the variables to include in the environmental (or soil) dataset, we partitioned variation among explanatory data and covariables using the varpart function in the “vegan” library (Oksanen et al. 2008). This method computes the proportion of variation in species abundance explained by: (1) the environmental dataset, (2) the spatial dataset, and (3) the fraction explained jointly by all spatial and environmental variables (Borcard et al. 1992, Peres-Neto et al. 2006). As a final step, we ran the RDA using Hellinger-transformed species response data, the reduced soil explanatory data, and spatial covariables (Borcard et al. 2011).

To better quantify the contribution of spatial and environmental variables to species abundance, we conducted RDA for a subset of samples that described the four islands in Channel Islands National Park (Anacapa, Santa Cruz, Santa Rosa and San Miguel Islands; Fig. 2). The geographical distance among the northern Channel Islands (CI) was small relative to other...
locations in the complete dataset, allowing study of finer spatial functions. Namely, the minimum spanning tree by which any two sites are connected using a single path had a truncation distance of 18.62 km. The truncation distance represents the single largest distance in the tree. Spatial coordinates among the CI sites were obtained with the geoXY() function in the SoDA package for R (Chambers 2008). Coordinates were used to construct a matrix of spatial explanatory variables using the method of Moran’s eigenvector maps (MEM; Borcard and Legendre 2002, Dray et al. 2006). Distance-based MEM is a method that identifies orthogonal spatial variables across multiple scales and can model both positive and negative correlations among species abundance data (Borcard et al. 2011). MEM spatial variables were only calculated for the four northern islands because these variables may be distorted if the truncation distance among sampled sites is too large (Borcard and Legendre 2002, Borcard et al. 2011).

The CI-only species data were Hellinger transformed, and standardized soil data included second and third order polynomials similar to analysis of the full dataset. Forward selection was conducted separately for spatial and soil variables. In the case of the soil dataset, we modified the analysis to use the significance value \( P \leq 0.10 \) as the cutoff with the goal to identify variables that approached significance at \( P = 0.05 \). Variation partitioning was also conducted for the CI dataset. Final data for RDA analysis included the Hellinger-transformed species data, the reduced soil environmental data, and matrices of (positive or negative) MEM spatial variables.

While forward selection reduced the number of explanatory variables in analyses, correlations among remaining variables may have inflated standard errors and obscured significant environmental and spatial patterns in the data. We therefore calculated variance inflation factors, which measure the degree of multicollinearity for each variable given the presence of other variables, for each RDA dataset. Inflation factors less than 10 indicated that correlations among variables were minimized (Borcard et al. 2011).

Our goals included testing the application of these methods, and so we examined the potential for individual soil variables identified by canonical ordination to accurately predict species presence or absence at a site. We conducted these analyses with logistic regression of selected soil variables separately for each of the three species. Logistic regression analysis of transformed soil variables and binary species data with a logit link function was performed in JMP version 9.0 (SAS Institute, Cary, North Carolina, USA).

**Results**

**Island and mainland locations**

Forward selection for samples among the five islands and two mainland locations included seven soil variables that explained a significant (0.05 level) portion of the variance in the distribution data. The first four variables were the percentage clay, magnesium-calcium ratio, CEC and the net nitrogen mineralization rate. The remaining three selected variables were polynomial functions that included cubic values of percentage silt and the magnesium-calcium ratio, and the quadratic value of CEC. Variance inflation factors were \( \leq 2.66 \), and were well within the accepted range of values for multivariate analysis.

Selected soil variables explained 27% (adjusted \( R^2 \) or \( R_a^2 \)) of the variation in species presence-absence data when modeled with spatial covariables. Spatial covariables, however, explained none of the variation in the species data. Permutation tests were significant for environmental variables (\( P = 0.0001 \)) but indicated no effect of spatial variables (\( P = 0.9208 \)). The first two canonical axes of the RDA were significant, and explained 19.0% of the variation in the bunchgrass distributions (Table 2, Fig. 3). Namely, the first axis described soil variables of CEC, the magnesium-calcium ratio and % clay, and net nitrogen mineralization. The second canonical axis described polynomials of silt and CEC. The RDA biplot of results distinguished among the three native bunchgrass species (Fig. 3). Specifically, the presence of *N. pulchra* was correlated with clay-rich, serpentine soils. Presence/absence of *B. carinatus* was associated with CEC, although the relationship was non-linear. *Elymus glaucus* presence was associated with soil texture (silt), low magnesium-calcium ratios, and net nitrogen mineralization.
Four islands, soils and MEM

Four islands, soils only

Islands and mainland, soils only

Channel Islands National Park

Table 2. Results of analyses including permutation tests and canonical coefficients of the two significant axes identified by each RDA. Quadratic (second-order) and cubic (third-order) polynomials of soil variables are indicated.

| Variable                         | RDA1     | RDA2     |
|----------------------------------|----------|----------|
| Islands and mainland, soils only | 0.173    | 0.018    |
| Eigenvalues                      | 0.014    | 0.027    |
| F ratio                          | 46.54*** | 4.77**   |
| Canonical coefficients           |          |          |
| Clay                             | −0.790  | −0.013   |
| N-min                            | 0.267   | 0.211    |
| (Mg/Ca)^3                        | 0.210   | −0.684   |
| Mg/Ca                            | 0.297   | 0.379    |
| (Silt)^3                         | −0.341  | 0.119    |
| CEC                              | 0.410   | −0.234   |
| Four islands, soils only         |          |          |
| Eigenvalues                      | 0.143    | 0.027    |
| F ratio                          | 21.40*** | 4.06*    |
| Canonical coefficients           |          |          |
| Mg/Ca                            | −0.458  | 0.264    |
| (NH4^+)^2                        | 0.339   | 0.528    |
| (CEC)^2                          | 0.334   | 0.633    |
| Clay                             | −0.692  | 0.477    |
| CEC                              | 0.510   | −0.441   |
| Four islands, soils and MEM      |          |          |
| Eigenvalues                      | 0.272    | 0.115    |
| F ratio                          | 78.44*** | 33.13*** |
| Canonical coefficients           |          |          |
| Mg/Ca                            | −0.317  | 0.232    |
| (NH4^+)^2                        | 0.161   | −0.174   |
| (CEC)^2                          | 0.083   | −0.120   |
| Clay                             | −0.323  | −0.322   |
| CEC                              | 0.262   | 0.288    |
| MEM 1                            | 0.409   | 0.035    |
| MEM 2                            | −0.049  | 0.558    |
| MEM 3                            | 0.165   | −0.314   |
| MEM 4                            | −0.199  | −0.099   |
| MEM 5                            | 0.301   | −0.021   |
| MEM 6                            | −0.263  | −0.009   |
| MEM 7                            | 0.216   | −0.019   |
| MEM 8                            | −0.016  | −0.387   |
| MEM 9                            | 0.305   | −0.099   |
| MEM 10                           | −0.076  | −0.310   |
| MEM 11                           | 0.132   | −0.349   |

*p < 0.05, **p < 0.01, ***p < 0.001.

Channel Islands National Park

Spatial data for analysis of the four northern Channel Islands included 70 MEM eigenfunctions. Forward selection retained 11 of the original 70 spatial variables, but none of these represented positive spatial autocorrelation (P = 0.272, forward selection of first positive MEM variable). The absence of significant positive spatial variables agreed with results for the complete island and mainland dataset, suggesting a lack of spatial structuring in these grasslands. Although the use of negative eigenfunctions in community analysis is not well-defined, negative MEM variables may model biotic interactions such as competition and niche differentiation (Borcard et al. 2011). We therefore ran RDA for the forward selected soil variables and Hellinger-transformed species data both with and without negative MEM spatial variables.

Forward selection of soil variables for samples among the four Channel Islands included the magnesium-calcium ratio, percentage clay and CEC. Also included were quadratic values of initial NH4^+ and CEC. The value of alpha was 0.05 or less for each of these variables despite the 0.10 cutoff. RDA without spatial functions was highly significant (P = 0.0001) and soil variables explained 22% (R^2 = 0.22) of the variation in species abundance data. Variance inflation factors were ≤ 1.9 for this analysis. The first two canonical axes were significant and explained 17.0% of the variation in the bunchgrass abundance data (Table 2). The first axis described CEC, the magnesium-calcium ratio and % clay. The second canonical axis described polynomials of initial NH4^+ and CEC. RDA biplot results indicated separation between N. pulchra and B. carinatus, with weaker evidence for an association between soil characters and the presence/absence of E. glaucus (Fig. 4).

Each of the first two RDA analyses identified a significant association between soil properties and species presence-absence data, but residual eigenvalues were high (>70%). The addition of negative MEM spatial functions to the model reduced residual eigenvalues. RDA was significant for soils (P = 0.0008), and variance inflation factors were low (≤1.91). Soil variables explained 9%, and spatial MEM functions 29%, of the variation in species abundance data. The variance fraction explained jointly by spatial and soil variables was 13%, and residual eigenvalues were reduced to 49%. In sum, the 22% of the variation in species data explained by soil properties in the CI analysis was divided into 9% explained solely by soil variables and 13% explained by spatially structured soil data. The first two canonical axes were significant, and N. pulchra populations were correlated with the percentage clay and magnesium-calcium ratio (Table 2, Fig. 5). Bromus carinatus was correlated with initial NH4^+ and the quadratic value of CEC. There
was some evidence for the association of *E. glaucus* and soil CEC (Fig. 6).

**Logistic regression**

Forward selected soil variables determined in RDA analysis were run in separate logistic regression analyses for each species and results indicated that individual soil variables can predict species presence or absence at a site. Results reported here list values derived from logistic likelihood ratio tests tables (chi-square degrees of freedom = 1). The two variables with
the greatest overall effect were the magnesium-calcium ratio and nitrogen mineralization rate. There was also some effect of soil texture, which was specific to the percentage clay. *Bromus* carinatus populations were negatively correlated with magnesium-calcium ratios ($\chi^2 = 6.87, P = 0.0088$) and somewhat positively correlated with nitrogen mineralization rates ($\chi^2 = 3.72, P = 0.0539$). *Elymus glaucus* distributions were negatively correlated with the percent clay ($\chi^2 = 3.90, P = 0.0484$) and positively correlated with nitrogen mineralization rates ($\chi^2 = 5.79, P = 0.0161$). The greatest number of variables predicted *N. pulchra* distributions (Mg/Ca, $\chi^2 = 4.99, P = 0.0254$; N-min, $\chi^2 = 9.19, P = 0.0024$; %clay, $\chi^2 = 13.28, P = 0.0003$). The presence of *N. pulchra* was positively correlated with magnesium-calcium ratios and percent clay, and negatively correlated with nitrogen mineralization rates.

**DISCUSSION**

Determining how to effectively reestablish California native grasses requires an understanding of the environmental factors that contribute to the persistence of focal species. However, given that large stands of native-dominated grasslands are no longer extant, identifying those factors is difficult. Our goal for this study was to assess the relative contribution of soil properties and spatial structure to species distributions. Canonical analysis confirmed that soil properties...
explained a significant proportion of the variance in the distributions of the three species, but no positive spatial autocorrelation was detected. This indicated that contagious processes such as dispersal factors (e.g., wind and animals) did not explain species occurrence among sampled grasslands (Peters et al. 2006, Borcard et al. 2011). These three species are capable of dispersing to all sites among sampled island and mainland grassland locations, and environmental factors subsequently select for their persistence (Soininen et al. 2007, Kramer et al. 2011).

The absence of dispersal limitations among mainland and Channel Island sites appears to contradict a prior study of native grassland recruitment, which concluded that low rates of bunchgrass seed production and restricted dispersal affected the competitiveness of these species in invaded grasslands (Seabloom et al. 2003). The relative importance of spatial and environmental factors, however, is dependent on scale and our work focused on existing native grasslands (Legendre and Legendre 1998). We evaluated soil characteristics associated with species presence and absence at sites currently occupied by remnant native bunchgrass populations. Consequently, these results do not address the extent to which the three species can disperse to unoccupied (non-native) sites, particularly if species are niche-limited (Moore and Elmendorf 2006). Moreover, recruitment limitation noted in earlier studies of California grasslands may be caused by low rates of seed production, rather than poor rates of dispersal among existing seed pools (Moore et al. 2011).

The presence of significant negative spatial autocorrelation among sites for each species may be a consequence of species ecology, or a sampling effect. We sampled grassland sites specific to these three species in order to characterize environmental variables relevant for their persistence. As a result, many sites represented one species out of three, with 12 of 118 collections representing more than one native bunchgrass population. If sampling did not identify all species at a site, the sampling protocol may represent a source of experimental error. However, sites were revisited frequently and occurrence data were corroborated during each visit. It is therefore likely that data reflect tangible spatial and biotic processes, perhaps due to niche differentiation among species (Leibold and McPeek 2006, Aanderud and Bledsoe 2009). This explanation is supported by the significant environmental variables identified in subsequent ordination and logistic regression analyses. For example, the distributions of *N. pulchra* and *B. carinatus* were negatively correlated among sites.

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Fig. 6. RDA biplot for the three native bunchgrass species and five selected soil variables for the analysis of four Channel Islands and 11 MEM spatial eigenfunctions. Soil variables are described in Fig. 4. Scaling = 1.
for soil magnesium-calcium ratio and nitrogen mineralization potential. In effect, the two species occupied contrasting environments.

Although we identified edaphic factors that predict species presence or absence, this does not confirm causation. Plants alter their environment by redistributing soil nutrients via root structures and litter accumulation as well as by producing allelopathic compounds (Weidenhamer and Callaway 2010, Lankau et al. 2011). In the case of abiotic soil properties, mineral and physical factors are a recognized cause of non-random species distributions (Brady and Weil 2002). The question remains, however, whether biological and chemical soil properties such as nitrogen mineralization and cation exchange capacity represent causes or consequences of plant species distributions. Sites occupied by B. carinatus and E. glaucus were often more mesic and situated on deeper soils relative to sites occupied by N. pulchra (K. Hufford, personal observation). In addition, B. carinatus and E. glaucus did not grow as monocultures and instead were patchily distributed. These characteristics predict that biological and chemical soil properties are a function of the larger community, and may also be a causal factor of bunchgrass distribution in a nutrient-poor environment (John et al. 2007).

In the case of the four northern Channel Islands, 13% of the 22% of the variance explained by soil variables was spatially distributed. Spatial heterogeneity may result from patchy distributions of soil properties, such as the occurrence of serpentine outcrops among sedimentary soils (Borcard et al. 2011). Serpentine soil is widely known to drive species distributions (Kruckeberg 1951, Schechter and Bruns 2008) and the ratio of magnesium to calcium was a significant factor determining species presence or absence in both ordination and logistic regression analyses. Bromus carinatus was less likely to occur on serpentine soils while N. pulchra populations appeared to favor serpentine substrate. Nassella pulchra was once considered to be a historically dominant species in California grasslands (Heady 1977), but later research noted that N. pulchra is adapted to disturbance, suggesting it is more likely a marginal species (Bartolome and Gemmill 1981, Lombardo et al. 2007). Invasive species may have forced N. pulchra populations to occupy serpentine soils as a refuge from intense competition for resources (Harrison et al. 2003). Results were not as conclusive for E. glaucus, possibly reflecting lower sample sizes and the need for additional environmental data as its distribution may be influenced by biotic or abiotic factors not included in this study. We note that island populations of E. glaucus were collected after extensive searches and were representative of the observed distribution.

The soil properties identified in canonical ordination closely matched logistic regression results, but were not identical in all analyses. This outcome may indicate the uneven predictive role of soil properties across a species range, as well as the varying power of different statistics. In addition, while environmental data explained a significant proportion (22–27%) of the variance in species abundance, a majority of the variation in the dataset was unexplained. Our set of environmental variables likely missed measures such as phosphorus and moisture content, as well as biotic interactions such as competition and plant-microbial relationships, that contribute to species distributions (Sea-bloom et al. 2003, Hawkes et al. 2005, Hausmann and Hawkes 2009). As a result, soil properties play a role in species distributions in this landscape, but other factors will likely also affect establishment. A next step would be to verify the ability of edaphic factors to predict revegetation success, supporting the use of individual soil variables in restoration planning.

In sum, the significant associations between our focal species’ distributions and magnesium-calcium ratios, percentage clay and nitrogen mineralization potential are consistent among analyses, and suggest that differences among the preferred soil habitats for the three species can assist in restoration of native bunchgrasses. This result offers potential tools for restoration practitioners who could incorporate knowledge of the association of key species with soil properties into decision making for seed mixes and seeding plans. A combination of additional research and practical testing would be useful to determine if the variance in species’ occurrence explained by soil properties is sufficient to influence restoration outcomes. Ultimately, practitioners will benefit from an understanding of local and regional patterns of diversity in contemporary, degraded ecosystems, and this understanding
may well assist species selection for each restoration site.

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LITERATURE CITED

Aanderud, Z. T., and C. S. Bledsoe. 2009. Preferences for $^{15}$N-ammonium, $^{15}$N-nitrate, and $^{15}$N-glycine differ among dominant exotic and subordinate native grasses from a California oak woodland. Environmental and Experimental Botany 65:205–209.

Allen, R. B., and J. B. Wilson. 1991. A method for determining indigenous vegetation from simple environmental factors, and its use for vegetation restoration. Biological Conservation 56:265–280.

Bartolome, J. W., J. S. Fehmi, R. D. Jackson, and B. Allen-Diaz. 2004. Response of a native perennial grass stand to disturbance in California’s Coast Range grassland. Restoration Ecology 12:279–289.

Bartolome, J. W., and B. Gemmill. 1981. The ecological status of Stipa pulchra (Poaceae) in California. Madroño 28:173–184.

Bartolome, J. W., S. E. Klukkert, and W. J. Barry. 1986. Opal phytoliths as evidence for displacement of native California grassland. Madroño 33:217–222.

Bell, C. E., T. Easley, and K. R. Goodman. 2008. Effective fennel (Foeniculum vulgare) control with herbicides in natural habitats in California. Invasive Plant Science and Management 1:66–72.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Forward selection of explanatory variables. Ecology 89:2623–2632.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer, New York, New York, USA.

Borcard, D., and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153:51–68.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045–1055.

Brady, N. C., and R. R. Weil. 2002. The nature and properties of soils. Prentice Hall, Upper Saddle River, New Jersey, USA.

Chambers, J. M. 2008. SoDiA: functions and examples for “Software for Data Analysis”. R package version 1.0-4. http://cran.r-project.org/web/packages/SoDA/

Chapin, F. S., III, B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500–504.

Corry, P. M., and A. K. McEachern. 2000. Native shrub recovery in non-native annual grasslands, California Channel Islands. Pages 182–183 in D. R. Browne, K. L. Mitchell, and H. W. Chaney, editors. Proceedings of the fifth California Islands symposium. OCS Study MSS99-0038. US Department of the Interior, Minerals Management Service, Pacific OCS Region, Washington, D.C., USA.

Cramer, W. P., and R. Leemans. 1992. Assessing impacts of climate change on vegetation using climate classification systems. Pages 190–217 in A. M. Solomon and H. H. Shugart, editors. Vegetation dynamics and global change. Chapman and Hall, New York, New York, USA.

D’Antonio, C. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent Carpobrotus edulis. Ecology 74:83–95.

Donlan, C. J., D. A. Croll, and B. R. Tershy. 2003. Islands, exotic herbivores, and invasive plants: their roles in Coastal California restoration. Restoration Ecology 11:524–530.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). Ecological Modelling 196:483–493.

Drayton, B. and R. B. Primack. 2012. Success rates for reintroductions of eight perennial plant species after 15 years. Restoration Ecology 20:299–303.

Fahselt, D. 2007. Is transplanting an effective means of preserving vegetation? Canadian Journal of Botany 85:1007–1017.

Falk, D. A., C. I. Millar, and M. Olwell. 1996. Restoring diversity. Island Press, New York, New York, USA.

Gates, D. H., L. A. Stoddart, and C. W. Cook. 1956. Soil as a factor influencing plant distribution on salt-deserts of Utah. Ecological Monographs 26:155–175.

Goldberg, D. E. 1982. The distribution of evergreen and deciduous trees relative to soil type: an example from the Sierra Madre, Mexico, and a
general model. Ecology 63:942–951.
Grman, E., and K. N. Suding. 2010. Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. Restoration Ecology 18:664–670.
Halle, S., and M. Fattorini. 2004. Advances in restoration ecology: insights from aquatic and terrestrial ecosystems. Pages 10–33 in V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, D.C., USA.
Halvorson, W. L. 1994. Ecosystem restoration on the California Channel Islands. Pages 485–490 in W. L. Halvorson and J. G. Maender. The Fourth California Islands Symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.
Hamilton, J. G. 1997. Changing perceptions of pre-European grasslands in California. Madroño 44:311–333.
Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology 17:837–845.
Hausmann, N. T., and C. V. Hawkes. 2009. Plant neighborhood control of arbuscular mycorrhizal community composition. New Phytologist 183:1188–1200.
Hawkes, C. V., I. F. Wren, D. J. Herman, and M. K. Firestone. 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecology Letters 8:976–985.
Heady, H. F. 1977. Valley grassland. Pages 491–514 in: M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. John Wiley and Sons, New York, New York, USA.
Hickman, J. C. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California, USA.
HilleRisLambers, J., S. G. Yelenik, B. P. Colman, and J. M. Levine. 2010. California annual grass invaders: the drivers or passengers of change? Journal of Ecology 98:1147–1156.
Hobbs, R. J. and J. A. Harris. 2001. Restoration ecology: repairing the Earth’s ecosystems in the new millennium. Restoration Ecology 9:239–246.
Holstein, G. 2001. Pre-agricultural grassland in Central California. Madroño 48:253–264.
Jackson, L. E. 1985. Ecological origins of California’s Mediterranean grasses. Journal of Biogeography 12:349–361.
John, R., J. W. Dalling, K. E. Harms, J. B. Yavit, R. F. Stallard, M. Mirabello, S. P. Hubbell, R. Valencia, H. Navarrete, M. Vallejo, and R. B. Foster. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences USA 104:864–869.
Junak, S., S. Chaney, R. Philbrick, and R. Clark. 1997. A checklist of vascular plants of Channel Islands National Park. Southwest Parks and Monuments Association, Tucson, Arizona, USA.
Knapp, J. J., C. Cory, R. Wolstenholme, K. Walker, and B. Cohen. 2009. Santa Cruz Island invasive plant species map. Pages 245–252 in C. C. Damiani and D. K. Garcelon, editors. Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, California, USA.
Kramer, H. A. C., D. M. Montgomery, V. M. Eckhart, and M. A. Geber. 2011. Environmental and dispersal controls of an annual plant’s distribution: How similar are patterns and apparent processes at two spatial scales? Plant Ecology 212:1887–1899.
Kruceberg, A. R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. American Journal of Botany 38:408–419.
Lankau, R. A., E. Wheeler, A. E. Bennett, and S. Y. Strauss. 2011. Plant-soil feedbacks contribute to an intransitive competitive network that promotes both genetic and species diversity. Journal of Ecology 99:176–185.
Lavkulich, L. M. 1981. Methods manual: pedology laboratory. Department of Soil Science, University of British Columbia, Vancouver, British Columbia, Canada.
Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.
Legendre, P., and L. Legendre. 1998. Numerical ecology. Second English edition. Elsevier, Amsterdam, The Netherlands.
Leibold, M. A., and M. A. McPeek. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87:1388–1410.
Lombardo, K., J. S. Fehmi, K. J. Rice, and E. A. Laca. 2007. Nassella pulchra survival and water relations depend more on site productivity than on small-scale disturbance. Restoration Ecology 15:177–178.
Makarenkov, V., and P. Legendre. 2002. Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. Ecology 83:1146–1161.
McCrea, A. R., I. C. Trueman, M. A. Fullen, M. D. Atkinson, and L. Besenyei. 2001. Relationships between soil characteristics and species richness in two botanically heterogeneous created meadows in the urban English West Midlands. Biological Conservation 97:171–180.
Moore, K. A., and S. C. Elendendorf. 2006. Propagule vs. niche limitation: untangling the mechanisms behind plant species’ distributions. Ecology Letters 9:797–804.
Moore, K. A., S. P. Harrison, and S. C. Elmentorf. 2011. Can spatial isolation help predict dispersal-limited
sites for native species restoration? Ecological Applications 21:2119–2128.
Norris, R. M. 2003. The geology and landscape of Santa Barbara County, California and its offshore islands. Santa Barbara Museum of Natural History Monographs Number 3, Santa Barbara, California, USA.
Oksanen, J., R. Kindt, P. Legendre, B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2008. Vegan: community ecology package. R package version 2.0-5. http://cran.r-project.org/web/packages/vegan/index.html
Pan, D., A. Bouchard, P. Legendre, and G. Domon. 1998. Influence of edaphic factors on the spatial structure of inland halophytic communities: a case study in China. Journal of Vegetation Science: 9:797–804.
Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625.
Peters, D. P. C., J. Yao, L. F. Hueneke, R. P. Gibbens, K. M. Havstad, J. E. Herrick, A. Rango, and W. H. Schlesinger. 2006. A framework and methods for simplifying complex landscapes to reduce uncertainty in predictions. Pages 131–146 in J. Wu, K. B. Jones, H. Li, and O. L. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and applications. Springer, Dordrecht, The Netherlands.
Pregitzer, K. S., and B. V. Barnes. 1982. The use of ground flora to indicate edaphic factors in upland ecosystems of the McCormick Experimental Forest, Upper Michigan. Canadian Journal of Forest Research 12:661–672.
Prentice, C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties, and climate. Journal of Biogeography 19:117–134.
R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rein, F. A., M. L. Huertos, and K. D. Holl. 2007. Restoring native grasses as vegetative buffers in a coastal California agricultural landscape. Madroño 33:249–257.
Seabloom, E. W. 2011. Spatial and temporal variability in propagule limitation of California native grasses. Oikos 120:291–301.
Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences USA 100:13384–13389.
Schechter, S. P., and T. D. Bruns. 2008. Serpentine and non-serpentine ecotypes of Collinsia sparsifolia associated with distinct arbuscular mycorrhizal fungal assemblages. Molecular Ecology 17:3198–3210.
Schoenherr, A. A., C. R. Feldmeth, and M. J. Emerson. 1999. Natural history of the islands of California. University of California Press, Berkeley, California, USA.
Sheldrick, B. H., and C. Wang. 1993. Particle size distribution. Pages 499–511 in M. R. Carter, editor. Soil sampling and methods of analysis. Canadian Society of Soil Science, Lewis Publishers, Ann Arbor, Michigan, USA.
Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. Ecography 30:3–12.
Vallano, D. M., P. C. Selmans, and E. S. Zavaleta. 2012. Simulated nitrogen deposition enhances the performance of an exotic grass relative to native serpentine grassland competitors. Plant Ecology 213:1015–1026.
Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13.
Volis, S., M. Dorman, M. Blecher, Y. Sapir, and L. Burdeniy. 2011. Variation partitioning in canonical ordination reveals no effect of soil but an effect of co-occurring species on translocation success in Iris atrofusca. Journal of Applied Ecology 48:265–273.
Weidenhamer, J. D., and R. M. Callaway. 2010. Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. Journal of Chemical Ecology 36:59–69.
Weintraub, M. N., and J. P. Schimel. 2003. Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. Ecosystems 6:129–143.
Whittaker, R. H. 1956. The ecology of serpentine soils. Ecology 35:258–288.
Zhang, L., X. M. H. Shao, and K. Ma. 2011. Strong plant-soil associations in a heterogeneous subtropical broad-leaved forest. Plant Soil 347:211–22.