Distribution of plants in a California serpentine grassland: are rocky hummocks spatial refuges for native species?

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Abstract

Invasions by non-native taxa can have severe consequences for native species. In the heavily invaded serpentine grasslands of central California, many native species appear to be restricted to isolated outcrops of shallow serpentine soil, or "hummocks," although the extent to which these hummocks function as refuges for native vegetation has never been quantified. We tested whether native plant species were restricted to hummocks within a serpentine grassland at the University of California Sedgwick Reserve near Santa Barbara, California by sampling species along hummock-grassland gradients. We also examined the influence of soil parameters, hummock area, proximity to other hummocks, and spatial location on species composition across 16 hummocks at this site. Both the hummocks and the surrounding grassland had high Mg, low Ca, and low Ca to Mg ratios typical of serpentine systems. Hummocks appeared to be more stressful environments because of their shallower soils, lower cation exchange capacity, and greater percent sand. Of the 27 most common plant species sampled along hummock-grassland transects, we identified 8 hummock specialists, 7 edge specialists, 8 matrix specialists, and 4 generalists. Importantly, both the hummock and matrix specialist groups included native species. Plant community composition was correlated with spatial positioning of the hummocks and with soil Ca, Na, K, and N. The number of species increased and community composition changed with increasing hummock area. Species composition was most similar among hummocks in close proximity to each other, and decreased with increasing distance between hummocks. Our results suggest that the community structure of serpentine grasslands is spatially complex and an effective management or restoration plan must address this complexity.

Introduction

Invasions by non-native species can significantly alter ecological communities and ecosystems (e.g., Drake et al. 1989; Hobbs and Humphries 1995; Mooney and Drake 1986; Shea et al. 1998; Vitousek et al. 1997). One outcome of many invasions is the restriction of native species to spatial refuges. For example, different abiotic requirements of native and non-native species may generate spatial refuges for native species in systems such as wetlands (Galatowitsch and van der Valk 1996) and serpentine grasslands (Harrison 1997; Harrison 1999a; Harrison 1999b; McNaughton 1968; Mooney et al. 1986; Murphy and Ehrlich 1989). The distribution of native species in and among these refuges may provide information about community processes that can be used to guide future restoration efforts.

California grasslands, a classic example of a heavily invaded community, provide an excellent system in which to study remnant populations of native species (Armstrong and Huenneke 1992; Baker 1978; Mooney et al. 1986). Native perennial grasslands may have originally covered 9.2 million ha in California, but nearly all of this area is currently dominated by exotic species, most of which are ruderal and early successional Mediterranean annuals (Baker 1978; D'Antonio and Vitousek 1992; Heady 1977; Jackson 1985). Currently, serpentine-derived substrates containing many of California's remnant populations of native species (Harrison 1997; Harrison 1999a; Harrison 1999b; Murphy and Ehrlich 1989) cover only 285,000 ha; the majority of these grasslands are grazed by cattle. Serpentine grasslands are increasingly invaded by exotic plants, some of which appear to be pre-adapted to serpentine conditions (e.g., *Aegilops triuncialis*, K. Lyons, pers. comm.).

In some areas, including our serpentine study site in central California, native species appear to be restricted to spatially isolated outcrops, or "hummocks" within a grassy matrix. However, the extent to which these hummocks function as refuges for native vegetation has not been quantified. Recently, both resource managers and landowners have become interested in restoring California grasslands to their pre-settlement condition to reduce dominance by exotic species, improve summer grazing fodder, and increase nutrient retention (Adams et al. 1999; Menke 1992). An understanding of the role that serpentine hummocks play as refuges for native species is therefore extremely timely and can provide important guidance for conservation and restoration of California grasslands.

Although native grasses and forbs persist on outcrops of serpentine soils (Armstrong and Huenneke 1992; Harrison 1997; Harrison 1999a; Harrison 1999b; Huenneke et al. 1990; Murphy and Ehrlich 1989), the relationships between geochemical constraints and historical events in these systems are not well understood. Serpentine-derived soils in central, coastal California have low calcium to magnesium ratios, low levels of available macronutrients (such as phosphorus and nitrogen), and high levels of toxic heavy metals (Brooks 1987; Proctor 1971; Proctor and Woodell 1975; Walker 1954). In addition, the soil is usually shallow, which limits moisture holding capacity, makes plant growth difficult (Huenneke et al. 1990), and excludes gophers (*Thomomys bottae*) that are common in the surrounding grasslands (Lobo et al. 1998).

Previous studies have identified several mechanisms that can alter the balance between native and non-native species in serpentine grassland systems, including (1) physiological tolerance for "toxic" conditions and tolerance of low nutrient conditions (Harrison 1999b; Huenneke et al. 1990); (2) disturbance regimes (e.g., due to burrowing rodents: Hobbs and Hobbs 1987; Hobbs and Mooney 1985; Moloney and Levin 1996); and (3) differential response to precipitation (Heady 1956a; Heady 1956b; Heady 1958; Hobbs and Mooney 1991; Pitt and Heady 1978). Thus, species that are successful on serpentine outcrops often tolerate drier soils, low nutrient levels, low calcium to magnesium ratios, and high levels of heavy metals.

We examined the distribution of native and non-native plant species on hummocks and in the surrounding grassland matrix as a function of physical and spatial attributes of the study site. We first characterized physical attributes of the study site to determine underlying physical gradients that may influence plant species distribution, because any successful restoration effort must consider these underlying gradients and their influence on species composition. Second, we tested whether native plant species are restricted primarily to hummocks by sampling species along hummock-grassland gradients; the presence of native species in the matrix would favor restoration strategies that control abundance of exotic plants without adversely affecting native species. Third, we assessed the among-year consistency
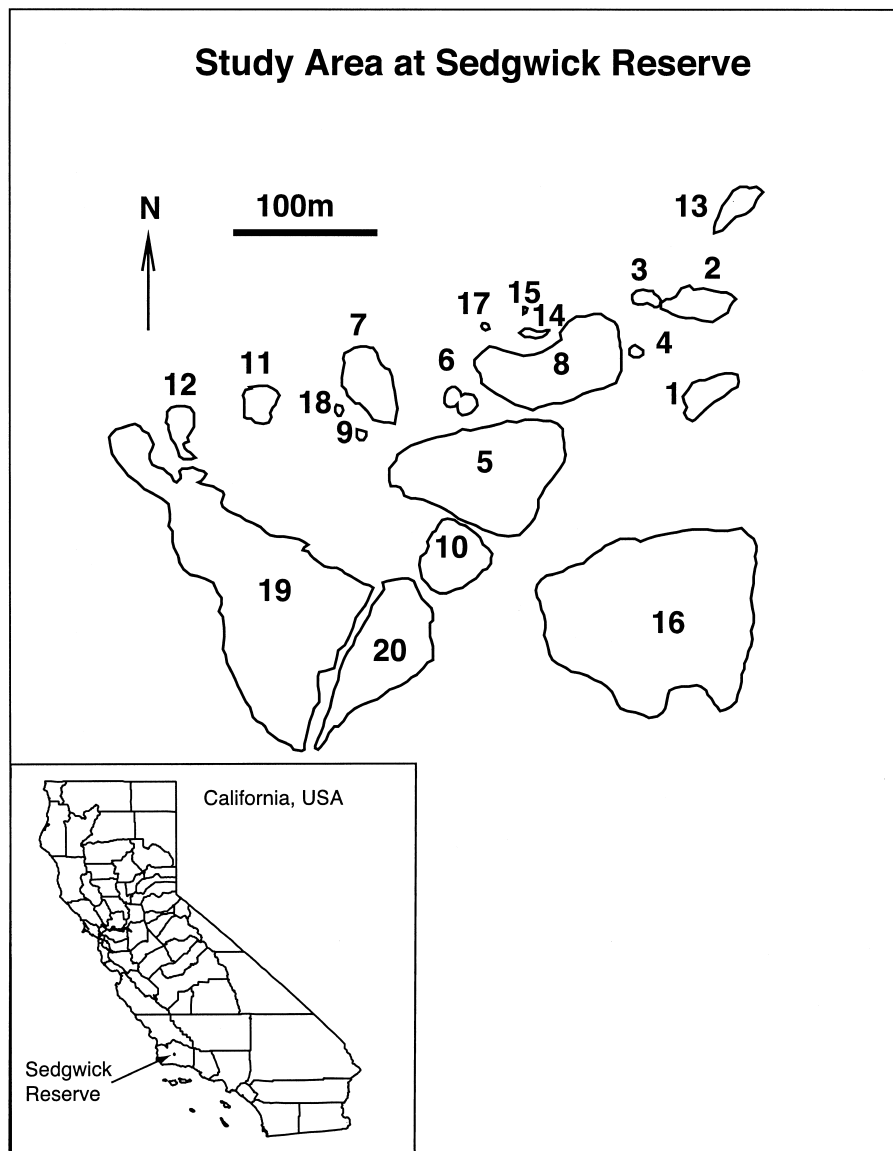
Study Area at Sedgwick Reserve

Figure 1. Map of the hummocks at the study site in the Sedgwick Reserve, located in central California. Area around the hummocks is serpentine grassland. Data from hummocks 3, 11, 12, and 17 were only collected in 1998 and are not included in this study. Transect data were collected across hummocks 1 and 5.

of spatial patterns of species associations among hummocks by comparing species distributions and community structure on 16 hummocks in two years with widely contrasting rainfall.

Methods

Study site

We studied the distribution of plant species on a 15-ha serpentine site in the Sedgwick Reserve, a 2364-ha research facility of the University of California approximately 50 km northeast of Santa Barbara, California (Figure 1). The study site is an upland (730 m elevation), south-facing slope dominated by three

Mediterranean annual grasses: *Avena barbata*, *Bromus hordeaceus*, and *B. madritensis*. The site was grazed by cattle for approximately 150 years before the cattle were permanently removed in 1996. Areas of deeper soil ("matrix") are interspersed with isolated rocky serpentine outcrops ("hummocks") that range in size from 10 to 15,000 m^2 (Figure 1). The non-native annual grasses are dramatically less abundant on the hummocks where native herbs and shrubs appear to be relatively much more abundant. Gopher (*Thomomys bottae*) activity, which is prevalent in the grassland, is nearly nonexistent on the hummocks.

We distinguished between hummock and grassland matrix habitat at our 15 ha study site visually, using plant density and composition as well as soil appearance to identify boundaries; ambiguities were rare. We also constructed a map by outlining the boundaries of each hummock with a stereo pair of color aerial photographs taken in the spring of 1998, when there was a distinct color contrast between vegetation on and off the hummocks. We delineated hummock boundaries at four ground control points as an aid in calibrating hummock boundaries and field checked areas where boundaries were unclear on the aerial photographs. We digitized the map of hummock boundaries (Figure 1) and calculated hummock area and nearest edge distance between each pair of hummocks.

We conducted plant community surveys on 16 hummocks in 1997 and 1998. These years varied widely in rainfall due to a drought in 1997 and heavy rains in 1998 associated with the El Niño Southern Oscillation between September 1997 and September 1998. Rainfall at Sedgwick Reserve was 361 mm from September 1996 through August 1997, and 795 mm for the following 12-month period.

Physical characteristics of hummocks versus grassland matrix

Patterns of plant species distribution are often constrained by environmental conditions such as soil characteristics. To quantify hummock soil characteristics, we collected and composited soil samples in Fall 1998 from six random locations on each of the 16 hummocks for which we sampled plant communities (Figure 1; all hummocks except 3, 11, 12, and 17). To quantify soil characteristics in the grassland matrix, we collected soil samples at 1, 5, 10, and 20 meters from the edge of hummocks 1, 5, and 10 in April 2000. Because Hummock 5 was extremely

large, we set up two transects on opposite ends of this outcrop, for a total of four transects. At each distance from the hummock edge, we collected and composited six soil samples taken at 1 meter intervals perpendicular to the transect line. All soil samples were analyzed by A&L Western Agricultural Laboratories (Modesto, CA) for total nitrogen (ppm), phosphorous (Weak Bray method, ppm), extractable potassium (ppm), total magnesium (ppm), total calcium (ppm), total sodium (ppm), soil pH, cation exchange capacity (meq/100g), percent sand, percent silt, percent clay, and percent organic matter. We also measured soil depth with a 25 cm steel spike at 25 random points on hummocks 1, 5, and 10, and at the same locations along the grassland transects from which we collected soils.

We used a variety of analyses to compare soil characteristics on hummocks with soil characteristics in the surrounding matrix. In these analyses, we found that the large among-hummock variability masked the finer-scale changes in soil chemistry along each transect. Accordingly, we centered each soil metric by subtracting mean value of the hummock from which it was taken. This transformation made the mean for samples taken from a single hummock equal to 0.0. We used these centered values in five analyses.

First, we determined whether hummock soil was different from matrix soil by extracting the linear combination of soil measurements that had the strongest correlation with distance from hummock with canonical correlation analysis; a significant canonical correlation indicated that hummock soil was different from matrix soil. We did not include percent silt because it was redundant with the sum of percent clay and percent sand (i.e., percent soils, silt, and sand sum to 100%). Second, we determined whether soil properties in the grassland matrix changed with distance from a hummock using correlations between individual soil characteristics and the distance from the edge of a hummock (locations on the hummock were assigned a distance of 0 m). Third, we compared mean soil depth on hummocks with mean soil depth in the grassland matrix. Fourth, we used linear regression to test whether the molar Ca:Mg ratio (a key measure of serpentinosity, Brooks 1987) decreased with increasing distance from the hummocks. Finally, we regressed each soil characteristic, including the Ca:Mg ratio, onto the west-east and south-north location of the centroid of each hummock to examine spatial patterns in soil characteristics.

Distribution of species on hummocks versus grassland matrix

We tested whether native species were primarily restricted to hummocks by sampling the distribution of plant species on two hummocks and in the surrounding grassland (hummocks 1 and 5, Figure 1) in April 1998. On each hummock, we sampled species along six radial transects that extended from the highest point of the hummock to a maximum of 109 m into the surrounding grassland matrix. The first radial transect was oriented on a random compass bearing, and each subsequent transect was turned by 60 degrees. Along each transect, we collected species frequency data every 10 m, starting 1 m from the highest point and using a 1.0 x 0.3 m quadrat. We divided the quadrat into thirty 0.1 x 0.1 m subplots and recorded the presence or absence of each species in each subplot. We sampled 2 to 15 (mean = 5.1) quadrats per transect, depending on the size of the hummock. All taxonomy follows Hickman (1997); a single person (VLB) resolved all taxonomic questions.

We used these data to determine the affinity of each plant species for hummocks or for the surrounding grassland matrix. First, we centered transect distances by subtracting the distance to the hummock edge from each point; a distance of 0.0 represented the hummock edge, negative distance values indicate samples taken on the hummock, and positive distances indicate samples taken in the matrix. We then classified each species' affinity for hummocks or grassland matrix using logistic regression. Each analysis tested for the significance of distance from hummock edge (*x*) using the following model:

$$\ln\left(\frac{p_i}{1-p_i}\right) = f(x) = b_{i0} + b_{i1}x + b_{i2}x^2 + h_{ik}$$

(1)

where p_i is the conditional probability of species *i* being present at a given distance *x* from the hummock edge, b_{ij} is the *j*th regression coefficient for species *i*, and h_{ik} is a dummy variable that represents the effect of hummock *k* on p_i. After testing for the significance of distance, we estimated the linear and quadratic slope terms using a model without the block terms, so that they represented the average response of the species across all hummocks. The inclusion of the blocking terms did not affect any classifications.

In this regression we counted each 1.0 × 0.3-m quadrat as a single sample. However, by using a quasi-likelihood approach we were able to take advantage of the additional precision afforded by the 30 presence-absence "surveys" within each quadrat (McCullagh and Nelder 1989). The quasi-likelihood approach calculates the ratio between the actual variance in the data and the expected variance. In our analysis, this ratio was always less than 1.0 (i.e., there was less variance than expected) due to the precision gained from the within-quadrat sub-sampling.

We classified each species *i* as a habitat specialist or generalist using the sign of the slope of species frequency as a function of distance, b_{i1} in Equation 1. If the slope was negative, we classified the species as a hummock specialist (the further from a hummock, the less likely an occurrence of that species). Conversely, if the slope was positive, we classified the species as a matrix specialist. Some species showed no overall trends in abundance along transects (i.e., $b_1 = 0$) and required further assessment. Three different distributions could cause the observed slope to be zero: the total frequency was too low to resolve a pattern, the species was clustered in the middle of the transect, or the species truly was a generalist. To address the first issue, we eliminated all species that were present in fewer than five quadrats across all transects and hummocks. To address the second issue, we examined the quadratic term in the regression (b_2 in Equation 1). If this term was negative and significantly improved the fit ($p < 0.05$), we examined the location of the peak of the quadratic function. If the peak was within 1 m of the hummock edge, we classified the species as an edge specialist; otherwise, we classified it as a hummock or matrix specialist, depending on peak location. We classified the remaining species as generalists.

Species distribution among hummocks

Species distribution in a heterogeneous environment is the result of many factors, including species-area relationships and environmental constraints. To identify which plant species occurred on hummocks, we did a complete survey of all vascular plants on 16 hummocks that spanned a wide range of hummock sizes (Figure 1; hummocks 3, 11, 12, and 17 were not sampled) in the spring when most native species were flowering (13 − 19 March 1997 and 10 − 29 April 1998). We compiled species lists by systematically walking across the hummocks until no additional

species were found. At least two people compiled lists on each hummock, and discrepancies were rare. All data were recorded as presence/absence of each species on each hummock in each of the two years.

We examined the effects of hummock area on species richness with a series of linear regressions relating the natural log of species richness (r_i) to the natural log of hummock area in m^2 (a_i) and a dummy variable coding for a year effect (y_i), which had a value of 0 for 1997 and 1 for 1998. The expectation function was

$$r_i = \beta_0 + \beta_1 a_i + \beta_2 y_i + \beta_3 a_i y_i \qquad (2)$$

We chose this statistical approach because it facilitated tests of whether the slope and intercept of the species-area relationship were different in the two years of our study (Neter et al. 1985). We tested for a significant change ($\alpha = 0.05$) in the intercept using β_2 and a significant change in the slope using β_3, and used backwards elimination to arrive at a final model.

We applied this multiple regression procedure to 10 datasets: all species that occurred on the hummocks, plus subsets of species to determine which species groups responded most strongly to hummock area. These subsets were native species, exotic species, woody species, herbaceous species, monocots, dicots, annuals, perennials, and hummock specialists as determined by the transect analysis. Species for which any classification was uncertain were omitted from that particular regression.

We characterized patterns of community composition among hummocks using ordination and Mantel tests. In these analyses, we used the complete list of species found on each hummock regardless of year, thereby providing an estimate of the total species pool on each hummock. We obtained similar results for each year independently but do not report those results here. Inclusion of rare species had little effect on either analysis so we report only analyses with the full species list.

First, we used principal coordinates ordination (PCO) to assess site-scale geographic patterns of community composition, the effects of hummock area on species composition, and the relationship between community composition and soil characteristics. We used PCO to extract linear axes summarizing the variation in hummock communities; specifically, we applied eigenanalysis to a similarity matrix calculated using Jaccard's index for presence/absence data. We

then assessed site-scale geographic patterns of community composition by determining the correlation between the scores for the first two PCO axes and the west-east and south-north location of each hummock. We determined the effects of hummock area on species composition by correlating the PCO scores and the area of each hummock. Finally, we determined the relationship between community composition and individual soil characteristics by regressing the PCO scores on each of the soil variables.

We also used two-way Mantel tests (Manly 1986; Mantel 1967) to test whether there was a correlation between (a) hummock community composition and soil properties, and (b) community composition and the distance between hummocks. We measured dissimilarity among hummocks using Jaccard's index for community composition, Euclidean distance for soil properties, and the shortest distance between each pair of hummocks for geographic distance. For each test, significance was assessed at $\alpha = 0.05$ by a permutation test with 5000 iterations.

Results

Characteristics of hummocks and the grassland matrix

Both hummocks and the grassland matrix at the Sedgwick study site had high Mg, low Ca, and low Ca:Mg ratios typical of serpentine systems (Table 1; Brooks 1987), but the soil conditions in the hummocks were more stressful than those in the matrix (canonical $R^2 = 0.88$, $p = 0.03$). Most, but not all, of the hummock soils that we sampled were serpentine, with average molar Ca:Mg ratios of approximately 0.3, which increased only weakly with increasing distance from hummocks ($R^2 = 0.168$; $p = 0.082$; n = 19). Hummocks had a higher percentage of sand and more shallow, rocky soils than the matrix (Table 1). Although some soil elements (Mg, Ca, Na) and parameters that affect nutrient availability (pH, cation exchange capacity, percent clay) increased significantly with increasing distance from hummocks, P concentrations declined with increasing distance from hummock (Table 1). Only P and K showed systematic spatial variation across the hummocks (Table 1, correlations with west-east hummock location).

Table 1. Properties of hummock and matrix soils and spatial pattern of soil properties among 16 hummocks

Soil metric	Hummocks[1]	Grassland Matrix[1]	r, distance from hummock[2]	r, west-east hummock location[3]	r, south-north hummock location[3]
P (ppm)	13.50 ± 1.68	7.25 ± 1.21	**-0.51**	**0.57**	0.17
K (ppm)	182.94 ± 11.14	210.63 ± 14.96	0.32	**0.63**	0.08
N (ppm)	1911.06 ± 127.17	1886.88 ± 109.32	0.15	0.26	0.09
Mg (ppm)	2044.13 ± 137.29	262 ± 116.16	**0.75**	− 0.18	− 0.41
Ca (ppm)	1020.94 ± 185.14	832.13 ± 109.79	**0.62**	− 0.42	0.18
Ca:Mg (on a molar basis)	0.165 ± 0.01	0.92 ± 0.03	0.40	− 0.31	0.29
Na (ppm)	18.69 ± 1.14	23.50 ± 3.36	**0.55**	− 0.33	0.03
pH	7.01 ± 0.07	7.31 ± 0.03	**0.67**	− 0.40	− 0.34
Cation exchange capacity (meq/100g)	22.77 ± 1.60	26.36 ± 1.23	**0.80**	− 0.33	− 0.14
Percent Organic Matter	3.35 ± 0.35	3.12 ± 0.43	− 0.11	0.35	0.11
Percent Sand	57.44 ± 2.81	43.44 ± 2.44	**-0.77**	0.12	0.26
Percent Silt	19.19 ± 1.56	25.56 ± 0.87	0.41	− 0.16	− 0.40
Percent Clay	23.63 ± 1.65	31.00 ± 2.17	**0.79**	− 0.07	− 0.09
Soil Depth[4] (mm)	132.76 ± 10.27	> 250	−	−	−

[1]Mean (± 1 SE) of soil metrics on 16 serpentine hummock outcrops (Hummocks) and at distances of 1, 5, 10 and 20 m away from hummocks into the associated grassland matrix (Grassland Matrix).

[2]Correlations between each of the soil metrics and distance from the hummock (r, distance from hummock) were calculated along four transects which extended 20 m into the surrounding grassland matrix (see Methods). Correlations that are significant at $\alpha = 0.05$ are indicated in bold.

[3]For the among-hummock spatial pattern analyses, correlations of each soils metric with west-east hummock location and south-north hummock location ($n = 16$; $|r| > 0.497$ for $p < 0.05$).

[4]Soil depth was measured on only 3 hummocks so these data are not included in the correlation analyses.

Distribution of species among hummock and grassland

Many plant species showed clear affinities for either hummock or grassland in the radial transects around hummocks 1 and 5 (Table 2). Fifty-three of the 116 species that we identified in the study area in 1997 and 1998 were found within the radial transects. Of these species, 42 are native to California and 11 are non-native annuals introduced from Europe. In our transect samples, we found 35 native species and 9 non-native species on the hummocks and 31 native species and 9 non-native species in the grassland matrix. Of the 27 species that we classified, we found 8 hummock specialists, 7 edge specialists, 8 matrix specialists, and 4 generalists (Table 2). All but one of the hummock and edge specialists were native species (the genus *Vulpia* contains a native and an exotic on the site, which we were unable to distinguish reliably), and three of the eight matrix specialists were exotic species. The generalists were evenly split between native and exotic species.

Species distribution among hummocks

Community composition on hummocks was related to hummock area, geographic position, and soil parameters. We identified 116 native and exotic species in the study area during 1997 and 1998. Most of these species were natives (80%) and herbaceous (88%). Just over half of the species were annuals (59%), while 75% were dicots.

The number of species on serpentine hummocks increased significantly with increasing hummock area for most plant groups (Table 3). Slopes of the species-area relationship for 9 of the 10 analyses fell between 0.15 and 0.21, with standard errors between 0.015 and 0.037. Interestingly, the relationship for exotic species was opposite the others, with a small but significant negative slope. Species-area relationships for perennials, woody species, and the hummock specialists were similar between years. In contrast, the intercept increased significantly from 1997 to 1998 for all species pooled, native taxa, dicots, and annuals, and both the slope and the intercept changed from 1997 to 1998 for monocots and exotic species.

Table 2. Affinity grouping for each species found in the hummock transects based on species-specific linear and quadratic logistic regression estimates

Species	Native/ Exotic	n[1]	Linear Coeff.	Linear p-value	Quadratic Coeff.	Quadratic p-value	Peak Location (m)	Affinity Group[2]
Chaenactis glabriuscula var. *lanosa*	n	8	− 0.053	0.023	−	−	−	Hummock
Eriogonum fasciculatum	n	22	− 0.087	0.0001	−	−	−	Hummock
Gilia achilleifolia	n	21	− 0.061	0.001	−	−	−	Hummock
Lotus strigosus	n	9	− 0.040	0.044	−	−	−	Hummock
Melica imperfecta	n	9	− 0.035	0.138	− 0.012	0.017	− 3.00	Hummock
Minuartia douglasii	n	14	− 0.039	0.049	−	−	−	Hummock
Poa secunda	n	7	− 0.019	0.341	− 0.009	0.017	− 2.21	Hummock
Vulpia spp.	-	18	− 0.020	0.268	− 0.005	0.021	− 4.29	Hummock
Astragalus gambelianus	n	8	− 0.004	0.748	− 0.009	0.014	− 0.47	Edge
Hazardia squarrosa	n	7	0.029	0.209	− 0.061	0.002	0.47	Edge
Lasthenia californica	n	15	− 0.003	0.920	− 0.006	0.023	− 0.51	Edge
Lotus wrangelianus	n	6	0.000	0.808	− 0.006	0.011	0.00	Edge
Plantago erecta	n	5	0.004	0.987	− 0.187	0.027	0.02	Edge
Trifolium albopurpureum	n	10	0.020	0.420	− 0.020	0.003	0.98	Edge
Trifolium willdenovii	n	6	− 0.000	0.809	− 0.010	0.020	− 0.02	Edge
Amsinckia menziesii	n	6	0.045	0.076	− 0.021	0.004	2.08	Matrix
Bromus hordeaceus	e	24	0.092	0.0002	−	−	−	Matrix
Dichelostemma captitatum	n	10	0.137	0.0001	−	−	−	Matrix
Hemizonia congesta	n	7	0.046	0.093	− 0.012	0.021	3.75	Matrix
Hordeum murinum	e	16	0.056	0.017	−	−	−	Matrix
Lactuca serriola	e	12	0.088	0.001	−	−	−	Matrix
Nassella pulchra	n	13	0.054	0.014	−	−	−	Matrix
Thysanocarpus curvipes	n	5	0.076	0.003	−	−	−	Matrix
Avena barbata	e	44	0.013	0.526	0.001	0.640	−	None
Bromus madritensis	e	6	0.024	0.308	− 0.003	0.224	−	None
Coreopsis bigelovii	n	9	− 0.002	0.865	− 0.001	0.426	−	None
Plagiobothrys spp.	n	7	− 0.015	0.559	0.003	0.003	−	None

[1]The number of quadrats in which the species appeared is represented by *n*.
[2]See text for affinity classification criteria.

Table 3. Parameters for ten linear regressions relating species richness to hummock area[1]

Response Variable	$\beta_0 \pm 1$ SE (Intercept)	$\beta_1 \pm 1$ SE (Slope)	$\beta_2 \pm 1$ SE (Change in intercept in 1998)	$\beta_3 \pm 1$ SE (Change in slope in 1998)	n	R^2 (%)
Total species richness	0.95 ± 0.05	0.16 ± 0.02	0.17 ± 0.03		32	82.8
Native species	0.75 ± 0.06	0.20 ± 0.02	0.15 ± 0.04		32	82.5
Exotic species	0.80 ± 0.12	− 0.07 ± 0.04	− 0.07 ± 0.16	0.12 ± 0.05	31	52.8
Monocots	0.73 ± 0.08	0.04 ± 0.03	− 0.17 ± 0.12	0.10 ± 0.04	32	58.0
Dicots	0.71 ± 0.05	0.19 ± 0.02	0.20 ± 0.03		32	87.3
Annuals	0.76 ± 0.05	0.15 ± 0.02	0.21 ± 0.03		32	79.9
Perennials	0.42 ± 0.10	0.18 ± 0.03			32	49.9
Woody	− 0.10 ± 0.11	0.16 ± 0.04			30	39.7
Herbaceous	0.93 ± 0.05	0.16 ± 0.02	0.18 ± 0.03		32	83.6
Hummock specialists	0.17 ± 0.11	0.21 ± 0.04			30	55.1

[1]Only parameters in the final model are listed here.

Community composition as summarized by PCO was correlated with hummock spatial position, hummock area, and hummock soil characteristics. The first PCO axis explained 31.9% of the variation in the data (Table 4), and was negatively associated with hummock south-north location on the study site ($r = − 0.65$, $p = 0.006$) and positively associated with hummock area ($r = 0.71$, $p = 0.002$). However,

Table 4. Plant species for which there was a significant correlation between presence-absence on a hummock and that hummock's scores on the first two principal coordinates axes[1]

Principal Coordinate 1		Principal Coordinate 2	
Species	r	Species	r
Trifolium willldenovii	0.844	*Astragalus gambelianus*	− 0.826
Minuartia douglasii	0.826	*Plagiobothrys* sp	− 0.602
Medicago polymorpha	− 0.823	*Uropappus lindleyi*	− 0.577
Coreopsis bigelovii	0.792	*Claytonia perfoliata*	0.574
Thysanocarpus curvipes	0.778	*Poa secunda*	0.550
Chorizanthe palmeri	0.768	*Vulpia myorus*	0.542
Trifolium fucatum	0.764	*Claytonia parviflora*	0.540
Salvia columbariae	0.757	*Lomatium utriculatum*	0.537
Gilia achilleifolia	0.743	*Bromus hordeaceus*	− 0.529
Hazardia squarrosa	0.739	*Callandrinia ciliata*	− 0.529
Bloomeria crocea	0.717	*Lepidium nitidum*	0.516
Eschscholzia californica	0.717	*Zigadenus fremontii*	0.515
Dudleya lanceolata	0.713	*Athysanis pusillus*	0.509
Sisyrinchium bellum	0.711	*Bowlesia incana*	0.509
Pellea andromedifolia	0.709	*Galium andrewsii*	0.509
Phacelia imbricata	0.700	*Phlox gracilis*	0.509
Agoseris heterophylla	0.693	*Senecio vulgaris*	0.509
Calystegia collina subspp *venusta*	0.691	Unknown 1	0.509
Hemizonia fasciculata	0.671	Unknown 2	0.509
Silene gallica	0.671	*Lupinus bicolor*	0.504
Yucca whipplei	0.671	*Microseris douglasii*	− 0.501
Filago californica	0.652		
Lupinus bicolor	0.646		
Crassula connata	0.644		
Melica imperfecta	0.635		
Lotus wrangelianus	0.629		
Claytonia parviflora	0.623		
Lomatium utriculatum	0.607		
Eriophyllum confertiflorum	0.597		
Chaenactis glabriuscula var. *lanosa*	0.594		
Galium porrigens	0.593		
Vulpia microstachys	0.589		
Plagiobothrys sp 2	0.585		
Lotus strigosus	0.584		
Nassella pulchra	0.566		
Cirsium occidentale	0.566		
Cuscuta californica	0.566		
Eriogonum fasciculatum	0.566		
Salvia leucophylla	0.566		
Selaginella bigelovii	0.566		
Rafinesquia californica	0.556		
Linanthus parviflorus	0.537		
Navarretia attractyloides	0.523		
Lupinus succulentus	0.517		
Trifolium gracilentum	0.517		
Fritillaria biflora	0.498		

[1]Only species with significant correlations ($n = 15$; $|r| > 0.497$ for $p < 0.05$) are listed.

hummock sizes decreased from south to north ($r = −0.596$, $p = 0.015$), confounding the effects of hummock spatial positioning and area. The second PCO axis explained 13.8% of variation in the data (Table 4), and exhibited a negative but non-significant trend with west-east location on the study site ($r = −0.21$, $p = 0.435$). For species on hummocks where we also sampled soils, the first PCO axis was nega-

Table 5. Correlations between the first Principal Coordinate axis (PCO 1) and the second Principal Coordinate axis (PCO 2) with each soil metric

Soil metric	r, PCO 1[1]	r, PCO 2[1]
Percent Organic Matter	0.193	− 0.308
Extractable P (ppm)	0.090	− 0.313
Total K (ppm)	0.224	**-0.532**
Total Mg (ppm)	− 0.144	0.159
Total Ca (ppm)	**-0.524**	0.417
Total Na (ppm)	**-0.510**	0.354
Ph	− 0.006	0.273
Cation Exchange Capacity (meq/100g)	− 0.418	0.351
Percent Sand	0.185	− 0.186
Percent Silt	− 0.017	0.226
Percent Clay	− 0.288	0.100
Total N (ppm)	0.143	**-0.525**
Ca:Mg (on a molar basis)	− 0.396	0.434

[1]Correlations that are significant at $\alpha = 0.05$ are indicated in bold ($n = 16$; $|r| > 0.497$ for $p < 0.05$).

tively correlated with Ca and Na, and the second PCO axis was negatively correlated with K and N (Table 5).

In addition, the two-way Mantel tests revealed that community composition was correlated with both hummock location and soil characteristics ($p < 0.05$). In particular, community dissimilarity increased with increasing geographic distance between hummocks and with increasing dissimilarity in soil properties.

Finally, the Ca to Mg ratio was a good predictor of the number of exotic species per hummock in the drier year of our study: there were more species on hummocks with higher Ca:Mg ratios ($R^2 = 0.62$, $p < 0.001$). This relationship did not persist in the wetter year, however ($R^2 = 0.1$, $p = 0.212$).

Discussion

Our quantitative analyses of species distribution and community composition confirm the visual impression that hummocks were spatial refuges for several native plant species at the Sedgwick Reserve study site. Although the hummocks are not isolated patches of serpentine soils, they represent higher-stress environments than the surrounding grassland matrix (Table 1) and contain some native species not found in the matrix (Table 2). These findings suggest that the sandy, shallow soils, and low cation exchange capacity may limit colonization of hummocks by exotic

species (Harrison 1999b; Huenneke et al. 1990; Kruckeberg 1984).

Our results, however, show that spatial partitioning of native and exotic species in the grassland matrix and hummocks is incomplete: some exotic species were found on hummocks and some native species were found primarily in the grassland matrix. The complex patterns of species distribution between the hummock and matrix habitat suggest that effective restoration of serpentine grassland-hummock systems to pre-settlement conditions will require a deeper understanding of the processes underlying the distribution of native species within specific habitats, as well as care in the choice of restoration models. The community structure of serpentine grasslands is spatially complex and an effective management or restoration plan must address this complexity.

Hummocks as refuges for native plant species

In this serpentine outcrop-grassland system, hummocks were habitat refuges for several native plant species (Table 2). The matrix specialists were a mixture of both native and exotic species, while fifteen of the sixteen hummock and edge specialists were native species. There were similar numbers of edge specialists (7) and hummock specialists (8), although three of the hummock specialists were clustered within a few meters of the edge. Restriction of some native species to serpentine hummocks may be due to low dispersal ability, specific physiological requirements, or poor competitive ability in the matrix. Because soil properties change gradually with increasing distance from hummock edges, conditions along the hummock-matrix edge may represent a compromise between Mg toxicity, nutrient availability, and soil depth. The physical and chemical conditions on hummocks are stressful and thus unsuitable for species that are not adapted to these conditions (mostly exotic species but some native). As distance from a hummock edge increases, physical and chemical conditions become less stressful and support a greater proportion of exotics.

The contrasting composition of native species assemblages in the matrix and on the hummocks suggests that any efforts to shift the balance of biomass towards native species must take into account the life-history traits and ecological processes underlying the observed distributions. For example, our results suggest that restoration via non-selective removal of plants from the grassland matrix using broad-

spectrum herbicides or cultivation would adversely affect both exotic and native species. Non-selective removals in the matrix might reduce competition with invaders, but the remaining natives may not be sufficiently abundant, have sufficient dispersal ability, or have sufficient reproductive output on the remaining hummocks to act as sources for re-populating the surrounding matrix. Results from an experiment at the same study site suggest that seed limitation and abiotically mediated competition exclude some native annual forbs from the grassland matrix (Seabloom et al. In press).

Successful restoration strategies might exploit life-history differences between the native species in the matrix, which tend to be perennials, and the non-native annual grasses. Possible management strategies might combine burning at the time of maximum growth for the annual exotics, reduction of disturbance by grazing cattle to limit exotic annual plant growth, and promotion of perennial growth and survival, including *N. pulchra*. Several studies in central California have found that early-spring burning promotes native grasses and forbs (Hatch et al. 1999; Meyer and Schiffman 1999; Pollak and Kan 1998; Shoulders 1994). However, because of the potential for complex interactions in multi-species assemblages, and our interest in managing for both native perennials and native annuals, such interventions should follow the principles of adaptive management (Parma et al. 1999; Walters 1986).

Hummock community composition

The site-scale gradients in community composition and the positive relationship of distance between hummocks and community dissimilarity indicate that environmental factors may play a key role in structuring these communities. Specifically, plant community composition on hummocks at our study site was influenced by hummock area, the spatial configuration of serpentine patches, soil chemistry, and inter-annual variability in rainfall. Furthermore, community composition varied along site-scale geographic and soil chemistry gradients (Ca, Na, K, and N).

The greater number of exotic species on hummocks with higher Ca:Mg ratios suggests that hummocks with lower Ca:Mg ratios than the surrounding grassland may resist invasion by exotic species abiotically, as seen by Harrison (1999b). However, this invasion pattern appears to be strongly affected by water availability. In 1998, the Sedgwick Reserve experienced twice the amount of rainfall of 1997, changing the composition of the plant community. In particular, the total number of exotic species found on hummocks doubled from 1997 (10 species) to 1998 (19 species): exotics were less excluded from low Ca:Mg soils in the year of heavy rainfall. This pattern is consistent with studies at Jasper Ridge, California, that show that *Bromus hordeaceus* colonization of serpentine areas increased in high rainfall years (Hobbs and Mooney 1991). At our site, *Hordeum murinum*, another exotic grass, was identified as a matrix specialist but was found on more hummocks in the wetter year. The relative exclusion of exotic species from hummocks during dry years might be due to the toxic soil chemistry, the low water holding capacity, or shallow depth of the serpentine soils, all three of which were implicated in a recent study of serpentine communities (Harrison 1999b). Increased water availability may facilitate invasion of hummocks, causing serpentine outcrop communities to be more susceptible to invasion by exotics during years with high rainfall.

A positive relationship between number of species and the area of patch habitats could result from the colonization-extinction dynamics of species within patches of varying size (MacArthur and Wilson 1967). Large hummocks may have a greater diversity of habitats, particularly relative to nutrient levels, than do smaller hummocks, which may promote more diverse plant communities on larger hummocks (Harrison 1997; Harrison 1999a). Furthermore, differences in disturbance regimes (e.g., habitat stability) across larger hummocks can significantly change habitat and promote establishment of particular plant species (Hobbs and Hobbs 1987; Hobbs and Mooney 1985; Hobbs and Mooney 1991; Hobbs and Mooney 1995).

Colonization-extinction dynamics, habitat diversity, and disturbance regime may also explain the observed correlation between community composition and hummock area. Species with low colonization potential or specific habitat requirements may persist only on large hummocks. Although hummock area and location were partly confounded at our study site (Figure 1), there is some evidence that hummock area *per se* may influence community composition. For example, hummocks 4 and 14 had similar areas and communities, in spite of their spatial separation by hummock 8, which was larger and differed in community composition (see Figure 1). The independence of exotic and monocot diversities from hummock size

suggests that these groups are maintained by invasion from the matrix, as opposed colonization-extinction dynamics among the hummocks.

Conclusions

We found that hummocks were spatial refuges for several native plant species but other native species were found primarily in the grassland matrix. For many native species, the shallower, lower quality soils of hummocks may cause them to function as refuges from intense competition with exotic annual grasses. An effective management strategy will incorporate our knowledge of the life-history traits of the species that we are trying to reduce, as well as those we are trying to enhance. Spring burning to decrease the dominance of exotic annuals in combination with adaptive management techniques has worked successfully in past studies (Hatch et al. 1999; Meyer and Schiffman 1999) and may work in these systems as well. Restoration of serpentine hummock-grassland systems provides both a formidable challenge and an excellent opportunity to study community dynamics in a complex ecosystem.

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