

PATTERNS IN POST-GRAZING VEGETATION CHANGES AMONG SPECIES AND ENVIRONMENTS, SAN MIGUEL AND SANTA BARBARA ISLANDS

PATRICIA M. CORRY¹ AND A. KATHRYN MCEACHERN²

¹*P.O. Box 185, Helena, MT 59624; pat_corry@yahoo.com*

²*U.S. Geological Survey-WERC, Channel Islands Field Station, 1901 Spinnaker Dr., Ventura, CA 93001; kathryn_mceachern@usgs.gov*

Abstract—Nonnative herbivores were removed from San Miguel and Santa Barbara islands by the late 1970s and early 1980s. To characterize post-grazing vegetation change while controlling for variable climate, we analyzed long-term (1984–2002) vegetation transect data on both islands for cover trends of individual plant species and correlations of plant community composition with physical site characteristics. We also analyzed species cover and environmental data from 28 vegetation plots sampled in 1983 and 2002 on San Miguel Island. Regression modeling of transect data for both islands and paired t-test analyses of San Miguel plot data found that both natives and exotics of various life histories have increased significantly since the early 1980s while other taxa and functional groups have declined. Species trends are generally consistent across different plant communities and both islands. Ordinations of species and environmental data indicate that soil texture and related soils variables are the environmental parameters most consistently correlated with species composition. Exotic grass cover is associated with fine-grained soils and native species cover with coarse-grained substrates. Results can be used to direct and prioritize native vegetation restoration and weed control efforts by indicating which native species are recovering and which exotic species are declining without intervention, and which environments are most likely to require active restoration efforts.

INTRODUCTION

The Channel Islands were used as ranches throughout the past two centuries, much like mainland California. Herbivory and farming quickly reduced native insular vegetation to remnant communities persisting in relatively inaccessible sites, within a matrix of non-native annual grassland. The five northernmost islands are now part of Channel Islands National Park, managed for recovery and conservation of native island ecosystems. One of the first large-scale management actions taken by the National Park Service was the eradication of nonnative herbivores from San Miguel and Santa Barbara islands. On San Miguel, sheep were reduced in number throughout the mid-twentieth century and eliminated in 1966; the last nonnative herbivores (feral burros) were removed ca. 1977 (Roberts 1991). Sheep were removed from Santa Barbara in the late 1920s and the last nonnative herbivores (feral rabbits) were eliminated in 1981 (Rugel 1995). A management

expectation was that natural succession would result in the spread of native plants from their refugia in response to the release from herbivory.

Indeed, field observations and repeat photography show evidence of vegetation change since removal of herbivores on the Channel Islands (Philbrick 1972; Brumbaugh 1980; Johnson 1980; Philbrick and Haller 1995; Santa Cruz Island Foundation 2004). This change appears to vary spatially and temporally, similar to the findings of mainland studies (e.g., Hobbs 1983; Hobbs and Mooney 1986; Young et al. 1999; Allen et al. 2002; Zavaleta et al. 2001; Stromberg et al. 2007). For example, some areas that were dominated by exotic annual grasses 20 or 30 years ago now host dense native shrub stands with minimal exotic species cover, while other exotic communities sharing a similar land use history appear to have changed very little. Recent studies have shown that weather has a strong influence on demographic performance of several rare island endemic taxa (Levine et al. 2008) but the relationship between weather and plant

community change on the islands is not well documented. Channel Islands National Park initiated long-term vegetation monitoring on San Miguel Island in 1983 and Santa Barbara Island in 1984, to document plant community change in response to the removal of grazing animals (Halvorson 1994; Johnson and Rodriguez 2001). We used these data for 1983/84 through 2002 to investigate vegetation change on those islands. Our goals were to investigate change over time in species' cover, after accounting for species' individual responses to fluctuations in precipitation. Because observations indicated that change occurred at various rates across different landscape positions, we also investigated the relationship of environmental factors, such as soils, to vegetation pattern.

METHODS

Study Area

San Miguel is a 37 km² island underlain by Cretaceous, Tertiary, and Quaternary marine sediments, volcanics, and eolianite deposits (Johnson 1967, 1980). Santa Barbara, the smallest Channel Island at 2.6 km², is predominantly Miocene basalt with localized veneers of Quaternary sediments (Vedder and Howell 1976). The region has a maritime Mediterranean climate, with nearly all precipitation falling between November and April. The 30-year mean annual precipitation for the period 1971–2000 at Oxnard, California, the nearest climate station to the islands, was 397 mm (Western Regional Climate Center 2003). Because the region has a semiarid climate and is affected by El Niño Southern Oscillation events (Schoenherr et al. 1999), annual precipitation fluctuates considerably. San Miguel's climate is cooler and foggier than Santa Barbara's because of the island's position in the cold outer waters of the California Current; Santa Barbara Island is in the warmer waters of an eddy flowing up from the south.

Vegetation Sampling with Plots

San Miguel Island vegetation was sampled in 1983 on 85 unmarked plots as part of an effort to classify island plant communities. Plots were of varying dimensions, generally 1200–3600 m².

Cover for each species on a plot was visually estimated within the five cover classes of the Braun-Blanquet scale (Class 1=1–5% cover, 2=5–25%, 3=25–50%, 4=50–75%, 5=75–100%; Mueller-Dombois and Ellenberg 1974). In 2002, we resampled 28 plots that had sufficient photographic and other documentation for reliable relocation. Species cover was visually estimated using the five cover classes of the Braun-Blanquet scale. Within each plot we established and sampled a 5 x 20 m subplot. The subplots have no 1983 counterpart, but they simplify analyses of current vegetation by eliminating potential effects of variable plot size on species composition. We collected environmental site data and documented plot locations by photography, global positioning systems, topographic maps, and aerial photos.

Vegetation Sampling with Monitoring Transects

The National Park Service (NPS) established permanent vegetation monitoring transects on San Miguel and Santa Barbara islands in 1984 and has sampled them annually most subsequent years (Johnson and Rodriguez 2001). Most transects are 30 m in length; several transects on Santa Barbara Island are 20 m or 40 m. Point poles are used to determine every species present at points on 30 cm intervals along the transect. Data from 1984 through 2002 were used for this study.

Environmental Data

Environmental variables measured or estimated on all plots and transects in 2002 include slope, aspect, and the categorical variables slope shape, topographic position, and soil drainage. Aspect was converted to a heat load index (McCune et al. 2002). Elevations were estimated from USGS topographic quadrangles. Percent bare ground and percent cryptobiotic crust cover were visually estimated in the field at plot sites in 2002. Percent bare ground is routinely measured by point-count on transects.

The upper 10 cm of soil was sampled in 2002 at all transect and plot sites via 4-point composites. Samples were oven-dried, passed through a 2-mm sieve, and analyzed by Brookside Laboratories of New Knoxville, Ohio, for soil texture (percent sand/silt/clay), bulk density, and a standard suite of soil chemistry parameters including pH, electrical conductivity, percent organic matter, cation exchange capacity, major cations and anions, and

macro- and micronutrients. Soil nitrogen was measured via NO_3 and NH_4 concentrations and estimated nitrogen release (ENR). Soil analytical results for San Miguel transect 18 were also used for adjacent transect 11, which was replaced by transect 18 in 1994. Transect 16 was not sampled due to archaeological protection constraints; soil analytical results for transect 13, which is on a very similar sand substrate and geomorphic position about 2 km distant, were also used for transect 16.

Species Cover Trend Analysis

Statistical analyses were conducted using R 1.9.1 (R Development Core Team 2004) unless otherwise noted. Taxonomic nomenclature follows the USDA Plants database (USDA NRCS 2001). Analyses were designed to determine which species experienced significant changes in cover over time while accounting for effects of precipitation, and to show the magnitudes and directions of the changes. San Miguel plot and transect datasets were analyzed separately because of differences in the data structure and data collection methods.

The paired difference in cover class (the number of cover classes spanned by the change between 2002 and 1983) on each San Miguel plot and the mean paired difference over all plots were calculated for species present on at least eight plots in either or both years. A paired t-test determined whether a species' mean cover class was significantly different in 2002 vs. 1983 ($\alpha = 0.05$). For comparison, we also used the nonparametric Wilcoxon's signed rank test to test for significant changes in cover class among species. In both analyses, multiple testing (multiple species present on a given plot) was accounted for using Benjamini and Hochberg's (1995) step-up procedure to control the false discovery rate (FDR) at 5%. The FDR is defined as the expected percentage of significant tests that could be falsely significant.

For each San Miguel and Santa Barbara transect in each year, the point count for each species was converted to percent cover by dividing the number of point-interceptions for the species by the total number of points on the transect. To limit multiple testing and focus on common species, analyses were confined to species present at least two years of the monitoring period, with a minimum cover of 4% for at least one of the years. To account for multiple

tests, Benjamini and Hochberg's (1995) step-up procedure was used to control the FDR at 5%.

We used a linear mixed-effects regression modeling approach to determine which species experienced significant changes in percent cover over time. We used a model structure that is suitable for time-series data such as the transect data because it automatically accounts for autocorrelation and heteroscedasticity (Singer and Willett 2003), characteristics that can make ordinary least-squares regression inappropriate for repeated-measures data. We used annual water-year (July to June) precipitation as a covariate to account for its contribution to variability in species cover, because species do not all respond similarly to precipitation variability. Water-year precipitation was calculated from monthly totals for the Oxnard NOAA reporting station (Western Regional Climate Center 2003). A moving three-year average for water-year precipitation was used because plant cover response appears to be a function of several years' precipitation rather than just the current year.

Each island's data were analyzed separately. The basic framework for the regression model can be expressed as:

$$Y_{ijk} = \alpha_{0ij} + \alpha_{1ij} \text{TIME}_{ijk} + \alpha_{2ij} \text{PPT}_{ijk} + \varepsilon_{ijk}$$

where TIME is the number of years since 1984 (i.e., 1984 = 0), and PPT is total water-year precipitation for year k . The cover value (Y) for species j on transect i at time k is due to the initial cover at time 0 (α_{0ij} , the intercept), the partial rate of change in cover with respect to time, the partial rate of change in cover with respect to precipitation, and random error. Each species' regression coefficient for the time term (α_1) represents its cover trend (the percent change in cover class category per year). The variable PPT was included in the model to remove the variation due to annual precipitation from the analysis, so we could examine the temporal trend in vegetation cover independent of precipitation.

In linear mixed-effects modeling, comparative versions of models can be constructed that vary in which parameters (intercepts and regression coefficients) are fixed at mean values (in this case, the mean value for a given species over all transects on which it occurs), and which parameters are random (allowed to assume the actual values on

each transect). Our reported results are from a model in which the intercept is random but both time and precipitation coefficients are the mean values across all transects. However, a mean time trend may not be meaningful if a species' cover trend differs markedly among transects, increasing over time on some transects and decreasing on others. To check whether mean time coefficients are reasonable representations of species' cover trends, we fitted a second model which differed from the first in allowing the time coefficient to be random, and compared the two models to determine whether any species have a significant random time effect, indicating heterogeneity in cover trend among transects. For species that did exhibit heterogeneity among transects, we examined model results and raw data to evaluate the source of heterogeneity and to assess whether a mean value across transects was a meaningful representation of cover trend.

To assess the generality of trends, we combined data from both islands and used a variation of the model described above to test whether species' temporal trends are significantly different between the two islands. The combined dataset included only species present on transects on both islands at the specified minimum-presence levels. Additionally, four similar congeneric pairs, such as *Eriogonum grande* v. *rubescens* on San Miguel Island and *E. giganteum* on Santa Barbara Island, were renamed by genus only, so that each pair was treated as the same taxa in the analysis. *Astragalus*, *Calystegia*, and *Claytonia* were the other genera treated this way. Multilevel models were fit with and without a dummy variable that identified the island on which a transect occurs. An analysis of deviance assessed whether inclusion of the island term changed results significantly for any species. FDR significance ($\alpha = 0.05$) was calculated to correct for multiple testing.

Species Composition and Environmental Correlations

Species composition patterns and correlations with environmental variables were assessed using nonmetric multidimensional scaling (NMS) ordinations in PC-ORD 4.32 (McCune and Mefford 1999). NMS solutions are graphically displayed in ordination diagrams showing the vegetation plots in two-dimensional ordination space; the proximity of plots indicates the degree of species-compositional

similarity between them. The Sorenson (Bray-Curtis) distance measure was used to calculate the dissimilarity matrix. We evaluated the acceptability of an NMS solution by its final stress and instability, using criteria of final stress <17, per Clarke's (1993) rules of thumb, and final instability <0.001 (McCune et al. 2002). Effectiveness of NMS solutions was assessed by calculating the proportion of variance in the original data that is represented by each ordination axis. The metric is the coefficient of determination (r^2) between distances in the original data and distances in ordination space. An ordination solution was considered effective when at least 50% of the variance was represented by two ordination axes (McCune et al. 2002).

Ordinations included a secondary matrix of the environmental variables measured or estimated at plot and transect locations. Ordination correlates environmental variables with ordination axes that represent gradients of species composition, calculating Pearson's r^2 to describe the linear relationship between environmental variables and ordination scores, and Kendall's tau to describe the rank relationship. Pearson's r^2 is the proportion of variance in a sample's position on an ordination axis that is explained by a given environmental variable.

Data for San Miguel plots, San Miguel transects, and Santa Barbara transects were ordinated separately. To assess whether species composition and environmental correlations are changing over the time, we ordinated data from a recent monitoring year (1998–2002), combined early (1983/84) and recent years, and various combinations of multiple years throughout the 19-year period. We also ordinated data from a very dry year (1990) and a very wet year (1998) to evaluate whether water-year precipitation affects species composition and environmental relationships. Multiple-year analyses included only transects present in each of the subject years; several sporadically sampled transects on both islands were eliminated from these analyses.

The San Miguel plots were only sampled twice, in 1983 and 2002. For current vegetation patterns, we ordinated data from the 5 x 20 m subplots we established in 2002 within the original plots. The subplots have the advantage of standard size. To combine 1983 and 2002 data, we used 2002 data from the larger plots (of the 1983 dimensions). Because the plots are of varying sizes, we included

plot size as a quantitative variable in the secondary matrix to assess its correlation with species composition (i.e., the extent to which varying plot sizes may have affected species composition via sampling effect).

RESULTS

Species Cover Trends on San Miguel Plots

The combined 1983 and 2002 data included 93 species; 29 met minimum presence criteria and were included in the analysis. Eleven of the 29 species had significant differences in Braun-Blanquet cover class categories between 1983 and 2002 (Table 1). The FDR significance level of 5% indicates that less than one significant test (5% of 11 tests) could be spurious, suggesting all tests remain significant after accounting for effects of multiple testing. The nonparametric Wilcoxon signed-rank test produced very similar results.

Species that significantly increased include the native shrubs *Lupinus albifrons*, *Coreopsis gigantea*, and *Baccharis pilularis*, the native grass *Distichlis spicata*, and the native thistle *Cirsium occidentale*. The annual grass *Bromus hordeaceus* was the only exotic species that increased. Only one native species, the subshrub *Malacothrix incana*, decreased. Exotic species that decreased in cover are the annual grass *Hordeum murinum*, a species common in saline waste areas; the herbs *Melilotus indicus* and *Sonchus oleraceus*, and the salt-tolerant subshrub *Atriplex semibaccata*.

Species Cover Trends on San Miguel and Santa Barbara Transects

Graphical examination of modeling results for species with significant heterogeneity in temporal cover change among transects found that the mean time trend is generally an appropriate representation of species trend. For example, Figure 1 compares observed temporal trends of *Eriogonum giganteum* v. *compactum* cover for the three transects on which

Table 1. Significant paired t-test and Wilcoxon signed-rank test results for San Miguel plots. Species with significant ($\alpha = 0.05$) mean change in Braun-Blanquet cover class category from 1983 to 2002 are listed in descending order of direction and magnitude of change, using paired t-test results. N = number of plots on which species occurs. Lifeform/life history: P. = perennial, A. = annual, * = exotic.

Species	Lifeform/life history	N	Mean change in cover class	<i>p</i>	Wilcoxon <i>p</i>
<i>Bromus hordeaceus</i> soft chess	A. grass*	10	1.500	0.001	0.004
<i>Lupinus albifrons</i> silver lupine	P. shrub	11	1.000	0.002	0.008
<i>Distichlis spicata</i> saltgrass	P. grass	18	0.778	0.015	0.026
<i>Coreopsis gigantea</i> giant coreopsis	P. shrub	13	0.615	0.005	0.016
<i>Baccharis pilularis</i> coyote brush	P. shrub	23	0.478	0.008	0.019
<i>Cirsium occidentale</i> California thistle	P. forb	24	0.292	0.016	0.039
<i>Sonchus oleraceus</i> sow thistle	A. forb*	24	-0.417	0.009	0.020
<i>Malacothrix incana</i> dunedelion	P. shrub	19	-0.632	0.001	0.003
<i>Atriplex semibaccata</i> Australian saltbush	P. subshrub*	13	-0.769	0.002	0.011
<i>Melilotus indicus</i> yellow sweetclover	A. forb*	18	-0.778	0.001	0.003
<i>Hordeum murinum</i> foxtail	A. grass*	8	-1.375	<0.001	0.008

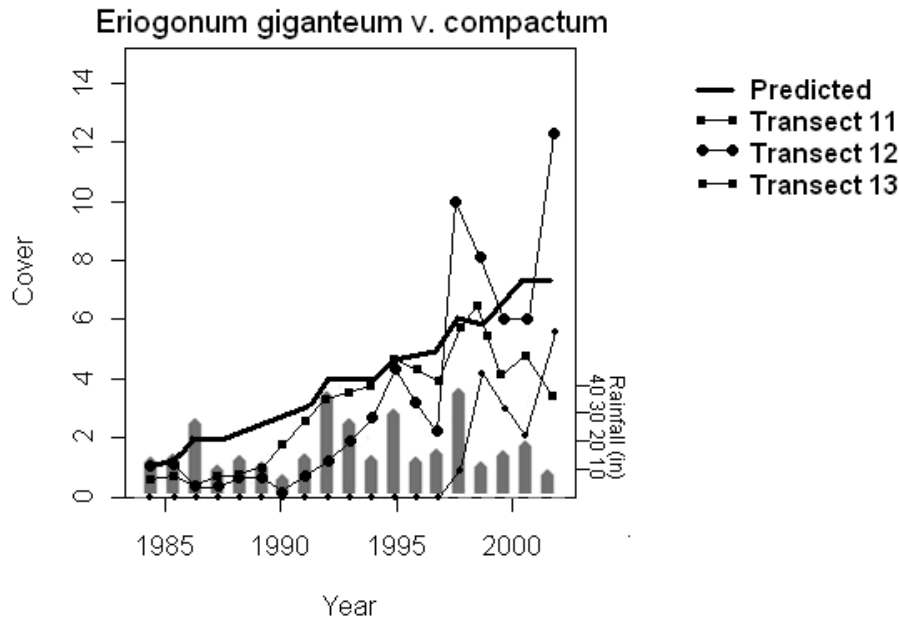


Figure 1. Observed and predicted trends of percent cover for *Eriogonum giganteum v. compactum* from 1984 to 2002. Bulleted lines represent observed trends on the three Santa Barbara Island transects on which the species occurs. The solid line represents percent cover estimated by the multilevel regression model, averaged over all three transects. Bars at the bottom of the graph indicate annual variation in precipitation. Percent cover generally increases over time on all transects; the heterogeneity is due primarily to differences in the magnitude of the increase rather than opposing trends.

it occurs, with the mean temporal trend predicted by the multilevel regression model. Variability in percent cover due to annual precipitation has been accounted for in the model, resulting in a smoother temporal trend line compared to observed values. This figure illustrates a typical example of a species that displays significant heterogeneity among transects. However, where heterogeneity among transects was found, it generally reflected large differences in initial cover that affected the magnitude of change, rather than divergent trends. For example, some species' cover declined on all transects, but could not decline as much on transects where initial cover was low.

San Miguel transects captured 103 species, of which 79 met minimum presence criteria. Twenty-three of the 79 species had significant ($\alpha = 0.05$) temporal trends (Table 2). The FDR ($\alpha = 0.05$) suggests that one of the 23 significant tests could be spurious. Positive values of α_1 indicate that seven native species (four shrubs and three herbs) and three exotic species exhibit significant increases in cover (Table 2). Negative values of α_1 indicate that

eight native species and five exotic species decreased in cover (Table 2), including both native vines (*Calystegia macrostegia* and *Marah macrocarpus*), salt-tolerators (*Hordeum murinum* and both species of *Atriplex*), and several species that tend to increase under grazing pressure (exotic herbs *Erodium cicutarium* and *Medicago polymorpha* and the native cactus *Opuntia littoralis*). Most of the other declining species are associated with sand dunes and other open habitats.

Santa Barbara Island transects captured 67 species, of which 50 met minimum presence criteria for analysis. Thirteen of the 50 species had significant ($\alpha = 0.05$) temporal trends (Table 3). The FDR ($\alpha = 0.05$) suggests that all tests remain significant after accounting for multiple testing. Only three species, all native, increased in cover. The 10 decreasing species include five out of six salt-tolerators in the analysis: both *Atriplex* species, both *Mesembryanthemum* species, and *Suaeda taxifolia*. Other decreasing species include a native shrub, cactus, and grass, an exotic grass, and another exotic herb.

Table 2. Regression coefficients and p -values for species with significant temporal trends on San Miguel Island transects, ordered by direction and magnitude of temporal trend. α_1 is the regression coefficient for the partial rate of change in a species' percent cover due to time. α_2 is the regression coefficient for the partial rate of change in a species' percent cover due to annual precipitation. N = number of transects on which species occurs. Lifeform/life history: P. = perennial, A. = annual, * = exotic.

Species	Lifeform/life history	N	Time		Ppt	
			α_1	p	α_2	p
<i>Eriophyllum confertiflorum</i> golden yarrow	P. shrub	1	1.392	0.001	0.251	0.438
<i>Coreopsis gigantea</i> giant coreopsis	P. shrub	4	1.244	<0.001	0.877	0.008
<i>Sisyrinchium bellum</i> blue-eyed "grass"	P. forb	2	0.901	<0.001	0.086	0.526
<i>Bromus hordeaceus</i> soft chess	A. grass*	8	0.896	0.001	0.258	0.322
<i>Carpobrotus chilensis</i> iceplant; sea-fig	P. subshrub*	9	0.807	<0.001	0.449	0.030
<i>Eriogonum grande</i> v. <i>rubescens</i> red buckwheat	P. shrub	2	0.539	<0.001	0.138	0.042
<i>Lotus dendroideus</i> v. <i>dendroideus</i> deerweed	P. shrub	3	0.482	0.004	0.104	0.508
<i>Dudleya greenii</i> Greene's dudleya	P. subshrub	2	0.436	<0.001	0.097	0.358
<i>Pterostegia drymarioides</i> fairy mist	A. forb	3	0.182	0.004	0.334	<0.001
<i>Sonchus oleraceus</i> sow thistle	A. forb*	12	0.176	0.007	0.125	0.047
<i>Atriplex californica</i> California saltbush	P. subshrub	8	-0.260	<0.001	-0.048	0.469
<i>Erodium cicutarium</i> filaree	A. forb*	8	-0.428	0.001	0.160	<0.001
<i>Medicago polymorpha</i> bur-clover	A. forb*	8	-0.462	0.003	0.259	0.085
<i>Marah macrocarpus</i> wild cucumber	P. forb	4	-0.550	0.013	0.340	0.115
<i>Atriplex semibaccata</i> Australian saltbush	P. subshrub*	4	-0.602	0.010	0.440	0.050
<i>Calystegia macrostegia</i> island morning-glory	P. subshrub	7	-0.631	<0.001	0.222	0.174
<i>Lupinus succulentus</i> succulent lupine	A. forb	1	-0.862	0.005	-0.088	0.727
<i>Malacothrix incana</i> dunedelion	P. shrub	6	-0.987	<0.001	0.308	0.138
<i>Bromus diandrus</i> ripgut brome	A. grass*	12	-1.035	<0.001	0.614	0.004
<i>Ambrosia chamissonis</i> beachbur	P. shrub	1	-1.174	0.007	-0.144	0.696
<i>Hordeum murinum</i> foxtail	A. grass*	6	-1.424	<0.001	0.529	0.062
<i>Artemisia californica</i> coastal sagebrush	P. shrub	3	-1.684	0.008	0.410	0.411
<i>Opuntia littoralis</i> coastal pricklypear	P. shrub	2	-1.930	<0.001	-0.193	0.546

Table 3. Regression coefficients and p -values for species with significant temporal trends on Santa Barbara Island transects, ordered by direction and magnitude of temporal trend. α_1 is the regression coefficient for the partial rate of change in a species' percent cover due to time. α_2 is the regression coefficient for the partial rate of change in a species' percent cover due to annual precipitation. N = number of transects on which species occurs. P. = perennial, A. = annual, * = exotic.

Species	Lifeform/life history	N	Time		Ppt	
			α_1	p	α_2	p
<i>Melica imperfecta</i> Coast Range melic	P. grass	1	1.837	0.001	0.972	0.139
<i>Opuntia littoralis</i> coastal pricklypear	P. shrub	3	0.528	0.011	0.134	0.528
<i>Eriogonum giganteum</i> v. <i>compactum</i>	P. shrub	4	0.358	<0.001	-0.003	0.968
<i>Malva parviflora</i> cheeseweed	A. forb*	11	-0.265	0.008	0.036	0.799
<i>Atriplex californica</i> California saltbush	P. subshrub	3	-0.465	0.001	0.091	0.639
<i>Hemizonia clementina</i> island tarweed	P. shrub	5	-0.509	<0.001	0.301	0.103
<i>Atriplex semibaccata</i> Australian saltbush	P. subshrub*	16	-0.651	<0.001	0.735	<0.001
<i>Opuntia prolifera</i> coastal cholla	P. shrub	4	-0.820	0.003	-0.775	0.017
<i>Suaeda taxifolia</i> sea-blite	P. shrub	7	-0.914	<0.001	0.517	0.071
<i>Bromus rubens</i> red brome	A. grass*	17	-1.333	<0.001	1.907	<0.001
<i>Mesembryanthemum nodiflorum</i> small-flowered iceplant	A. forb*	2	-1.359	0.005	0.804	0.224
<i>Mesembryanthemum crystallinum</i> crystalline iceplant	A. forb*	12	-1.882	<0.001	0.473	0.106
<i>Muhlenbergia microsperma</i> littleseed muhly	A. grass	2	-4.578	0.001	1.567	0.044

Testing for Differences in Species Cover Trends between Islands

The two islands have 31 taxa in common on transects. Modeling of combined data for both islands found no significant difference in trends between islands for any of the 31 taxa, when multiple testing is accounted for via the FDR. Two species, *Chenopodium californicum* and *Opuntia littoralis*, have significantly different trends between islands before correction for multiple testing.

Species Composition and Environmental Correlations from Ordinations

All acceptable NMS solutions had three dimensions and were deemed effective, with 55–68% of the original data's variance explained by two axes. Species composition gradients and their Pearson's r^2 and Kendall's tau correlations with environment were similar in all ordinations for a given island, regardless of which years' data were used; species composition-environment

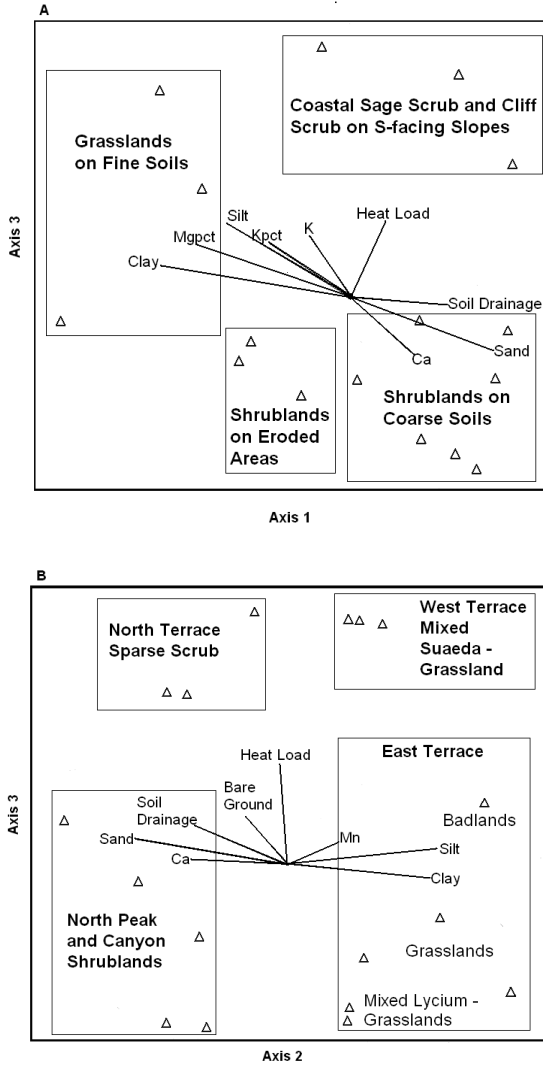


Figure 2. Nonmetric multidimensional scaling (NMS) ordinations of transect species data, with vectors showing relative strengths of Pearson's r^2 correlations with some environmental variables measured at the sites. a) San Miguel Island 2002 data, b) Santa Barbara Island 1998 data.

relationships do not appear to be changing over time or fluctuating with annual precipitation.

San Miguel plots and transects generally sort along two types of species compositional gradients: 1) grasslands (predominantly exotic) vs. native-dominated shrub vegetation, and 2) dense vegetation of any type on relatively deep soils vs. sparse vegetation on thin soils or erosion pavements (Fig. 2a). Most native-dominated shrub communities such as lupine, *Coreopsis*, and *Isocoma* scrub tend to group together despite differences in dominant species. Exceptions are

coastal sage scrub and cliff scrub on south-facing slopes, which tend to group separately from other native communities, and *Baccharis* scrub and the few grasslands with a native graminoid component, which generally group with or near exotic grasslands. Ordination axes also reflect site environmental conditions, most commonly representing gradients between fine- and coarse-grained substrates and between warm/xeric sites such as south-facing slopes and cool/mesic sites such as canyons and north-facing slopes.

Santa Barbara transects generally group by geographic regions of the island: mixed shrub-grassland (*Suaeda taxifolia* – *Hordeum murinum*) communities on the west terrace, sparsely vegetated annual-rich low scrub communities on the north terrace near Arch Point, native shrub communities on North Peak and in canyons, and east terrace communities (Fig. 2b). Within the latter, three subgroups are evident: exotic grasslands, mixed shrub- (*Lycium californicum*) grassland, and a heavily eroded *S. taxifolia* – *H. murinum* badlands site. The east terrace sites share a large *Avena* component that appears to separate this group from the others. Similarly to San Miguel, ordination axes appear to represent gradients between fine- and coarse-grained substrates and between warm/xeric and cool/mesic sites.

On both islands, soil texture (percent sand, silt, and clay) and soil drainage are the strongest, most consistent environmental correlates with species composition, with Pearson correlation coefficients (r^2) up to 0.80 (Table 4). Native-dominated communities are associated with well-drained soils with high sand content, while predominantly exotic grasslands are associated with slower-draining soils with high silt and clay. These correlations are significant but weaker on San Miguel plots compared to the transects, possibly because sand dune habitats were underrepresented due to the difficulty of reliably relocating plots on shifting sands.

Major cations covary with soil texture and are also consistent, although generally weaker, correlates with species composition. High calcium is associated with native communities on coarse soils while magnesium, potassium, and, less consistently, sodium are associated with grasslands on finer-grained soils. Heat load is another frequently significant correlate, supporting the

Table 4. Pearson's r^2 correlation coefficients for environmental variables and NMS ordination axes (see Fig. 2) for 16 San Miguel Island transects, 2002 data; and 18 Santa Barbara Island transects, 1998 data. Variables with Pearson's $r^2 \geq 0.2$ are in bold.

	San Miguel		Santa Barbara	
	Axis 1	Axis 3	Axis 2	Axis 3
Sand	0.63	0.23	0.67	0.07
Silt	0.42	0.24	0.59	0.03
Clay	0.80	0.14	0.52	0.10
TEC	0.23	0.28	0.48	0.10
pH	0.26	0.30	0.02	0.02
OM	0.13	0.18	0.15	0.00
ENR	0.16	0.33	0.17	0.00
S	0.15	0.32	0.14	0.15
P	0.06	0.00	0.00	0.39
Ca	0.28	0.30	0.44	0.00
Mg	0.01	0.00	0.09	0.14
K	0.22	0.26	0.15	0.15
Na	0.11	0.03	0.01	0.17
Capct	0.45	0.34	0.26	0.02
Mgpct	0.48	0.24	0.30	0.04
Kpct	0.35	0.27	0.08	0.02
Napct	0.66	0.16	0.04	0.16
B	0.14	0.25	0.15	0.12
Fe	0.24	0.07	0.16	0.04
Mn	0.26	0.26	0.25	0.01
Cu	0.11	0.07	0.00	0.00
Zn	0.06	0.32	0.10	0.35
Al	0.33	0.12	0.14	0.08
EC	0.05	0.02	0.03	0.06
Cl	0.05	0.02	0.05	0.12
BulkDensity	0.24	0.37	0.08	0.01
NO3	0.54	0.00	0.05	0.07
NH4	0.16	0.06	0.02	0.13
CaCO3	0.23	0.22	0.01	0.21
Elev	0.07	0.01	0.01	0.05
Slope	0.22	0.03	0.44	0.01
HeatLoad	0.05	0.34	0.07	0.37
SoilDrainage	0.80	0.07	0.62	0.05
BareGr	0.00	0.03	0.24	0.16

observation of compositional sorting between warm/xeric sites and cool/mesic sites. Percent bare ground is a frequent correlate, reflecting compositional gradients between densely vegetated sites on deeper soils and more sparsely vegetated areas such as Arch Point on Santa Barbara and erosion pavements and sand dunes on San Miguel. Less consistent correlates include some soil chemistry variables such as pH, cation exchange capacity, sulfur, and some micronutrients, all of which appear to covary with soil texture. The macronutrients nitrogen and phosphorus generally have insignificant or inconsistent correlations with species composition.

DISCUSSION AND CONCLUSIONS

Many factors can affect species' trends, including changes in land use, environmental setting, and climate fluctuations. Precipitation is highly variable in a Mediterranean climate regime, and it can affect the relative abundances of species across years of high rainfall and drought, with some species exhibiting stronger responses than others to rainfall variations. Our analyses were designed specifically to look at change independent of precipitation effects on individual species abundances. Therefore, we included precipitation as a covariate in our analyses, to account for the effect of varying moisture in the analysis of species cover trend. Results (Tables 2 and 3) show that when species' varying responses to precipitation are accounted for, significant differences in cover trends among species still emerge. Future analyses will focus on species trends as they relate to precipitation and temperature fluctuations, for species life-history forms and other functional groups. Our results do show that species are responding individually over time, within the context of changing management and climate regimes. Post-grazing cover trends are significantly different among some species, and a given species' trend is generally consistent across all plots and plant community types in which it occurs. Species cover trends do not vary significantly between the two islands despite climatic, edaphic and land use differences, suggesting generality of trends for other Channel Islands and possibly coastal mainland

systems recovering from similar anthropogenic impacts.

Most species that increased significantly are native, particularly native shrubs. These include fast-growing wind-dispersed shrubs such as *Coreopsis gigantea* and *Baccharis pilularis*, and species such as nitrogen-fixers with traits that facilitate colonization of low-nutrient sandy and rocky substrates. *Eriogonum* species on both islands increased; this genus appears to be a successful early colonizer on damaged lands. Stylinski and Allen (1999) found that the common mainland buckwheat *E. fasciculatum*, along with a *Baccharis* species, were the only native shrubs that colonized heavily damaged southern California scrub communities after cessation of anthropogenic disturbance.

Despite general increases in native species cover, some native species did decline in the 18–19 years of censusing. Both native vines, *Marah macrocarpus* and *Calystegia macrostegia*, decreased significantly on San Miguel transects; possibly their niches overlap with the exotic subshrub *Carpobrotus*, which has a prostrate, sprawling habit and is increasing. Native shrubs *Ambrosia chamissonis* and *Malacothrix incana* and the native annual herb *Lupinus succulentus* are all colonizers of sand dunes and other open sites; their decline on San Miguel may be due to competition from nitrogen-fixing shrubs and/or *Carpobrotus*, or loss of habitat as sand dunes and other open sites created by grazing-induced erosion stabilize and revegetate. Declining forb and graminoid species on both islands are mostly exotic; increasers are mostly native. Declining exotic forbs on both islands were nearly all halophytes or species such as *Medicago polymorpha*, *Melilotus indica*, and *Erodium cicutarium* that are associated with grazing disturbance.

The decline of certain exotic taxa appeared to be associated with functional traits; specifically, saline tolerance. Exotic taxa associated with saline disturbed areas declined significantly on San Miguel (*Hordeum murinum*) or on both islands (*Atriplex semibaccata*, *Mesembryanthemum* spp), possibly indicating a reversal of soil compaction and concomitant decrease in soil salinity that can follow grazing cessation (Chaneton and Lavado 1996; Belsky and Blumenthal 1997). The decline of *Mesembryanthemum crystallinum* on Santa Barbara

may be at least partially attributable to experimental removal projects conducted ca. 1987 near North and Signal peaks (Halvorson 1994; Rugel 1995). Although the projects presumably avoided the immediate vicinity of monitoring transects, they may have decreased the abundance of *M. crystallinum* propagules sufficiently to affect cover on the transects. The decline of *Hordeum murinum* on San Miguel is supported by photo evidence from the late 1970s showing dense *H. murinum* covering large areas that are currently dominated by native vegetation. Native halophytes displayed a more equivocal trend: *Suaeda taxifolia* decreased on Santa Barbara and *Atriplex californica* decreased on both islands, but the saltgrass *Distichlis spicata* increased on San Miguel plots.

We found that native and exotic communities segregated according to environmental characteristics. Correlation of environmental variables with vegetation composition supports field observations of the affinity between exotic grasslands and fine-grained, slowly draining soils and between native scrub communities and coarse, well-drained substrates. Major cations were also frequent correlates. An experimental approach would be required to disentangle the effects of major cations and soil texture and assess whether either or both have a causative relationship with species composition, but the stronger, more consistent correlation of soil texture suggests it is the primary driver of the relationship with species composition.

On both islands sites tend to also sort by heat load. On San Miguel, native communities tend to associate with cooler, more mesic sites and exotic grass cover with warmer, drier sites. This relationship is more equivocal in Santa Barbara ordinations, but repeat photography on the island provides some qualitative evidence of the association, showing more extensive native plant colonization on north-facing gully slopes while the opposite slopes are generally dominated by exotic grasses.

Coarse-grained substrates are often thought of as xeric from a plant's perspective; therefore, native island communities' apparent preference for sites with both lower heat load (i.e., lower xericity) and coarse-grained, well-drained substrates may seem contradictory. However, for the deeper-rooted perennials that dominate native island communities,

coarse-grained substrates are probably less xeric than slower-draining soils because more moisture can percolate to the natives' deeper rooting zones. In arid and semiarid climates, slower-draining soils are often effectively more xeric than coarse-grained soils due to higher evaporative loss of moisture retained near the surface (Wells 1962). This effect would be compounded in the presence of the shallow-rooted annual vegetation that dominates island exotic communities; the annuals can more thoroughly deplete moisture retained near the surface in slower-draining, fine-grained soils. This has been proposed as a mechanism by which exotic annual grasses outcompete native perennials in Mediterranean-climate communities (Kirkpatrick and Hutchinson 1980; Hobbs 1983; Vila and Sardans 1999), and is supported by experimental studies (Gordon et al. 1989; Melgoza et al. 1990; Eliason and Allen 1997).

Characterizing patterns of vegetation change can inform vegetation management and restoration efforts by identifying taxa and environments most in need of active intervention and providing evidence of factors that control native vegetation recovery. We have identified specific native taxa, such as *Coreopsis*, *Baccharis*, and *Eriogonum*, and groups with shared traits such as nitrogen-fixers, as successful colonizers needing less active intervention but perhaps having utility as nurse plants or site remediators in restoration efforts. Exotic species and functional groups can be prioritized for removal efforts based on their cover trends: exotic halophytes and many grazing-associated forbs are apparently decreasing on their own, while some exotics such as *Carpobrotus* on San Miguel are spreading.

Native perennial colonizers appear to be at greatest advantage on sites where well-drained soils or rocky, fractured substrates such as erosion pavements allow more percolation to deeper rooting zones. Active restoration is most likely to be needed on sites with fine-grained soils. Results from San Miguel, at least, also indicate that spontaneous native recovery is favored where aspect results in relatively lower moisture stress. Our results suggest that competition with exotic annuals for soil moisture is an important factor controlling native vegetation recovery. Fruitful avenues for further research include restoration experiments involving fog drip capture or other methods of altering soil

moisture competition between native perennials and exotic annual vegetation.

ACKNOWLEDGMENTS

Funding and logistical support for this work was provided by University of North Carolina–Chapel Hill, W.C. Coker Fellowships, Alma Holland Beers Scholarships, Channel Islands National Park, and U.S. Geological Survey's Western Ecology Research Center. Channel Islands National Park supplied vegetation monitoring data. Jack Weiss provided statistical consultation. Patricia Corry acknowledges the assistance of Robert Peet, Peter White, Patricia Gensel, Aaron Moody, Dean Urban, Jim Lenihan, Dirk Rodriguez, Ian Williams, and Randy Nelson.

REFERENCES

- Allen, E.B., A.G. Sirulnik, L. Egerton-Warburton, S.N. Kee, A. Bytnerowicz, P.E. Padgett, P.J. Temple, M.E. Fenn, M.A. Poth, and T. Meixner. 2002. Air pollution and vegetation change in southern California shrublands. Pages 79–96. *In*: Kus, B.E., and J.L. Beyers (eds.), *Proceedings of the Symposium on Planning for Biodiversity: Bringing Research and Management Together*, Gen. Tech. Rep. PSW-GTR-195. USDA Forest Service Pacific Southwest Research Station, Albany, CA.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B* 57:289–300.
- Belsky, A.J., and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. *Conservation Biology* 11:315–327.
- Brumbaugh, R. 1980. *Erosion and Soils*, Santa Cruz Island, California. Report on file, Channel Islands National Park, Ventura, CA, 110 pp.
- Chaneton, E.J., and R.S. Lavado. 1996. Soil nutrients and salinity after long-term grazing exclusion in a flooding pampa grassland. *Journal of Range Management* 49:182–187.

- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Eliason, S.A., and E.B. Allen. 1997. Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology* 5:245–255.
- Gordon, D.R., J.M. Welker, J.W. Menke, and K.J. Rice. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia* 79:533–541.
- Halvorson, W.L. 1994. Ecosystem restoration on the California Channel Islands. Pages 485–490. *In*: Halvorson, W.L., and G.J. Maender (eds.), *Proceedings of the Fourth California Islands Symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Hobbs, E.R. 1983. Factors controlling the form and location of the boundary between coastal sage scrub and grassland in southern California [Ph.D. dissertation.] University of California, Los Angeles, CA, 307 pp.
- Hobbs, R.J., and H.A. Mooney. 1986. Community changes following shrub invasion of grassland. *Oecologia* 70:508–513.
- Johnson, D.L. 1967. Caliche on the Channel Islands. *Mineral Information Service* 20:151–158.
- Johnson, D.L. 1980. Episodic vegetation stripping, soil erosion and landscape modification in prehistoric and recent historic time, San Miguel Island, California. Pages 103–121. *In*: Power, D.M. (ed.), *The California Islands: Proceedings of a Multidisciplinary Symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Johnson, L., and D. Rodriguez. 2001. Terrestrial vegetation monitoring, Channel Islands National Park, 1996–2000, Technical Report 01–06. Report on file, Channel Islands National Park, Ventura, CA, 279 pp.
- Kirkpatrick, J.B., and C.F. Hutchinson. 1980. The environmental relationships of California coastal sage scrub and some of its component communities and species. *Journal of Biogeography* 7:23–38.
- Levine, J.M., A.K. McEachern, and C. Cowan. 2008. Effects of a fluctuating rainfall environment on rare island annual plants. *Journal of Ecology* 96:795–806.
- McCune, B., J.B. Grace, and D.L. Urban. 2002. *Analysis of Ecological Communities*. MjM Software, Glendon Beach, OR, 300 pp.
- McCune, B., and M.J. Mefford. 1999. *Multivariate Analysis of Ecological Data*, PC-ORD Software Version 4.32. MjM Software, Glendon Beach, OR.
- Melgoza, G., R.S. Nowak, and R.J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* and two native species. *Oecologia* 83:7–13.
- Mueller-Dombois, D., and H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology*. Wiley, New York, NY.
- Philbrick, R.N. 1972. The plants of Santa Barbara Island, California. *Madroño* 21:329–393.
- Philbrick, R.N., and R.J. Haller. 1995. The southern California islands. Pages 893–906. *In*: Barbour, M.G., and J. Major (eds.), *Terrestrial Vegetation of California*, Special Publication No. 9. California Native Plant Society, Davis, CA.
- R Development Core Team. 2004. R 1.9.1. Available <http://cran.r-project.org> [date visited 3/30/2004]
- Roberts, L.J. 1991. *San Miguel Island: Santa Barbara's Fourth Island West*. Cal Rim Books, Carmel, CA. 214 pp.
- Rugel, D.J. 1995. *The vegetation history of Santa Barbara Island, Channel Islands, California*. Ventura (CA): Channel Islands National Park. Report on file, Channel Islands National Park, Ventura, CA, 42 pp.
- Santa Cruz Island Foundation. 2004. *History of Santa Barbara Island*. Available <http://www.west.net/~scifmail/barbhist.html> [date visited 5/30/2004]
- Schoenherr, A.A., C.R. Feldmeth, and M.J. Emerson. 1999. *Natural History of the Islands of California*. University of California Press, Berkeley/Los Angeles, CA. 772 pp.
- Singer, J.D., and J.B. Willett. 2003. *Applied Longitudinal Data Analysis*. Oxford University Press, New York, NY, 644 pp.
- Stromberg, M., J. Corbin, and C.M. D'Antonio (eds.). 2007. *California grassland: ecology and management*. UC Press, Berkeley, CA.
- Stylinski, C.D., and E.B. Allen. 1999. Lack of native species recovery following severe exotic

- disturbance in southern California shrublands. *Journal of Applied Ecology* 36:544–554.
- USDA Natural Resource Conservation Service. 2004. The PLANTS database. Available <http://plants.usda.gov> [date visited: 2/20/2008]
- Vedder, J.G., and D.G. Howell. 1976. Neogene strata of the southern group of Channel Islands, California. Pages 80–126. *In*: Howell, D.G. (ed.), *Aspects of the Geologic History of the California Borderland*, Misc. Pub. 24. Pacific Section of American Association of Petroleum Geologists, Ventura, CA.
- Vila, M., and J. Sardans. 1999. Plant competition in Mediterranean-type vegetation. *Journal of Vegetation Science* 10:281–294.
- Wells, P.V. 1962. Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle, California. *Ecological Monographs* 32:79–103.
- Western Regional Climate Center. 2003. Oxnard, California, monthly total precipitation (046569). Available <http://www.wrcc.dri.edu> [date visited 7/29/2003]
- Young, J.A., C.D. Clements, and G. Nader. 1999. Medusahead and clay: the rarity of perennial seedling establishment. *Rangelands* 21:19–23.
- Zavaleta, E.S., R.J. Hobbs, and H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16:454–459.