

Temporal variability in California grasslands: Soil type and species functional traits mediate response to precipitation

B. M. FERNANDEZ-GOING,¹ B. L. ANACKER, AND S. P. HARRISON

Department of Environmental Science and Policy, University of California, One Shields Drive, Davis, California 95616 USA

Abstract. Plant communities on infertile soils may be relatively resistant to climatic variation if species in these communities have “stress-tolerant” functional traits that limit their ability to respond to climate. Alternatively, such communities may be more sensitive to climatic variation if their relatively sparse vegetative cover exposes species to more extreme changes in factors such as temperature or wind. We compared temporal variability in species richness and composition over 10 years between grasslands on infertile serpentine and “normal” sedimentary soils. Variability in species richness and species composition tracked mean annual precipitation on both soils, but variability was lower in serpentine grasslands. Communities on serpentine had lower functional diversity and had species with more “stress-tolerant” traits than non-serpentine communities (i.e., shorter stature, lower specific leaf area, and lower leaf area). Within and between soils, variability in species richness and temporal turnover were lower in communities scoring as more stress tolerant on a multivariate index of these traits; however, community variability was unrelated to functional diversity. Within 41 species found commonly on both soils, variability in occurrence and cover were also lower on serpentine soils, even though intraspecific trait differences between soils were minimal; this suggests a direct effect of soil type on species variability in addition to the indirect, trait-mediated effect. Communities with higher biomass had higher annual variability in species occurrence and cover. Our results suggest that infertile soils reduce compositional variability indirectly by selecting for stress-tolerant traits and directly by limiting productivity. We conclude that communities on infertile soils may respond more conservatively to predicted changes in precipitation, including increased variability, than communities on soils of normal fertility.

Key words: *climate; functional traits; grasslands; precipitation; serpentine; stability.*

INTRODUCTION

Climatic variation, perhaps the most important force structuring the world’s ecological communities, now receives growing attention from ecologists because of the incontrovertible evidence for climate change, including increases in variability and directional change (Parmesan and Yohe 2003, Kelly and Goulson 2008). One of the less understood aspects of climatic impacts is how they may be mediated by intrinsic differences among natural communities, in factors such as soil fertility, functional composition, functional diversity, invasion history, and human land use. For example, infertile “ancient” limestone grasslands showed only a weak response to multiple years of water and temperature alteration, while the response to these treatments was much higher in more fertile grasslands with a prior history of fertilization and cultivation (Grime et al. 2000, 2008). In another example, plant communities in the Arctic were remarkably stable in the face of long-

term experimental warming, despite the expectation that such temperature-limited communities should respond strongly to warming (Hudson and Henry 2010). In a paleoecological study, Briles et al. (2011) detected less Pleistocene-to-Holocene community change in forests on infertile ultramafic soils than those on “normal” diorite soils. In all of these cases, the authors cited a role for stress-tolerant functional traits, i.e., plant traits that confer slow resource acquisition, low mean and variance in growth rates, and slow nutrient cycling, in mediating community response to climate.

Plant communities on infertile soils may also be relatively resistant to climate change for reasons other than functional traits. Strong nutrient limitation may directly reduce the potential impact of changes in temperature and rainfall on plant growth, as evidenced by studies showing that communities respond to the alteration of one resource or condition (e.g., temperature) only after the removal of limitation by another resource or condition (e.g., nutrients; Klanderud and Totland 2005, Going et al. 2009). But in natural, unmanipulated communities, variation in nutrients may be tightly linked to functional trait variation, because traits that are adaptive to low soil-resource availability may also be adaptive to harsh climates (Chapin 1991). In

Manuscript received 8 November 2011; revised 15 March 2012; accepted 27 March 2012. Corresponding Editor: J. B. Yavitt.

¹ E-mail: bmggoing@ucdavis.edu

addition, communities on infertile soils may have higher levels of diversity in functional traits, and this may confer resistance to climatic variability through the enhanced potential for complementarity in species responses (Tilman and Downing 1994, McCann 2000).

There have been few examinations of climate sensitivity in adjacent natural communities that differ in species functional traits. Moreover, one study found that forest herb communities on serpentine and non-serpentine soils responded equally to long-term (57 years) climatic warming, and that the relatively rare endemic component of the serpentine communities showed the strongest response (Damschen et al. 2010). These authors speculated that the greater solar exposure of herbs under the sparser tree canopies on serpentine soils could be an important factor. Clearly, there is need for more exploration of community differences in sensitivity to climatic variation, and of the mediating role of species traits, to determine whether species growing on infertile soils will be either unusually resistant or sensitive to climate change (Damschen et al. 2011).

Here, we analyze the responses to 10 years of natural climatic variation of Mediterranean grassland communities, which are strongly influenced by interannual variation in precipitation (Pitt and Heady 1978). We compare grasslands on two soil types that differ in functional composition and diversity. Grasslands on unproductive serpentine soils have a greater diversity of native annual forbs, and higher total richness and diversity, while grasslands more fertile non-serpentine soil are heavily invaded by exotic annual grasses and forbs and have lower richness and higher dominance (see Methods). Experiments in serpentine grasslands show that many of these differences can be reversed or reduced by the addition of basic nutrients (N, P, K), making these grasslands a reasonable model system for nutrient-poor communities in general (Huenneke et al. 1990, Going et al. 2009, Harrison and Rajakaruna 2011).

We hypothesized that species richness and species composition will vary less over time in response to annual rainfall in serpentine than in non-serpentine grasslands. We also tested the following mechanisms to explain differences in community variability over time: (1) Soil type affects variability via functional group (i.e., annual/perennial, grass/forb); thus, serpentine soils will have higher levels of the more stable functional groups (e.g., perennials), although variability may not differ between soils within each of these groups. (2) Soils affect community variability via species functional trait composition; thus, serpentine grasslands will contain values of species functional traits consistent with stress tolerance, and community-level means of these functional traits will predict community variability. (3) Soils affect community variability via species functional diversity; thus, serpentine grasslands will support higher functional diversity, and functional diversity will predict

community variability (negatively). (4) Soils affect community variability directly, rather than via species traits; thus, species found on both soils will show lower temporal variability on serpentine than non-serpentine soils. We also used supplemental analyses to understand the influence of naturalized annual grasses, a species-poor, but dominant (on non-serpentine soils) functional group that is virtually all nonnative.

MATERIALS AND METHODS

Study site

We surveyed serpentine and non-serpentine annual grasslands over 10 years at the University of California McLaughlin Reserve, a 2776-ha reserve located in Napa, Yolo, and Lake Counties of California (38°51' N, 123°30' W). Elevation ranges from 366 to 914 m. The climate is Mediterranean, with cool, wet winters and hot, dry summers. Mean annual temperatures range from 8°C in January to 25°C in July and mean annual precipitation is 62 cm, falling primarily as winter rain. Annual precipitation during the study period was variable (Fig. 1, Appendix A). However, there was no significant trend in precipitation over the 10 year study period.

Grasslands on sedimentary-derived soils are dominated by a small number of exotic annual grass species (e.g., *Avena barbata*, *A. fatua*, *Bromus hordeaceus*, *Lolium multiflorum*, and *Taeniatherum caput-medusae*; taxonomy follows Hickman 1993) that germinate in fall and flower in spring, and are well known to suppress annual forb abundances by forming a dense layer of recalcitrant litter that inhibits forb germination (e.g., Pitt and Heady 1978, Levine and Rees 2004). Of the 19 species of annual grasses occurring in our plots, only two species are native to California (*Vulpia microstachys* and *V. octoflora*). Native perennial grasses and forbs are present in low abundance on non-serpentine soils. Grasslands on soil formed from serpentine (ultramafic) rock, which has high Mg^{+2} : Ca^{+2} and low primary nutrients, support a higher diversity of native forbs (mostly annuals) as well as native perennial grasses. Exotic species are present, but in relatively low abundances (<40% of species in a 1-m² plot, compared with >80% on non-serpentine) (Harrison 1999, Harrison et al. 2003). Previous analyses showed that species composition is highly nested temporally, such that most species are favored by cool, wet years that follow hot, dry years (Elmendorf and Harrison 2009).

We focus our analyses on rainfall because variability in annual rainfall is known to be a critical driver of natural variation in community composition for California annual grasslands (Pitt and Heady 1978, Levine and Rees 2004, Hobbs et al. 2007). Temperature has been shown experimentally to have little effect on California grasslands (Zavaleta et al. 2003). In addition, experimental work in California and elsewhere suggest that grassland productivity and composition are sensitive to changes in the magnitude and timing of rainfall

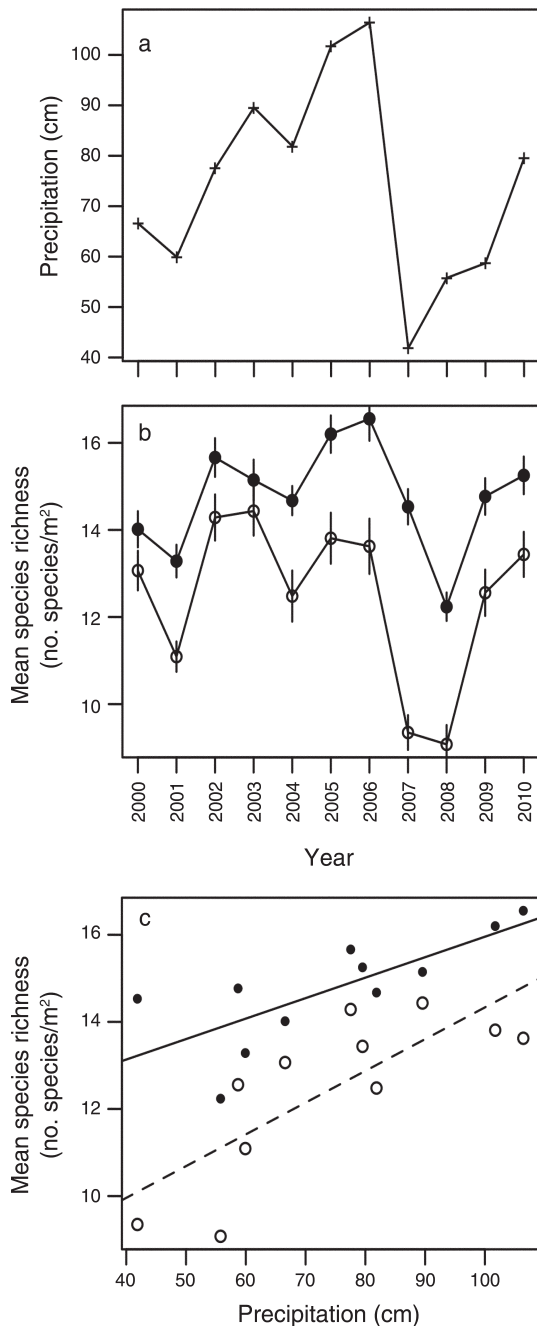


FIG. 1. (a) Annual precipitation over the 10-year study period, (b) species richness over the 10-year study period for non-serpentine (open circles, dashed line) and serpentine (closed circles, solid line) grasslands, and (c) relationship of plant species richness and annual precipitation for non-serpentine (open circles, dashed line) and serpentine (closed circles, solid line) grasslands. Values are means; error bars in panel (b) represent SE. Regression statistics for panel (c) non-serpentine are $y = 7.04 + 0.07(\text{precipitation})$ ($P = 0.0043$, $r^2 = 0.61$); for serpentine, $y = 11.25 + 0.05(\text{precipitation})$ ($P = 0.0075$, $r^2 = 0.57$).

(Zavaleta et al. 2003) and may be influenced by the presence of dynamic functional groups such as annual grasses (Suttle et al. 2007). Moreover, regional forecasts for ecological change in California strongly emphasize alterations in the amount, timing, and variability of precipitation, though the specific details of the predicted changes are highly uncertain (Cayan et al. 2008). Precipitation data came from the Knoxville Creek weather station (Western Regional Climate Center) and is shown in Fig. 1a and Appendix A (data available online).²

Sampling

Community composition was sampled twice annually (April and June) in 80 grassland sites (38 on serpentine, 42 on non-serpentine) since 2000. We combined the two surveys from each year by using the larger cover value for each species. Each site consisted of five 1-m² permanently marked quadrats placed evenly along a 50-m transect. The sites are ≥ 50 m apart and well interspersed throughout the reserve (no mean difference between soil types in latitude, longitude, slope, or aspect). Presence of each species was recorded from 2000 to 2006, and visual estimates of percent cover were recorded from 2006 to 2010. Soil samples were collected and analyzed to confirm site classifications as “serpentine” ($\text{Ca:Mg} < 1$) and “non-serpentine” ($\text{Ca:Mg} > 1$) (Appendix B). Additional details of sites and sampling methods can be found in Harrison (1999).

To obtain the maximum temporal scope, we base our analyses on the 10 years of frequency data (i.e., presence or absence in the five subplots per site), but we also ask whether key results are robust to the use of the five years of relative abundance (cover) data.

Functional traits and functional groups

Functional traits were measured on 10 individuals from each of the 191 species (297, including plants with populations on both soils) that were found at >10 sites (the sum of cover for these species represent $98.3\% \pm 3.1\%$ of the total cover in each plot). For 41 species occurring at >10 sites on each soil (referred to as “generalists”), we measured traits on 10 individuals from each home soil. We selected a set of traits that are associated with resource acquisition, mean and variance in growth rate, and tolerance to resource scarcity (Cornelissen et al. 2003, Cornwell and Ackerly 2009, Sandel et al. 2010). For all 191 species, we measured height, leaf area (LA), specific leaf area (SLA, fresh leaf area in mm² per g dry mass), leaf water content (LWC), and percent foliar nitrogen (%N). Collection and measurement of traits took place just prior to the peak flowering of each species and followed protocols in Cornelissen et al. (2003). We also classified species into

² <http://www.wrcc.dri.edu/cgi-bin/rawMAIN.pl?caCKNO>

the following groups: annual grasses, perennial grasses, annual forbs, and perennial forbs.

Analysis

Community variability.—To describe the temporal community variability of each site with the 10 years' presence-absence data, we used two occurrence-based metrics: the coefficient of variation (CV) of species richness over 10 years, and the mean Jaccard dissimilarity in composition between each pair of adjacent years at that site. Sites ($n = 80$), rather than years, provided the replication in these and many of our other key analyses. To measure the temporal community variability of each site with the five years of cover data, we calculated two abundance-weighted metrics: the CV of Shannon diversity and the mean value of Bray-Curtis dissimilarity between adjacent year pairs using the five years of cover data. All community variability metrics were calculated at the quadrat level and averaged to obtain one value for each site. Variability metrics were log-transformed when necessary to meet parametric assumptions.

To determine if community variability differed by soil type using the 10-year occurrence-weighted metrics, we used MANOVA with CV of richness and Jaccard dissimilarity as response variables and soil type as the predictor, with sites as replicates. To ask the same question using the 5-year abundance-weighted metrics, we conducted a second MANOVA, with CV of Shannon diversity and Bray-Curtis dissimilarity as response variables and soil type as the predictor. When MANOVAs were significant, we conducted F tests for individual response variables. To determine if functional group abundance and variability differed by soil type, we conducted two MANOVAs with functional group cover or CV of cover as response variables and soil type as the predictor variable. When MANOVAs were significant, we conducted F tests for individual response variables.

To test whether communities on the two soil types differ in the strength of the response of species richness to rainfall, we created a linear mixed effect model for each soil with a random effect for site and a first-order autoregressive error structure, *sensu* Adler and Levine (2007). Predictor variables were same-year and previous-year sum precipitation and their interaction; replicates in this case were year \times site observations. We compared coefficients across the two models using a t test with unequal variance and $df = (\text{number of year} \times \text{site observations} - 4)$.

Community variability and functional traits

To test whether the four functional groups (annual/perennial, grass/forb) differed in the functional traits we measured, we used MANOVA with species-level means of the five traits as response variables, functional group identity as the predictor variable, and the 191 species as replicates. When the MANOVA was significant we used

ANOVAs to determine which traits differed among functional groups.

To test whether the "generalist" species had different trait values depending on soil type, we used a paired t test with species-level means of the five traits (separate means for each soil) as response variables, home soil as the predictor variable, and the 41 generalist species as replicates. Traits were log-transformed to meet parametric assumptions.

To compare the functional traits by soil type, we calculated community-weighted mean traits (CWM) values for each of the five traits (based on the 191 species). CWM weights a species trait by its relative abundance in the plot and sums over all species, resulting in a single community trait value. We used a MANOVA, followed by F tests, to determine if these trait means differed by soil type, with sites as replicates.

To test whether functional diversity predicts community stability, we used an ANOVA with Bray-Curtis dissimilarity as the dependent variable; functional divergence, soil type, and their interaction as predictors; and sites as replicates. Functional divergence is a measure of functional diversity that is independent of species richness and accounts for species abundances (Laliberte and Legendre 2010). We calculated it using the FD package in R (Laliberte and Legendre 2010) (We also calculated functional evenness, which measures trait spacing; the results were qualitatively unchanged and are not shown.)

To test whether community-level functional properties predict temporal variability, we used ANOVAs with temporal Bray-Curtis dissimilarity as the dependent variable; traits, soil type, and trait by soil type interactions as predictor variables; and sites as replicates. Because functional traits are often correlated, we used principal components analysis (PCA) to create a multivariate trait index that described the suite of traits we measured. We chose Bray-Curtis dissimilarity as the focal metric to remain consistent with the abundance-weighted trait data and because results obtained with this metric were qualitatively similar to results obtained using CV of Shannon diversity.

Community variability and soil

To test for a direct effect of soil type on variability, we used two approaches. First, we compared the temporal CVs in frequency and cover for the 41 soil generalists using t tests with species as replicates. Second, we used ANOVAs with temporal Jaccard dissimilarity or Bray-Curtis dissimilarity as dependent variables, soil type and community biomass (as a proxy for soil fertility) and the interaction between soil and biomass as predictor variables, and sites as replicates. Soil properties differed significantly between soil types (serpentine and non-serpentine), but no soil variables were significant in models of community variability that also included soil type, probably reflecting the importance of multiple soil variables (including some that we did not measure) and

TABLE 1. Results of *F* tests for differences in 10-year (CV richness and Jaccard dissimilarity) and 5-year (CV Shannon diversity and temporal Bray-Curtis dissimilarity) variation in diversity and composition of serpentine and non-serpentine grasslands.

Stability metric	Non-serpentine	Serpentine	<i>F</i>	<i>P</i>
Including annual grasses				
CV species richness	0.28 ± 0.06	0.19 ± 0.03	63.3	<0.0001
Jaccard dissimilarity	0.43 ± 0.04	0.39 ± 0.05	21.7	<0.0001
CV Shannon diversity	1.39 ± 0.33	1.08 ± 0.15	29.6	<0.0001
Bray-Curtis dissimilarity	0.49 ± 0.09	0.54 ± 0.06	8.2	0.0053
Excluding annual grasses				
CV species richness	0.25 ± 0.12	0.14 ± 0.03	28.5	<0.0001
Jaccard dissimilarity	0.51 ± 0.05	0.42 ± 0.05	57.8	<0.0001
CV Shannon diversity	2.13 ± 0.46	1.88 ± 0.22	9.2	0.0033
Bray-Curtis dissimilarity	0.66 ± 0.11	0.58 ± 0.09	11.4	0.0011

Notes: Values shown for metrics are mean ± SD. CV stands for coefficient of variation. All df = 1, 78.

correlated plant community variation in determining responses. Community biomass was measured in 2002 by collecting all aboveground biomass from 30 × 30 cm² plots at each site. Biomass was oven-dried at 60°C for 24 hours and weighed.

Community variability and annual grasses

In contrast to the other three functional groups, annual grasses (*n* = 19 species) had higher temporal variability on serpentine, so to better characterize the influence of this functional group on community variability, we ran additional MANOVAs for temporal variability metrics after excluding annual grasses from the data. In addition, to ask whether variability in other groups was driven by annual grass cover, we used ANOVAs with Jaccard dissimilarity or Bray-Curtis dissimilarity for all other species as dependent variables and soil type, mean annual grass cover, and the interaction between soil type and mean annual grass cover as predictors. Finally, we repeated the multivariate traits analyses with annual grasses excluded from both the stability and trait data.

RESULTS

Community variability

Analyses using both the 10-year presence-absence data and the 5-year cover data were generally consistent with our prediction that serpentine communities are relatively more stable over time. Species richness was higher on serpentine than on non-serpentine soils (non-serpentine = 12.5 ± 2.6 species; serpentine = 14.8 ± 2.1 species; *t* test df = 78, *t* = 4.3, *P* < 0.0001) and temporal variation in species richness (10 year) and composition (5 and 10 year) were lower on serpentine than on non-serpentine soil (10-year MANOVA *F*_{2,77} = 33.9, *P* < 0.0001; 5-year MANOVA *F*_{2,77} = 14.6, *P* < 0.0001). The temporal CVs of species richness and Shannon diversity, as well as the temporal Jaccard dissimilarity between years within sites, were all lower on serpentine soil (Table 1). However, temporal Bray-Curtis dissimilarity

in the 5-year cover data set was significantly higher on serpentine soils than non-serpentine soils (Table 1).

Functional group abundance (mean percent cover; Appendix C) differed by soil type (MANOVA: *F*_{4,75} = 19.7, *P* < 0.0001), as expected, with perennials being more abundant on serpentine (perennial forb, non-serpentine cover = 2.3% ± 3.2%, serpentine cover = 4.5% ± 2.9%, *F*_{1,78} = 9.8, *P* = 0.0025; perennial grass, non-serpentine cover = 4.7% ± 6.3%, serpentine cover = 9.1% ± 8.%, *F*_{1,78} = 9.0, *P* = 0.0037) and annual grasses being more abundant on non-serpentine (non-serpentine cover = 63.4% ± 22.6%, serpentine cover = 33.6% ± 16.8%, *F*_{1,78} = 54.3, *P* < 0.0001). There was no difference in annual forb abundance by soil (non-serpentine cover = 30.2% ± 15.4%, serpentine cover = 34.8% ± 16.0%, *F*_{1,78} = 3.0, *P* = 0.0881). Functional group CV also differed by soil type (MANOVA *F*_{4,75} = 12.2, *P* < 0.0001; Appendix C). However, the major deviation from predictions was that the temporal CV of cover for annual grasses was higher on serpentine soil (*F*_{1,78} = 16.7, *P* = 0.0001), while temporal CVs of cover for annual and perennial forbs were significantly higher on non-serpentine, as expected (annual forb *F*_{1,78} = 7.1, *P* = 0.0095; perennial forb *F*_{1,78} = 19.8, *P* < 0.0001), and variation in perennial grass cover did not differ by soil type (*F*_{1,78} = 1.6, *P* = 0.2095). Temporal CVs of cover did not differ between native and exotic forbs (df = 151.1, *t* = -1.7, *P* = 0.0836).

For both soils, species richness was significantly affected by the present and previous year's rainfall and their interaction (non-serpentine, current-year precipitation df = 375, *t* = 8.2, *P* < 0.0001; previous-year precipitation df = 375, *t* = 5.2, *P* < 0.0001, current-year × previous-year precipitation df = 375, *t* = -6.0, *P* < 0.0001; serpentine, current-year precipitation df = 339, *t* = 6.1, *P* < 0.0001; previous-year precipitation df = 339, *t* = 5.8, *P* < 0.0001, current-year × previous-year precipitation df = 339, *t* = -4.7, *P* < 0.0001). The coefficient representing the strength of the response of species richness to the present year's rainfall was significantly lower on serpentine soils (df = 376, *t* = -2.3, *P* = 0.0200; Fig. 1c).

Community variability and functional traits

Species belonging to the four functional groups differed in trait values (MANOVA $F_{5,285} = 89.3$, $P < 0.0001$) for height ($F_{3,286} = 26.6$, $P < 0.0001$), SLA ($F_{3,286} = 15.2$, $P < 0.0001$), LA ($F_{3,286} = 26.3$, $P < 0.0001$), LWC ($F_{3,286} = 5.6$, $P = 0.0010$), and %N ($F_{3,286} = 27.6$, $P < 0.0001$) (Appendix C). Of the 41 generalist species, populations on serpentine soil had lower SLA than those on non-serpentine soil ($df = 40$, $t = -2.3$, $P = 0.0247$), but populations did not differ in other traits between soil types (height $df = 40$, $t = -1.3$, $P = 0.2139$; area $df = 40$, $t = 1.2$, $P = 0.2360$; LWC $df = 40$, $t = -1.1$, $P = 0.2957$; %N $df = 40$, $t = 1.5$, $P = 0.1290$).

Community-weighted mean trait values differed by soil type ($F_{5,75} = 41.4$, $P < 0.0001$). Serpentine communities had lower community-weighted mean values of SLA ($F_{1,78} = 155.3$, $P < 0.0001$) and LA ($F_{1,78} = 5.4$, $P = 0.0222$) and tended to be shorter ($F_{1,78} = 3.6$, $P = 0.0594$), but had higher %N ($F_{1,78} = 5.3$, $P = 0.0243$) than non-serpentine communities (Appendix D). There was no difference in LWC between soil types ($F_{1,78} = 0.2$, $P = 0.6995$). Functional divergence was significantly lower in serpentine communities than in non-serpentine communities ($df = 74.1$, $t = -4.7$, $P < 0.0001$).

There was a significant effect of soil type, but not functional divergence or the interaction between functional divergence and soil type, on Bray-Curtis dissimilarity ($F_{3,76} = 4.2$, $P = 0.0085$).

The first principal component of functional traits (trait PC1) explained 46.0% of the variation in community traits and was primarily associated with increasing LA, LWC, and %N; trait PC2 explained 27.5% of the variation and was primarily associated with increasing height (Appendix E). Soil type, trait PC1, and soil type \times trait PC2 affected temporal Bray-Curtis dissimilarity ($F_{5,74} = 6.6$, $P < 0.0001$; Table 2, Fig. 2a–d). The main effect of PC1 reflected that temporal variability was higher in communities with a correlated suite of fast-growth traits (high leaf area, leaf water content, and percent nitrogen). The soil type \times trait PC2 interaction signified that temporal variability was also higher in communities with greater mean height, but only on serpentine soils. (Means of functional traits of each soil type, and correlations of each trait to temporal variability, can be found in Appendix C).

Community variability and soil

The 41 generalist species had significantly lower temporal CVs of frequency and cover when they grew on serpentine soil than non-serpentine soil (CV frequency, paired $df = 40$, $t = -2.2$, $P = 0.0314$; CV cover, paired $df = 40$, $t = -4.9$, $P < 0.0001$).

Temporal Jaccard dissimilarity was significantly affected by soil type, biomass, and the soil \times biomass interaction (overall $F_{3,76} = 13.1$, $P < 0.0001$; soil $F = 14.4$, $P = 0.0003$; biomass $F = 4.0$, $P = 0.0486$; soil \times biomass $F = 13.1$, $P = 0.0005$). Compositional turnover

TABLE 2. Results of ANOVAs for the effects of soil type and trait indices on temporal Bray-Curtis dissimilarity of serpentine and non-serpentine grasslands.

Factor	<i>F</i>	<i>P</i>
Including annual grasses		
Soil	4.3	0.0422
PC1	6.4	0.0133
PC2	2.9	0.0905
Soil \times PC1	0.1	0.7355
Soil \times PC2	5.5	0.0222
Excluding annual grasses		
Soil	4.1	0.0466
PC1	1.1	0.3006
PC2	0.1	0.8093
Soil \times PC1	6.9	0.0104
Soil \times PC2	1.7	0.1969

Note: All $df = 1, 78$.

was higher and unrelated to biomass on non-serpentine soil, but on serpentine soil it increased linearly with biomass (non-serpentine $r = 0.22$; serpentine $r = 0.49$, Fig. 3a and b). Only soil type was significantly related to Bray-Curtis dissimilarity (overall $F_{3,76} = 3.0$, $P = 0.0357$; soil $F = 8.5$, $P = 0.0046$; biomass $F = 0.3$, $P = 0.6087$; soil \times biomass $F = 0.01$, $P = 0.8–65$).

Community variability and annual grasses

Annual grasses strongly influenced turnover patterns by increasing temporal variability in serpentine grasslands. When annual grasses were excluded from the data, overall variability remained lower on serpentine (10-year MANOVA, $F_{2,77} = 31.6$, $P < 0.0001$; 5-year MANOVA, $F_{2,77} = 16.3$, $P < 0.0001$) and temporal Bray-Curtis dissimilarity became significantly lower on serpentine than non-serpentine soil (Table 1). Further, mean annual grass cover was negatively correlated with annual grass variability on both soils (non-serpentine $F_{1,40} = 55.1$, $P < 0.0001$, $r = 0.76$; serpentine $F_{1,36} = 25.8$, $P < 0.0001$, $r = 0.65$). The latter result suggests that the greater variability of annual grass cover on serpentine soil may be due to the fact that at many sites (especially on non-serpentine soils), annual grass cover is too high to permit much additional variability.

Mean annual grass cover was positively correlated with temporal Jaccard dissimilarity of non-annual grasses on both soil types (i.e., significant effects of soil type and annual grass cover, but not the interaction between soil and grass cover) (overall $F_{3,76} = 27.8$, $P < 0.0001$; soil $F = 13.3$, $P = 0.0005$; grass $F = 15.1$, $P = 0.0002$; soil \times grass $F = 0.2$, $P = 0.6990$). Using the 5-year cover-based metric, Bray-Curtis dissimilarity, there was a positive correlation with temporal turnover and annual grass cover, but the relationship depended on soil type (i.e., there were significant effects of annual grass cover and the interaction between grass cover and soil type, but not of soil type alone) (overall $F_{3,76} = 7.2$, $P = 0.0003$; soil $F = 1.5$, $P = 0.2190$; grass $F = 4.2$, $P = 0.0437$; soil \times grass $F = 7.1$, $P = 0.0092$). There was no effect of annual grass cover on temporal Bray-Curtis

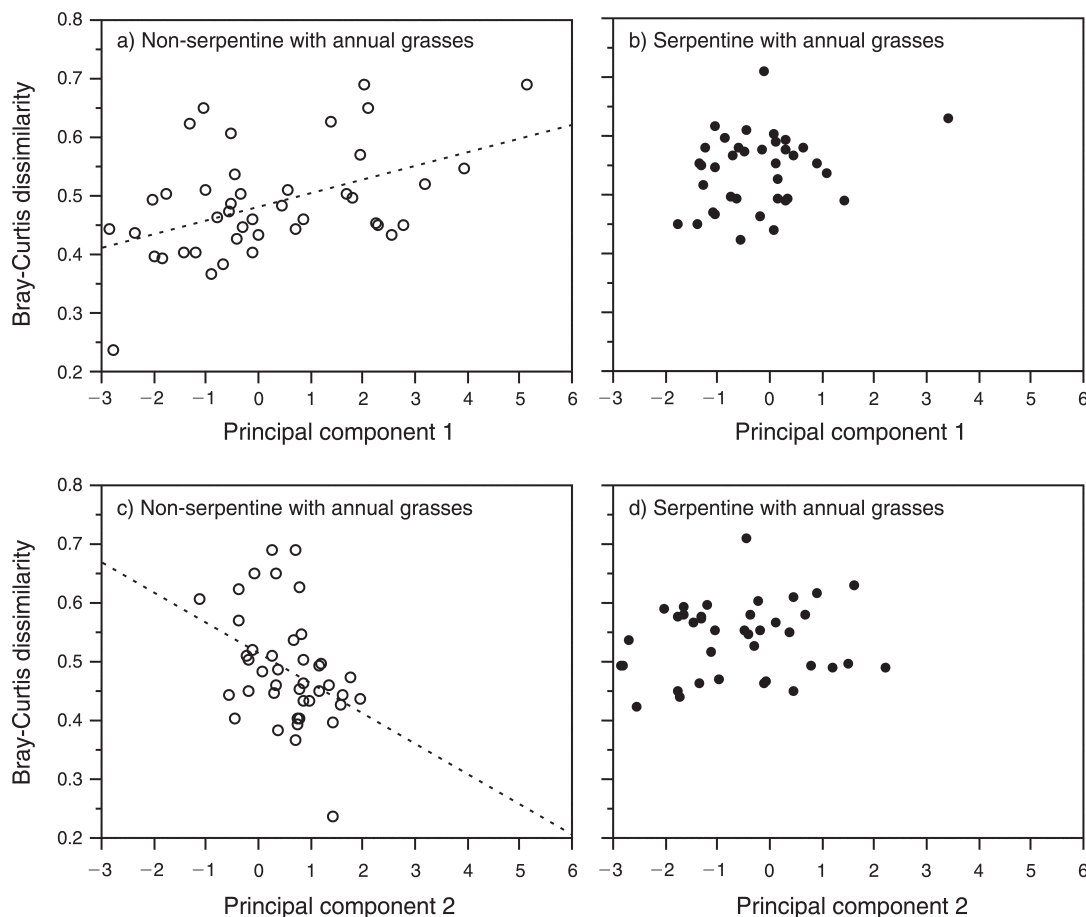


FIG. 2. The relationship between cover-based temporal turnover and indices of community-weighted mean functional traits for (a, c) non-serpentine (open circles, dashed lines) and (b, d) serpentine (solid circles) grasslands. Principal component 1 was associated with increasing leaf area (LA), leaf water content (LWC), and percentage nitrogen (%N), while principal component 2 was associated with increasing height. Regression statistics are: (a) $y = 0.48 + 0.02(\text{PC1})$, $P = 0.0016$, $r^2 = 0.22$; (b) $y = 0.54 + 0.01(\text{PC1})$, $P = 0.1452$, $r^2 = 0.06$; (c) $y = 0.52 - 0.05(\text{PC2})$, $P = 0.0106$, $r^2 = 0.15$; (d) $y = 0.54 + 0.01(\text{PC1})$, $P = 0.4095$, $r^2 = 0.02$.

dissimilarity on non-serpentine, and a significant, positive correlation on serpentine (non-serpentine $r = 0.10$, serpentine $r = 0.51$).

Excluding annual grasses from the data had little effect on most patterns in community-weighted trait means, which still differed by soil type ($F_{5,74} = 18.6$, $P < 0.0001$); serpentine communities had lower SLA ($F_{1,78} = 80.9$, $P < 0.0001$), LA ($F_{1,78} = 3.5$, $P = 0.0644$), and LWC ($F_{1,78} = 18.9$, $P < 0.0001$) values. However, %N became significantly lower for serpentine communities in the absence of annual grasses ($F_{1,78} = 18.3$, $P < 0.0001$). There was no difference in height between the communities ($F_{1,78} = 3.1$, $P = 0.0816$).

For species other than annual grasses, trait PC1 explained 44.5% of the variation and was associated with increasing SLA, LWC, and %N, while PC2 explained 27.2% of the variation and was associated with increasing height and LA (Appendix E). When annual grasses were excluded there was a significant effect of soil type and soil \times PC1, but not of the individual trait axes or the interaction between soil type

and PC2 on Bray-Curtis dissimilarity ($F_{5,74} = 4.9$, $P = 0.0006$, Table 2). High community variability was again associated with non-serpentine soils and a suite of fast-growing traits (SLA, LWC, and %N), with these traits having stronger positive correlations to variability on serpentine soils than non-serpentine soils (Fig. 4a–d).

DISCUSSION

Consistent with the limited number of experimental and paleoecological studies (Grime et al. 2000, 2008, Briles et al. 2011; but see Damschen et al. 2010), our analyses indicated that communities on low-fertility serpentine soils generally vary less in response to precipitation than do communities on more fertile soils. Moreover, we found that the lower community variability on infertile serpentine soils appears to reflect several underlying factors. First, serpentine communities contain species belonging to particular functional groups that have sets of functional traits associated with slow growth and lower community-level variability (perennial life form, short stature, low leaf area, low

specific leaf area, and low foliar N). Second, infertile serpentine soils also appear to lead directly to lower temporal variability, as shown by our analysis of species that occur on both soils (and this is not likely explained by intraspecific trait variation, for which we found little evidence). Third, the annual grass functional group, which is composed of a handful of exotic species and is highly dominant on fertile non-serpentine soils, shows higher temporal variability in cover on serpentine soils where it is less dominant, and this tends to influence community variability in the opposite direction (serpentine > non-serpentine). However, at the whole-community level, this third factor is less strong than the first two, leading to net results in the predicted direction (serpentine < non-serpentine). Fourth, functional diversity, which was lower on serpentine, did not appear to play an important role in explaining community variability. Our results generally support the prediction (Grime et al. 2000, 2008) that plant communities on nutrient-poor soils may be relatively resistant to perturbations in precipitation, especially if they are unaltered by fertilization, invasion by fast-growing exotic species, or other human impacts.

To our knowledge, this is the first study to use species trait information in addition to functional groupings to compare compositional turnover in time in contrasting plant communities. Previous studies have relied solely on functional groups or other indirect evidence for traits, such as differences in productivity (e.g., Grime et al. 2000, 2008). In a comparison of savannah communities along a productivity gradient, Sankaran and McNaughton (1999) found that compositional turnover in time was lower in *Aristida setacea*-dominated communities at the low end of a productivity gradient. In another example, White et al. (2000) found that low-resource communities composed of heat-tolerant C_4 grasses were less impacted by experimentally imposed heat and rainfall events than more productive communities containing a mix of C_3 and C_4 species. Based on this recent literature, we expected functional traits to explain more of the variation in community temporal variability than we observed (multivariate trait axes explained about 25% of compositional variability; i.e., $r^2 = 0.15$ and 0.25 with and without annual grasses, respectively). We believe that other, more difficult to measure traits, such as root depth, root density, and specific root length, are likely to play important roles in explaining the relative stability of grassland communities because they are linked to resource capture and stress tolerance. A recent study suggests that above- and belowground functional trait syndromes are not completely correlated in grassland species; specific leaf area and specific root length were positively correlated but leaf density and root density were not (Kembel and Cahill 2011). This suggests that considerable additional predictive power could be gained by measuring belowground traits, which is unfortunately nearly impossible in rocky soils such as serpentine.

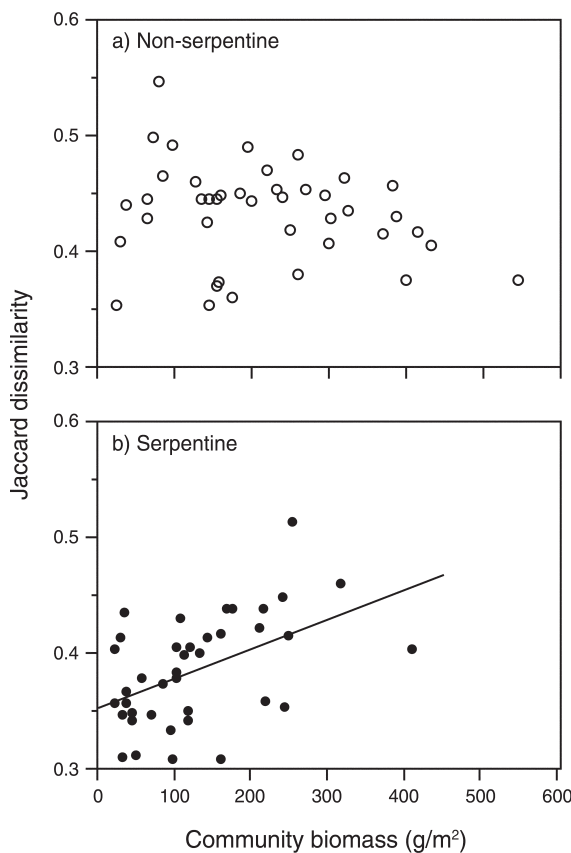


FIG. 3. Relationship between compositional turnover (Jaccard dissimilarity) and community biomass, a proxy for soil fertility (rescaled to 1 m^2). Regression statistics: (a) $y = 0.45 - 7.35 \times 10^{-5}(\text{biomass})$, $P = 0.1718$, $r^2 = 0.05$; (b) $y = 0.35 + 0.00026(\text{biomass})$, $P = 0.0014$, $r^2 = 0.24$.

We also found direct effects of soil type on community variability, in addition to the trait-mediated effects. One possible explanation is that low soil resource availability in serpentine soil is associated with higher allocation to belowground storage, which could reduce the variability of aboveground biomass. However, these grasslands are dominated by annual plants that regenerate from seed each year. Another possibility is that low nutrient availability limits the mean and variance in recruitment rates of species on serpentine, constraining their ability to respond to interannual variability in precipitation. Previous work has shown that low nutrient availability can suppress community responses to elevated CO_2 (Reich et al. 2001) and temperature (Klanderud and Totland 2005). Further, serpentine communities have been shown to be highly responsive to nutrient additions, but not to water manipulations (Huenneke et al. 1990, Going et al. 2009). There are also many other possible climate-soil interactions mediated by soil texture, pH, nutrient cycling, litter chemistry, and other factors (e.g., Sala et al. 1988). Since serpentine and non-serpentine soils differ in numerous chemical and physical properties and support very different plant

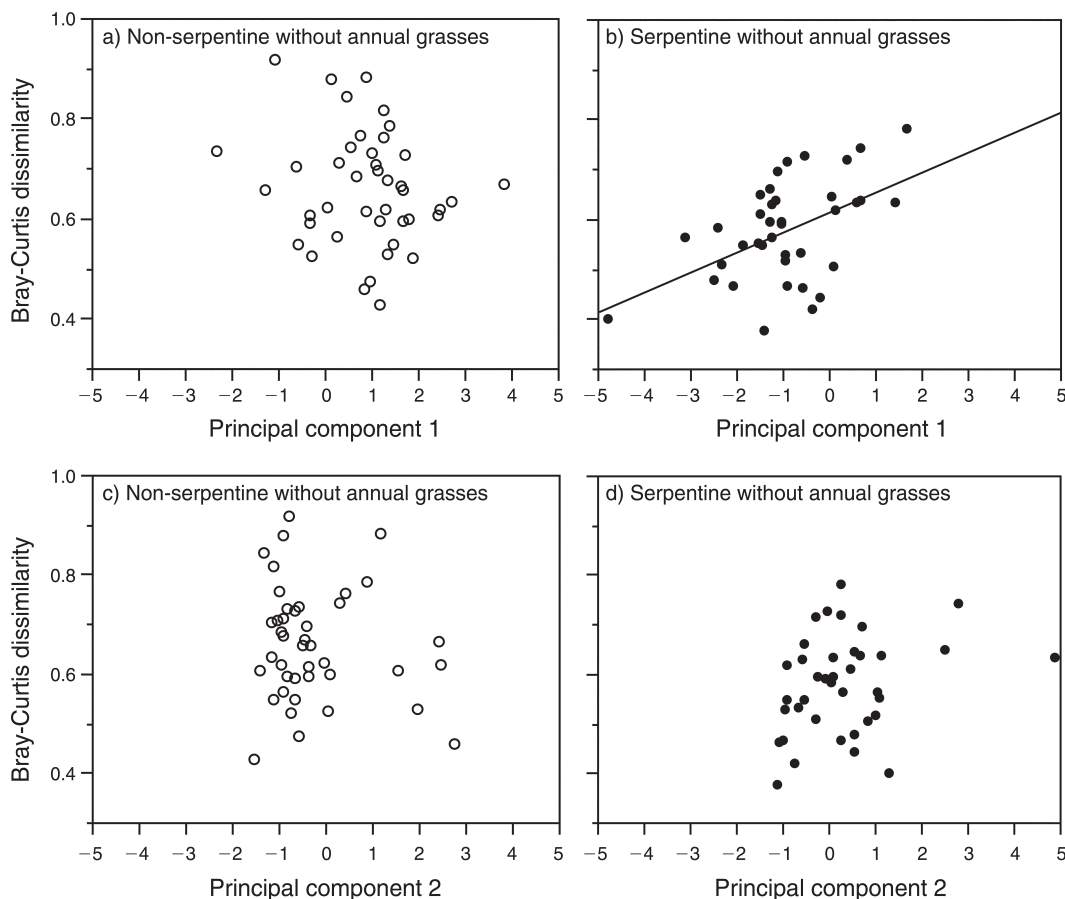


FIG. 4. The relationship between temporal turnover of communities excluding annual grasses and functional traits indices for (a, c) non-serpentine (open circles) and (b, d) serpentine grasslands (solid circles, solid line). Principal component 1 was associated with increasing SLA, LWC, and %N, and principal component 2 was associated with increasing height and LA. Regression statistics: (a) $y = 0.67 - 0.01(\text{PC1})$, $P = 0.2652$, $r^2 = 0.03$; (b) $y = 0.62 + 0.04(\text{PC1})$, $P = 0.0014$, $r^2 = 0.25$; (c) $y = 0.66 - 0.01(\text{PC2})$, $P = 0.4003$, $r^2 = 0.02$; (d) $y = 0.57 + 0.02(\text{PC2})$, $P = 0.0775$, $r^2 = 0.08$.

communities, our observational study was not the best avenue for understanding direct (non-trait-mediated) interactions between soil fertility and climate; this would be better accomplished by factorial manipulations of nutrients and climate within a single soil type.

Our results suggest that annual grasses have a fundamentally different response to the rainfall–soil interaction than other groups. This result is in agreement with prior work showing that *Bromus hordeaceus* is especially responsive to rainfall on serpentine soils (Hobbs et al. 2007). One possible explanation for this result is that the very high abundance of annual grasses on non-serpentine soils, often approaching 100% visual cover, precludes significant temporal variability in their abundance on these soils, which is supported by the negative relationship between annual grass cover and variability. Also, some evidence suggests that grasses are considerably less adversely affected than forbs by the low Ca:Mg ratio of serpentine soil, since they do not require Ca for their cell walls (O'Dell and Rajakaruna 2011). The differences between plant communities on

high- and low-nutrient soils may be also shaped by interspecific interactions with microbes, including pathogens (Blumenthal et al. 2009, Springer 2009) and belowground mutualists (Wardle et al. 2004, Ekelinen et al. 2009), that are only beginning to be explored.

There is a growing consensus that community stability should increase with functional diversity through either redundancy or complementarity (reviewed in Diaz and Cabido 2001). Most of the evidence comes from experimentally created communities in which diversity varies over a modest number of species and “all else” is held equal, including the abiotic filters that determine the means as well as ranges of functional traits in natural communities (Cornwell and Ackerly 2009). We found significantly lower mean values of resource-acquisition traits in serpentine communities, together with lower overall functional divergence. The lack of a role for functional diversity in explaining temporal stability suggests that the trait mean values mattered more than the diversity of traits within a community. This agrees with previous work indicating that species identities, but

not diversity, are important to ecosystem processes (Lepš et al. 2001, Emery and Gross 2006). Based on our study, we find no reason to believe that functional diversity buffers natural grassland communities against climate-driven variability.

Our results suggest that “stress tolerant” functional traits may act to limit climate-induced fluctuations in community composition on low nutrient soils. This lends support to Grime et al.’s (2000, 2008) experimental result that undisturbed, resource-poor communities should be more resistant to climatic change, including forecast increases in the variability of precipitation. Our work highlights important gaps in our understanding of how different communities respond to climatic variation, and suggests the need for more experiments, observations, and modeling.

ACKNOWLEDGMENTS

We thank Kara Moore O’Leary, Sarah Elmendorf, Peter March, Jill Baty, Annette Bieger, Florian Altermatt, Erica Case, Stella Copeland, Andy Kleinhesselink, Rebecca Crowe, and many SCA interns for assistance in the field. We also thank Paul Aigner and Catherine Koehler for logistical support. The manuscript was improved by reviews of earlier versions by Anu Eskelinen and Marko Spasojevic.

LITERATURE CITED

- Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. *Oikos* 116:221–232.
- Blumenthal, D., C. E. Mitchell, P. Pysek, and V. Jarosik. 2009. Direct and indirect effects of viral pathogens and the environment on invasive grass fecundity in Pacific Coast grasslands. *Journal of Ecology* 97:1264–1273.
- Briles, C. E., C. Whitlock, C. N. Skinner, and J. Mohr. 2011. Holocene forest development and maintenance on different substrates in the Klamath Mountains, Northern California, USA. *Ecology* 92:590–601.
- Cayan, D. R., E. P. Mauer, M. D. Dettinger, M. Tyree, and K. Hayhoe. 2008. Climate change scenarios for the California region. *Climatic Change* 87:S21–S42.
- Chapin, III, F. S. 1991. Integrated responses of plants to stress. *BioScience* 41:29–36.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335–380.
- Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79:109–126.
- Damschen, E. I., S. Harrison, B. L. Anacker, and B. M. Going. 2011. Climate change and special soil communities. Pages 359–381 in S. P. Harrison and N. Rajakaruna, editors. *Serpentine: the evolution and ecology of a model system*. University of California Press, Berkeley, California, USA.
- Damschen, E. I., S. Harrison, and J. B. Grace. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker’s Siskiyou sites (Oregon, USA). *Ecology* 91:3609–3619.
- Diaz, S., and M. Cabido. 2001. Viva la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16:646–655.
- Elmendorf, S. C., and S. P. Harrison. 2009. Temporal variability and nestedness in California species composition. *Ecology* 90:1492–1497.
- Emery, S. M., and K. L. Gross. 2006. Dominant species identity regulates invasibility of old-field plant communities. *Oikos* 115:549–558.
- Eskelinen, A., S. Stark, and M. Männistö. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. *Oecologia* 161:113–123.
- Going, B. M., J. HilleRisLambers, and J. M. Levine. 2009. Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia* 159:839–847.
- Grime, J. P., V. K. Brown, K. Thompson, G. J. Masters, S. H. Hillier, I. P. Clarke, A. P. Askew, D. Corker, and J. P. Kielty. 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* 289:762–765.
- Grime, J. P., J. D. Fridley, A. P. Askew, K. Thompson, J. G. Hodgson, and C. R. Bennett. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences USA* 105:10028–10032.
- Harrison, S. 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia* 121:99–106.
- Harrison, S., B. D. Inyone, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* 17:837–845.
- Harrison, S. P., and N. Rajakaruna. 2011. *Serpentine: the evolution and ecology of a model system*. University of California Press, Berkeley, California, USA.
- Hickman, J. C. 1993. *The Jepson manual, higher plants of California*. University of California Press, Berkeley, California, USA.
- Hobbs, R. J., S. Yates, and H. A. Mooney. 2007. Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs* 77:545–568.
- Hudson, J. M. G., and G. H. R. Henry. 2010. High Arctic plant community resists 15 years of experimental warming. *Journal of Ecology* 98:1035–1041.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in a Californian serpentine grassland. *Ecology* 71:478–491.
- Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences USA* 105:11823–11826.
- Kemmel, S. W., and J. F. Cahill, Jr. 2011. Independent evolution of leaf and root traits within and among temperate grassland plant communities. *PLoS ONE* 6:e19992.
- Klanderud, K., and O. Totland. 2005. Simulated climate change altered dominance hierarchies and diversity of an alpine diversity hotspot. *Ecology* 86:2047–2054.
- Laliberte, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.
- Lepš, J., et al. 2001. Separating the chance effect from other diversity effects in the functioning of plant communities. *Oikos* 92:123–134.
- Levine, J. M., and M. Rees. 2004. Effects of temporal variability on rare plant persistence in annual systems. *American Naturalist* 164:350–363.
- McCann, K. S. 2000. The diversity–stability debate. *Nature* 405:228–233.
- O’Dell, R. E., and N. Rajakaruna. 2011. Interspecific variation, adaptation, and evolution. Pages 97–137 in S. P. Harrison and N. Rajakaruna, editors. *Serpentine: evolution and ecology in a model system*. University of California Press, Berkeley, California, USA.

- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pitt, M. D., and H. F. Heady. 1978. Responses of annual vegetation to temperature and rainfall patterns in Northern California. *Ecology* 59:336–350.
- Reich, P. B., D. Tilman, J. Craine, D. Ellsworth, M. G. Tjoelker, J. Knops, D. Wedin, S. Naeem, D. Bahaeddin, J. Goth, W. Bengston, and T. D. Lee. 2001. Do species and functional groups differ in acquisition and use of C, N, and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *New Phytologist* 150:435–448.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States: spatial patterns and major controls. *Ecology* 69:40–45.
- Sandel, B., L. Goldstein, N. Kraft, J. Okie, M. Shuldman, D. Ackerly, E. Cleland, and K. Suding. 2010. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist* 188:565–575.
- Sankaran, M., and S. J. McNaughton. 1999. Determinants of biodiversity regulate compositional stability of communities. *Nature* 401:691–693.
- Springer, Y. P. 2009. Edaphic quality and plant/pathogen interactions: effects of soil calcium on fungal infection of a serpentine flax. *Ecology* 90:1852–1862.
- Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reserve grassland responses to changing climate. *Science* 315:640–642.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and sustainability in grasslands. *Nature* 367:363–365.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304:1629–1633.
- White, T. A., B. D. Campbell, P. D. Kemp, and C. L. Hunt. 2000. Sensitivity of three grassland communities to simulate extreme temperature and rainfall events. *Global Change Biology* 6:671–684.
- Zavaleta, E. S., M. R. Shaw, N. R. Chiarello, H. A. Mooney, and C. B. Field. 2003. Additive effects of simulated climate changes, elevated CO₂, and nitrogen deposition on grassland diversity. *Proceedings of the National Academy of Sciences USA* 100:7650–7654.

SUPPLEMENTAL MATERIAL

Appendix A

Description of precipitation by year (*Ecological Archives* E093-199-A1).

Appendix B

Means and standard deviations of non-serpentine and serpentine soil properties (*Ecological Archives* E093-199-A2).

Appendix C

Means and standard deviations of community properties by functional group (*Ecological Archives* E093-199-A3).

Appendix D

Means, standard deviations, and correlation coefficients of community weighted mean (CWM) trait values in relation to Bray-Curtis dissimilarity (*Ecological Archives* E093-199-A4).

Appendix E

Principal-component eigenvectors for community traits with and without annual grasses (*Ecological Archives* E093-199-A5).