

Temporal variability and nestedness in California grassland species composition

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Abstract. Nestedness occurs when species-poor assemblages contain a subset of the species that occur in more species-rich communities and is a commonly observed pattern in spatial data sets. Examination of nested distribution patterns across time rather than space are rarely conducted, even though they may have important implications for species coexistence. Nested temporal assemblages can occur when most species respond similarly to interannual variation in conditions. In contrast, assemblages might be non-nested when different sets of species occur in different years, either because of different resource requirements or as a result of competitive exclusion. Using eight years of plant occurrence data at 71 sites in California grasslands, we found strong signals of temporal nestedness with most species favored by similar conditions. High-quality years enabled the expansion of both grasses and forbs into locales where they were not found during poor-quality years. Native annual forb, exotic annual forb, and exotic annual grass species richness were all greatest in cool, wet years following hot, dry years. Together, these analyses support the hypothesis that, in the absence of community members that specialize on poor-quality years, interannual environmental variation can cause communities to form nested subsets across time much as they do across space.

Key words: *bad-year specialists; California grasslands; coexistence; grass vs. forb “years”; interannual environmental variation; native vs. exotic species; nestedness; species richness; temporal variation.*

INTRODUCTION

Ecologists have long been interested in how fluctuating environments contribute to the maintenance of diversity. The importance of seasonal niche specialization to coexistence was first recognized by Hutchinson (1961). In addition to seasonal variability, interannual fluctuations in weather conditions are also prevalent in many ecosystems. A longstanding but rarely tested hypothesis is that different species within a community are adapted to different types of years, such that interannual weather variability contributes to long-term coexistence (Talbot et al. 1939, Pitt and Heady 1978, Chesson and Huntly 1989, Hobbs and Mooney 1991, Pake and Venable 1996, Peco et al. 1998). For example, in an experimental Minnesota grassland some species increase in abundance during drought years (Tilman 1996) suggesting that “bad years are good” for at least some species. More recently, Adler et al. (2006) used modeling of long-term demographic data to illustrate how variable interannual weather conditions can promote long-term coexistence in Kansas prairie grasses.

Niche differentiation likely contributes to species coexistence in spatially heterogeneous environments (Amarasekare 2003). In California grasslands, distinct subsets of species are relegated to harsh soils, such as serpentine, due to their inability to tolerate competition on more benign soils (Kruckeberg 1954, Huenneke et al. 1990, Reynolds et al. 1997). It is not known whether a similar phenomenon occurs in response to temporal environmental variability. Interannual weather fluctuations may promote coexistence of competing species, if varying life history adaptations cause each species to have an advantage in some years (Levine and Rees 2004, Facelli et al. 2005). For example, a subset of species may be most fit in dry years, either because of physiological intolerance of higher moisture, or because dry conditions reduce the growth of their competitors and thus lead to increased light availability.

Mediterranean ecosystems are well known for year-to-year variability in environmental conditions (Noy-Meir 1973). It is possible that specialization on years when competitive pressure is reduced might contribute to diversity maintenance through time, much as specialization on harsh edaphic conditions appears to contribute to maintenance of diversity across space. Significant fluctuations in the relative abundance of species between years have been observed in annual grasslands plots in these climates (Heady 1958, Pitt and Heady 1978, Peco et al. 1998), but the relationship between these patterns and weather conditions is not well understood.

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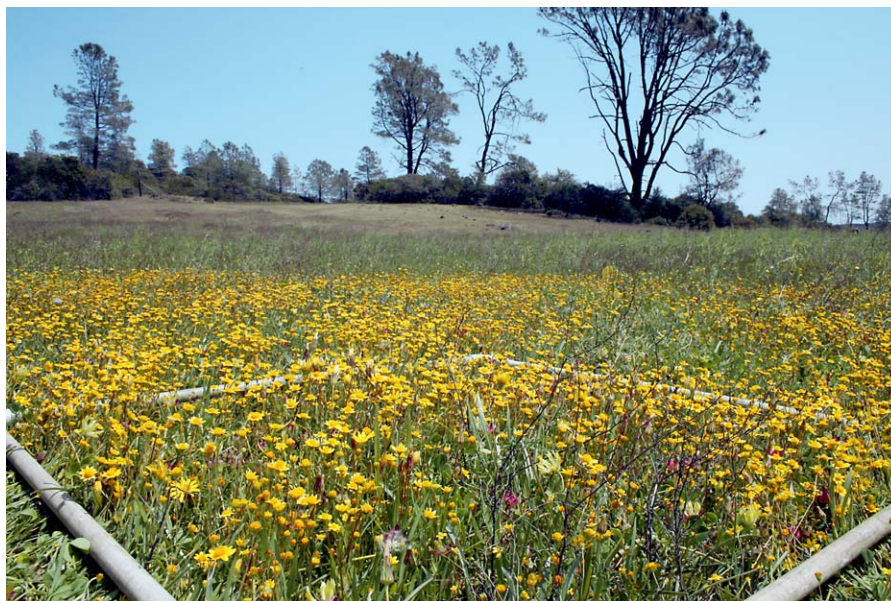


PLATE 1. Study plot dominated by the native annual forb *Lasthenia californica*. Photo credit: Brian Anacker.

In California grasslands, native annual forbs persist precariously among high densities of competitively dominant exotic annual grasses. Exotic grasses germinate early and grow rapidly, and can quickly overtop slower-growing species (Dyer and Rice 1999). They also form persistent dense thatch, which can affect plant growth in the next year (Bartolome et al. 1980). The presence of exotic thatch has been found to decrease the cover and diversity of shorter-statured forbs (Coleman and Levine 2007), and the decline of native annuals is commonly attributed to the successful invasion of these competitively dominant species (Biswell 1956, Murphy and Ehrlich 1988). Yet native forbs persist at low densities despite their apparent competitive disadvantage. Year-to-year weather variations are one explanation for this tenuous coexistence. The majority of exotic annual grasses seeds are thought to germinate every year, while many forbs form persistent seed banks, germinating only under favorable conditions (Young et al. 1981, Rice 1989). Cued germination could allow forbs to take advantage of temporal refuges and allow replenishment of seed banks in years where competition with exotic grasses is reduced (Levine and Rees 2004).

Empirical support for this hypothesis is equivocal. Observational accounts of “forb years” and “grass years” are consistent with the hypothesis that diversity is promoted by weather variation (Talbot et al. 1939, Pitt and Heady 1978), but other evidence suggests that the same types of weather (high rainfall and cool conditions) are favorable to both forbs and grasses (Seabloom et al. 2003).

Nestedness analysis is one way to test whether a community is characterized by broadly similar or differing responses to environmental variation. Nestedness occurs when species are lost in a consistent order,

such that more species-poor communities contain a subset of those species present in more species-rich ones (Atmar and Patterson 1993). When species respond differently to the major gradients associated with species richness (e.g., area, disturbance, resource availability), the community as a whole will not be nested (Urban 2004, Driscoll 2008). In contrast, when species differ quantitatively but not qualitatively in their responses to environmental conditions (i.e., some species are more vulnerable to resource-poor conditions, but all species are favored by the same type of conditions), communities will be nested. Species may be more likely to disappear under resource-poor conditions because they require a higher level of resources or have smaller population sizes.

When environmental conditions exhibit dramatic variability among years, communities containing few or no species specializing in “bad” years should exhibit temporal nestedness, whereas those containing many species that occur preferentially in species-poor years should not. Such patterns may differ among community types; in California grasslands, for example, temporal variation might be expected to be most important to diversity maintenance in grassland forbs on nonserpentine soils, where exotic grasses form dense stands. If forbs that specialize on good years have already been eliminated from these soils by competition from exotic grasses (Levine and Rees 2004), the remaining forbs might include many bad-year specialists, and the community would exhibit less temporal nestedness than the less-invaded grasslands on serpentine soils.

We used eight years of data at 71 grassland sites to investigate the following questions. First, do grassland plots show temporal nestedness? Second, does temporal nestedness occur equally in both native-rich serpentine

and exotic-dominated nonserpentine grasslands? Third, do native annual forbs, exotic annual forbs, and exotic annual grasses differ in their responses to spring environmental conditions? Finally, is the tendency of individual species to disappear in bad years a function of their spatial abundance, as predicted by metapopulation theory (Hanski 1982)?

METHODS

Study system and data

Species occurrence data were collected at 80 grassland sites within the University of California Donald and Silvia McLaughlin Reserve and nearby Fish and Game lands, located within Lake and Napa Counties, California, USA (Harrison 1999, Harrison et al. 2003; see Plate 1). Sites included both non-serpentine and serpentine soils. Serpentine soils typically have lower moisture, macronutrients and calcium, as well as higher heavy metal and magnesium content. They also support a higher diversity of native species, and are less dominated by exotic grasses. Each study site consists of five permanently marked 1-m² quadrats evenly spaced along a 40-m transect. Annual plant lists at each quadrat were compiled from two spring surveys/year timed to identify both early and late flowering species (Harrison et al. 2003); nine sites that burned during the study period were excluded from the analyses, leaving 71 sites as the basis for our analyses.

Temporal nestedness

We combined the data from each of the five quadrats at each site to create a single species list for each site in each of eight years. Nestedness was assessed by matrix temperature, a measure of the disorder in the observed matrices, where low temperatures indicate nestedness (Atmar and Patterson 1995). The most widely used test for nestedness randomizes presences of species among cells within the species–site (or species–year) matrix (Atmar and Patterson 1995), but this procedure is believed to be prone to Type I error (Rodriguez-Girones and Santamaria 2006, Ulrich and Gotelli 2007). We instead used a procedure in which the probability of a cell being occupied is the average of the fraction of presences for that row and column (Bascompte et al. 2003, Rodriguez-Girones and Santamaria 2006). Observed matrix temperatures were compared to those of randomly generated matrices permuted 1000 times, using the program Aninhado (Guimaraes and Guimaraes 2006).

We combined the 71 sites into a single study-wide assessment of temporal distribution patterns, using Stouffer's *Z* test (Whitlock 2005). The 71 *P* values (one per site) were transformed to their corresponding standard normal variates (Z_i). The sum of Z_i s divided by the square root of number of tests ($\sqrt{71}$) can then be compared to a standard normal distribution with mean $P = 0.50$ to evaluate the likelihood that real communities

are more or less nested than randomly permuted communities. Separate *Z* tests were also conducted on the 33 serpentine and 38 non-serpentine sites. Sites that were more nested than all 1000 randomized matrices were assigned *P* values of 0.0005 for the *Z* tests.

To ask whether the tendency of species to disappear in bad years was related to their spatial abundances, we calculated the order of each species' nestedness rank in a maximally packed matrix (a species–year matrix with rows and columns reordered based on the prevalence of species and diversity of years), converted this rank to a percentile to account for different richnesses between sites, averaged these percentiles for each species across all sites, and correlated the resulting values with the spatial abundances of species throughout the study area (total number of sites occupied). A negative correlation would indicate that more spatially abundant species are less likely to disappear species-poor years.

Species responses to yearly conditions

To test the relationship between species occurrences and yearly conditions, we defined favorable years in two ways, first using annual species richness, and second using weather data from sensors located within the study area (California Department of Water Resources, Knoxville Creek sensor; data *available online*).² Spring (March–May) mean daily rainfall and temperature were inversely correlated over the eight years of the study ($r = -0.76$), so we used principal components analysis (JMP version 4.1; SAS Institute, Cary, North Carolina, USA) to combine these into a single variable “PCAweather,” corresponding to increasing temperature and decreasing rainfall, which explained 88% of the variation in these two metrics and 59% of the interannual variation in total quadrat-level plant species diversity.

We used generalized mixed models to test the effect of species richness and PCAweather on species presence in 1-m² quadrats during the study period (PROC GLIMMIX, SAS version 9.1; SAS Institute 2003). Two separate analyses (using either species richness in the current year, or PCAweather in the current and previous years as the independent variable(s)) were conducted for each annual species that occurred in at least five sites for a total of 115 species. Weather in both the current and previous years were used in the weather analysis, as prior work suggests that temporal lags can be important in grassland systems (Levine and Rees 2004, Adler and Levine 2007). Sites and quadrats nested within sites were treated as random effects in all models. Any quadrat in which a species was either present or absent in all eight years were deleted prior to analysis.

To adjust for multiple comparisons, we used the Benjamini and Hochberg (1995) method to control the false discovery rate (FDR; proportion of erroneously rejected null hypotheses), rather than the more conser-

² (<http://cdec.water.ca.gov/>)

vative Bonferroni procedure, which controls the family-wise error rate (FWER; probability of obtaining one or more spurious rejections). Adjusted P values were calculated using the R multtest package (version 1.8.2; available online).³

Group responses to yearly conditions

We considered three definitions of “bad-year specialists” based on the above analyses: species that were more prevalent in species-poor years, hot dry years, or years following cool rainy years. We used Fisher’s exact tests to examine whether the number of bad-year specialists differed between grasses and forbs, or native vs. exotic forbs (R, version 2.3.1; see footnote 3). The study site included only one native annual grass, which was not used in these comparisons. We also used mixed models (PROC MIXED, SAS Institute 2003) to test the effects of weather in the current and previous years on richness of each of the three groups (native annual forbs, exotic annual forbs, and exotic annual grasses) at the quadrat scale. A separate analysis was run for each group, with PCAweather in the current and previous years treated as fixed effects and site and quadrat nested within site included as random effects.

RESULTS

Temporal nestedness

All sites had lower matrix temperatures than their corresponding randomized matrices (Fig. 1), indicating that species distribution patterns through time were significantly nested (Stouffer’s $Z = -20.68$, $P < 0.0001$). Nonserpentine sites were no more nested than serpentine sites (Fig. 1). Species that were more spatially abundant (occupied a greater number of sites) were less likely to disappear in bad years (Pearson $r = -0.52$, $P < 0.0001$).

Species responses to yearly conditions

Most species (57) were found in significantly more quadrats during species-rich years and only two were found in significantly more quadrats during species-poor years. Responses to weather were similar; 36 species were found in more quadrats during cool rainy years and only three were found in more quadrats during hot dry years (Appendix). Significant responses to weather conditions the previous year were equally common but in the opposite direction; 38 species were found in significantly more quadrats following hot dry years and only nine species were found in more quadrats following cool rainy years. The statistical model for one species (*Vulpia myuros*) failed to converge for the weather analysis.

Group responses to yearly conditions

There were no significant differences between grasses and forbs in the proportion of bad-year specialists

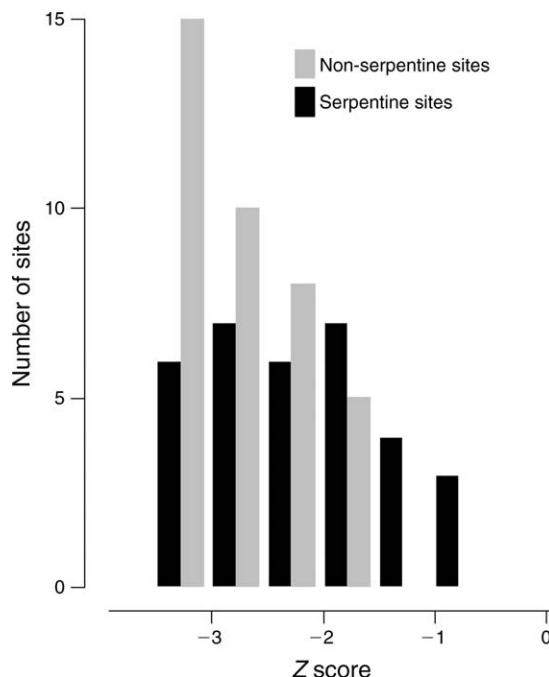


FIG. 1. Z scores for temporal nestedness by soil type at the 71 sites. Z scores less than 0 indicate that the nestedness of observed site data was greater than the median nestedness of randomized matrices; Z scores less than -2.0 indicate that temporal nestedness at an individual site was significant as compared to randomized matrices at the $P < 0.05$ level.

(Fisher’s exact test, species-poor years, $P = 1.0$; hot dry years, $P = 1.0$; years following cool rainy years, $P = 0.60$). There were also no significant differences between native and exotic forbs in the proportion of bad-year specialists (Fisher’s exact test, species-poor years, $P = 1.0$; hot dry years, $P = 0.16$; years following cool rainy years, $P = 0.22$).

Quadrat-level richness of all three response groups was significantly greater in years that were cool and wet and that followed warm dry years ($P < 0.0001$ for all six tests). Positive responses to cool wet years were strongest for native forbs (0.30 ± 0.03 , coefficient \pm SE for effect of current year’s weather PCA on quadrat-level richness), intermediate for exotic forbs (0.16 ± 0.02), and weakest for exotic grasses (0.10 ± 0.01). Similarly, negative responses to cool wet conditions in the previous year were strongest for native annual forbs (-33 ± 0.03), intermediate for exotic forbs (-0.11 ± 0.02) and weakest for exotic grasses (-0.06 ± 0.02).

DISCUSSION

As noted by Preston (1960), patterns of diversity in space are often repeated over time; for example, a number of recent studies have documented a species–time relationship resembling the better-known species–area relationship (White et al. 2006). Any factor that leads to the assembly or disassembly of communities over time in a consistent order will lead to temporal

³ www.r-project.org

nestedness (Wright and Reeves 1992), and this may have important implications for coexistence and the maintenance of diversity. However, despite hundreds of studies examining spatial nestedness patterns, to our knowledge temporal nestedness has previously been examined in only a single two-year study. Taylor and Warren (2001) found that fish assemblages in streams with more variable flow regimes had higher extinction rates, and because species were lost in a consistent order, more variable streams exhibited stronger temporal nestedness. Our data likewise illustrate how environmental variation can generate communities that are nested across time. Many species are most prevalent in climatically good years and very few are most prevalent in bad years. In the absence of bad-year specialists, common ("core") species are always present, while rare ("satellite") species disappear in bad years, largely as a function of their relative abundances (Hanski 1982).

A commonly held belief states that weather fluctuations lead to distinct "forb" vs. "grass" years in Mediterranean grasslands, and that specialization on particular weather conditions is an important component of species coexistence in these systems (Talbot et al. 1939, Heady 1958, Pitt and Heady 1978). However, these studies examined relative cover of species or response groups, which imposes a zero sum game in which any increase in proportional cover of one species or response group necessarily leads to a decrease in another group. By examining total rather than relative data, we found no evidence for the temporal niche-partitioning that had been previously hypothesized. Most species whose abundance varied among years had synchronous dynamics, with increased frequency in both cool wet years and years following hot dry years. Our interpretation agrees with a recent meta-analysis of community dynamics across time, which concluded that compensatory dynamics among species are rare, and that weather conditions are a more common driver of fluctuating abundance than competition (Houlahan et al. 2007).

Negative lag effects of the previous year's conditions are not unique to our system. Adler and Levine (2007) found similar patterns in a 36-year study of species composition in Kansas grasslands, and attributed the positive effect of past drought on diversity to breaking seed dormancy and increased seed germination in the subsequent year. In a simulation model, Levine and Rees (2004) illustrated how forbs could persist in invaded grasslands by germinating the majority of their seeds in low-competition, resource-rich, wet years following dry years. This strategy could enable them to escape competition from exotic annual grasses, whose abundance might be seed-limited in years following dry years. However, we found that exotic annual grass diversity increases under the same conditions that forb diversity increases, suggesting that the annual exotic grass seed bank is sufficient to permit species to take advantage of favorable conditions when they occur.

Good years may still provide windows of opportunity for forb growth and seed bank replenishment; even if both grasses and forbs are more common during good years, the net suppressive effect of grasses on forbs may be reduced in these years due to greater overall resource availability.

Despite widespread theoretical interest, the effects of temporal variability on species interactions and community membership are only beginning to be evaluated empirically (Colleen 2008). In our community-wide study, the best years for both exotic grasses and native and exotic forbs were those in which cool temperatures and abundant rainfall occurred in the current year, and hot and dry conditions occurred in the previous year. Recent theoretical work (Adler and Drake 2008), concluded that such positive correlations in species' responses to environmental conditions generally reduce the likelihood of long-term coexistence. However, these communities are also those for which, a relatively high degree of temporal environmental variation, such as that which is predicted to occur under most climate change scenarios, may be especially beneficial to species coexistence. Further empirical tests are necessary to understand the precise ramifications of increases in year to year environmental variation in individual systems.

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LITERATURE CITED

- Adler, P. B., and J. M. Drake. 2008. Environmental variation, stochastic extinction, and competitive coexistence. *American Naturalist* 172:E186–E195.
- Adler, P. B., J. HilleRisLambers, P. C. Kyriakidis, Q. F. Guan, and J. M. Levine. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences (USA)* 103:12793–12798.
- Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. *Oikos* 116:221–232.
- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6: 1109–1122.
- Atmar, W., and B. D. Patterson. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382.
- Atmar, W., and B. D. Patterson. 1995. The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices. AICS Research, University Park, New Mexico and The Field Museum, Chicago, Illinois, USA.
- Bartolome, J. W., M. C. Stroud, and H. F. Heady. 1980. Influence of natural mulch on forage production on differing California annual range sites. *Journal of Range Management* 33:4–8.
- Bascompte, J., P. Jordano, C. J. Melian, and J. M. Olesen. 2003. The nested assembly of plant–animal mutualistic

- networks. *Proceedings of the National Academy of Sciences (USA)* 100:9383–9387.
- 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-Methodological* 57:289–300.
- Biswell, H. H. 1956. Ecology of California grasslands. *Journal of Range Management* 9:19–24.
- Chesson, P., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology and Evolution* 4:293–298.
- Coleman, H. M., and J. M. Levine. 2007. Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. *Biological Invasions* 9:65–71.
- Colleen, K. K. 2008. Niche picking: the importance of being temporal. *New Phytologist* 180:745–747.
- Driscoll, D. A. 2008. The frequency of metapopulations, metacommunities and nestedness in a fragmented landscape. *Oikos* 117:297–309.
- Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80:2697–2710.
- Facelli, J. M., P. Chesson, and N. Barnes. 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. *Ecology* 86:2998–3006.
- Guimaraes, P. R., and P. Guimaraes. 2006. Improving the analyses of nestedness for large sets of matrices. *Environmental Modelling and Software* 21:1512–1513.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210–221.
- Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. *Ecology* 80:70–80.
- Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* 17:837–845.
- Heady, H. F. 1958. Vegetation changes in the California annual type. *Ecology* 39:402–416.
- Hobbs, R. J., and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* 72:59–68.
- Houlahan, J. E., et al. 2007. Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences (USA)* 104:3273–3277.
- 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 Californian serpentine grassland. *Ecology* 71:478–491.
- Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* 95:137–145.
- Kruckeberg, A. R. 1954. The ecology of serpentine soils III. Plant species in relation to serpentine soils. *Ecology* 35:267–275.
- Levine, J. M., and M. Rees. 2004. Effects of temporal variability on rare plant persistence in annual systems. *American Naturalist* 164:350–363.
- Murphy, D. D., and P. R. Ehrlich. 1988. Conservation biology of California's remnant native grasslands. Pages 201–212 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic, Dordrecht, The Netherlands.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25–51.
- Pake, C. E., and D. L. Venable. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* 77:1427–1435.
- Peco, B., T. Espigares, and C. Levassor. 1998. Trends and fluctuations in species abundance in Mediterranean annual pastures. *Applied Vegetation Science* 1:21–28.
- Pitt, M. D., and H. F. Heady. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59:336–350.
- Preston, F. W. 1960. Time and space and the variation of species. *Ecology* 41:611–627.
- Reynolds, H. L., B. A. Hungate, F. S. Chapin, and C. M. Dantonio. 1997. Soil heterogeneity and plant competition in an annual grassland. *Ecology* 78:2076–2090.
- Rice, K. J. 1989. Impact of seedbanks on grassland community structure and population dynamics. Pages 212–230 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Ecology of soil seed banks*. Academic Press, San Diego, California, USA.
- Rodriguez-Girones, M. A., and L. Santamaria. 2006. A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography* 33:924–935.
- SAS Institute. 2003. SAS version 9.2. SAS Institute, Cary, North Carolina, USA.
- Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications* 13:575–592.
- Talbot, M. W., H. H. Biswell, and A. L. Hormay. 1939. Fluctuations in the annual vegetation of California. *Ecology* 20:394–402.
- Taylor, C. M., and M. L. Warren. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology* 82:2320–2330.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.
- Ulrich, W., and N. J. Gotelli. 2007. Null model analysis of species nestedness patterns. *Ecology* 88:1824–1831.
- Urban, D. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology* 85:2971–2978.
- White, E. P., P. B. Adler, W. K. Lauenroth, R. A. Gill, D. Greenberg, D. M. Kaufman, A. Rassweiler, J. A. Rusak, M. D. Smith, J. R. Steinbeck, R. B. Waide, and J. Yao. 2006. A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos* 112:185–195.
- Whitlock, M. C. 2005. Combining probability from independent tests: the weighted Z-method is superior to Fisher's approach. *Journal of Evolutionary Biology* 18:1368–1373.
- Wright, D. H., and J. H. Reeves. 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia* 92:416–428.
- Young, J. A., R. A. Evans, C. A. Raguse, and J. R. Larson. 1981. Germinable seeds and the periodicity of germination in annual grasslands. *Hilgardia* 49:1–37.

APPENDIX

Response of individual species to richness or weather (principal components analysis of spring temperature and rainfall in the current and previous years) (*Ecological Archives* E090-102-A1).