Resistance and Resilience of Vernal Pool Vegetation

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ABSTRACT. Typically, vegetation is described as either resistant or resilient to stress. Vernal pool vegetation, however, is exceptional, being both resistant and resilient. Resistance of this unique vegetation type was tested by repeatedly sampling 80 vernal pools in the Sacramento Valley, California over a period of 5 years. Pools were quantified using whole-pool releves and data were analyzed by Twinspan, DCA, and standard phytosociological table methods. Resistance (calculated as "persistence," which is the proportion of visits to a given pool showing the presence of a given species) for diagnostic taxa at the class level ranged from 41% to 99%, averaging 72% for 15 taxa. Calculated persistence values were lower for diagnostic species at the association level, averaging 57% for 15 taxa that represent 11 distinct plant associations. If selected diagnostic taxa display high persistence values, then the resistance of vernal pool communities could be described as high, despite significant variation in annual rainfall. Resilience was tested by sampling 13 created (7-8 years old) and 13 natural pools at Wurlitzer Ranch in the Sacramento Valley. At Wurlitzer, cluster analysis revealed that there was no statistically significant difference between defined plant communities occupying created pools and plant communities in natural pools. This finding suggests that vernal pool vegetation can be resilient, able to reform itself into the pre-disturbance composition within half a dozen years, though these results hinge on localized mitigation undertaken with exceptional care and planning.

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INTRODUCTION

Our objective in this work was to quantify the degree of stability that is characteristic of plant communities in vernal pool habitats.

Among the many ways that plant communities can be described, quantified and compared is their stability in the face of stress, disturbance, or perturbation. Leps et al. (1982) and Leps (2003) have suggested that stability can be measured in terms of the presence of temporal variation, directional (successional) change, resilience and resistance. Leuschner (2003) described resistance as "…the speed at which an ecosystem returns to its initial [pre-disturbed] state. Resilient systems can be altered relatively easily, but [they] return to their pre-disturbance structure and function rapidly… Ecosystems that show relatively small changes upon disturbance are said to be resistant."

Resilient vegetation is characteristically herbaceous and offers little resistance to stress because small, herbaceous plants do not create a buffered microenvironment. In contrast, resistant vegetation is characteristically woody and thus exhibits low resilience, because it takes a long time for woody vegetation to recover its pre-stress biomass and physiognomy. Thus, a common dictum among systems ecologists is that a given vegetation or community type can be either resistant or resilient, but not both.

The question of how resistant and resilient vernal pool vegetation is to stress and disturbance is very important, because the answer gets to the very base of how to classify these annual-dominated community types. For half a dozen years, Barbour and his colleagues (Barbour et al., 2003, 2005; Barbour and Witham, 2004) have been creating a phytosociological syntaxonomy of vernal pool classes, orders, alliances and associations. These classification units are defined and named after one or more diagnostic species. If the diagnostic species are not resistant to such stresses as annual fluctuations in precipitation, then their abundance and even presence/absence will vary every year and so will the community type(s) that they represent. Classification systems should be robust, meaning that a given forest stand, patch of grassland, or hectare of chaparral can be keyed out to the same classification unit by different samplers at different times. Is the system used by Barbour and others sufficiently robust?

Another reason for quantifying resistance and resilience for vernal pool vegetation has to do with conservation and restoration. The “taking” of a vernal pool (i.e., the destruction of it) is the ultimate disturbance. The notion that destroyed pools can be recreated (constructed) by physically digging a new pool and seeding it with topsoil from the destroyed pool is founded on the premise that vernal pool vegetation is resilient, able in a few years to recover and reconstitute itself from stand-destroying disturbance. During the past 20 years, mitigation for the taking of pools has often included vernal pool construction, either on-site or off-site. The number of created pools and their area are high despite the fact that few long-term studies have evaluated this kind of mitigation. Those few studies of created pools that have been published (De Weese, 1998; Ferren et al., 1998; Black and Zedler, 1998) compared the flora of created pools to a generic state-wide list of vernal pool taxa. They did not compare the recovered flora with the composition of natural communities known to occupy similar habitats in the local area. Thus, vernal pool creation is a highly controversial process that has been frequently criticized for its inability to adequately and faithfully replace the original, predisturbance ecosystem (Ferren and Gevirtz, 1990; Leidy and White, 1998).

In order to quantify the resistance and resilience of vernal pool communities, we conducted two studies. First, we examined a data set for species presence and abundance collected from 156 vernal pools that had been annually sampled for 5 years. By quantifying the persistence of diagnostic species over the course of so many years that varied significantly in annual precipitation, we were able to measure the resistance of vernal pool vegetation (Buck, 2005). Then, by comparing the species assemblages in 14 created pools (8 years post-construction) to those in 13 adjacent natural pools at the Wurlitzer Ranch in the Sacramento Valley, we were able to measure the resilience of vernal pool vegetation (Starr, 2004).

METHODS

Test of Resistance

All field data for the resistance testing were provided by Carol Witham. She sampled 10 vernal pool complexes along a 300-km-long section of a proposed PGT/PGE gas pipeline corridor that largely ran through the Sacramento Valley, from Fall River Mills in Shasta County to Jepson Prairie in Solano County, California. A total of 156 vernal pools were permanently located within those complexes, but off the proposed pipeline. Eighty of the 156 pools were consistently visited twice each year (early spring and late spring) during the 5-year-period of 1994-1998. This subset of pools included seven vernal pool complexes, from Red Bluff in Tehama County to Wilson Creek in Glenn County (Table 1).

During each visit, the absolute percent cover for every species in each pool was recorded. The pool area sampled was defined as the area within the high water mark, or the zone where the vegetation composition shifts in dominance from wetland to upland plant species. In general, the width of this zone is < 1 m. Daily precipitation for each vernal pool complex was obtained from data available at the University of California’s Integrated Pest Management Program website (Statewide IPM Program, 2004). Weather stations used for these analyses include Gerber, Hastings, McArthur, Orland, Red Bluff and Vacaville. Precipitation totals were averaged and partitioned into seasonal components for analysis (Sep-Nov, Dec-Feb, Mar-May).

Statistical analyses were performed at the whole-pool scale and at the vernal pool complex scale. All 80 pools fell within a single vernal pool region, the Northwestern Sacramento Valley (Keeler-Wolf et al., 1998). The complete data set included 800 samples and 187 plant taxa. We used repeated measures analysis of variance, which takes into account co-variation within repeatedly sampled pools (Sokal and Rohlf, 1995), and linear regression to examine the relationship between precipitation and species richness.

Resistance for any given species was quantified as temporal persistence (P), calculated as:

$$P = \frac{100\ (\sum a/b)}{n}$$

where a = the number of occurrences of a species in one pool over time, b = the number of sample periods for that pool and n = the number of pools in which a particular taxon was present at least once during the 5 years of observation. Persistence is expressed as a percentage. It represents the average probability of finding a species in a pool in consecutive surveys over time.

TABLE 1. Location and elevation of seven vernal pool complexes, the number of pools within each that had been sampled twice a year for 5 years and average species richness per site for the entire period of observation. Sites are arranged from north to south.

Site name	County	Elevation (m)	No. pools	Richness
Red Bluff	Tehama	88	8	37
Coyote Creek	Tehama	82	1	45
Truckee Creek	Tehama	95	12	38
Thomes Creek	Tehama	99	18	40
Corning	Tehama	106	24	38
Hall-Stony Creek	Tehama	103	15	31
Wilson Creek	Glenn	77	2	34

A time lag analysis introduced by Collins et al. (2000) was used to measure the pattern and degree of variability within an individual vernal pool association. The analysis compares a Euclidean distance matrix along the square-root-transformation of time intervals, permitting a regression of temporal trends to be calculated.

Detrended correspondence analysis (DCA) for all pools within a single complex allowed the general pattern of species composition change within a pool to be tracked over time (McCune and Grace, 2002). DCA ordinations were run for three randomly selected complexes: Redding, Hall-Stony Creek and Truckee Creek.

A Mantel test was used to detect relationships between distances with 1000 runs of randomized data, for a Monte Carlo test of significance (McCune and Grace, 2002). Tests were run comparing the similarities of species composition among pools to eight variables: geographic distance apart (along the pipeline), habitat, year, season, annual precipitation and the three seasonal components of annual precipitation. Data were analyzed with the software package PC-ORD for Windows, Version 4.27 (McCune and Mefford, 1999).

Test of Resilience

Vernal pools examined were located in Wurlitzer Ranch, a 24-ha-preserve 10 km north of Chico in the Sacramento Valley. The site supports approximately 100 vernal pools, 60 of which were created and 40 are natural. Following a two-year period of preparation, planning and design, the pools were constructed over a span of three summers (1994-1996) and inoculated with onsite vernal pool topsoil or with offsite topsoil from pools a few kilometers to the south. All pools are on soils from Red Bluff and Modesto-Riverbank formations. At the time of our sampling, the created pools had been established for 7-8 years. During that period, the pools were protected from grazing by cattle, but some had undergone prescribed burning.

In April and May of 2003, a subset of the 100 pools was sampled: 10 constructed and burned, 3 constructed and unburned, 5 natural and burned and 8 natural and unburned, totaling 26 pools. Within each pool, a sample was taken for each visually distinctive community type, resulting in a total of 84 plots, each 10 square meters in area. The within-pool plots contained 35 plots of constructed and unburned vegetation, 10 of constructed and burned vegetation, 17 of natural and burned vegetation and 22 of natural and unburned vegetation.

Within each homogeneous and visually distinct patch, a single plot (releve) was subjectively located, and percent cover noted for every species present. In addition, the whole pool was surveyed to include any species missed in pool releves (an average of 3 releves per pool were sampled). Relative depth measurements were taken for each releve, by means of a laser level. The zero elevation line was defined as that narrow zone of high water (usually < 1 m), where vegetation shifts in dominance from wetland to upland plant species.

Releve data were entered in Turboveg format (Hennekens and Schaminee, 2001) and exported to Excel for formatting and analysis. Two statistical programs were used for community analysis: PC-ORD and Excel. PC-ORD was used for analyses involving vegetation cover values and community composition, while Excel was used for linear regression, chi-square tests, and t-tests of variables associated with the releves. Agglomerative hierarchical cluster analysis was also applied, similarity calculated by the Sorensen formula and the linkage method was flexible beta (-0.25; McCune and Grace, 2002). Multi-response permutation procedures (MRPP) were used to test for differences between cluster groups. Indicator species analysis (ISA; McCune and Mefford, 1999) was used to evaluate species for diagnostic value in defining syntaxonomic units. Indicator values can range from zero (no indication) to 100 (perfect indication). Whole-pool and within-pool data sets were analyzed independently.

Non-metric multidimensional scaling (NMS; McCune and Mefford, 1999) was used to ordinate sample units. It was run using Sorensen similarity measures, with 40 runs of real data and 50 runs of randomized data, for a Monte Carlo test of significance. Canonical Correspondence Analysis (CCA; McCune and Mefford, 1999) was used to discern the correlative strength of environmental variables with cluster types.

Regression analysis and t-tests were used to test the difference between species richness, species ratios and Shannon-Weiner diversity indices between groupings of whole pool and within-pool data sets. Chi-square analysis was used to test the difference in treatments among groups derived from cluster analysis.

RESULTS

Test of Resistance

Precipitation varied over the 5 years from a site-average low in 1993-1994 of 420 mm to an average high in 1997-1998 of 1050 mm (Figure 1). The average pool species richness over all sites rose and fell with rainfall, from a low of 33 species in 1993-1994 to 41 in 1997-1998 (Figure 2). The correlation between annual rainfall and richness was significantly positive at $p < 0.0001$. Partitioning of annual precipitation into seasonal components showed that winter and spring (but not fall) seasons were significantly correlated with species richness ($p < 0.0001$). Total plant cover also was positively correlated with annual precipitation, as represented by data from a single pool in the Coyote Creek complex: a low of 40-60% in the two driest years and a high of 70-90% in the two wettest years.

The magnitude of change in abundance or presence/absence of individual species was highly variable. Diagnostic species at the class level in general had higher persistence than those at the order level, and those at the association level were the lowest (73%, 63% and 51%, respectively; Table 2). The diagnostic species used in this analysis remain preliminary and will be refined as the classification is completed. Eleven listed rare taxa had the lowest persistence of all, averaging 40% (Table 3), but none of these had any diagnostic value for syntaxonomic units at any level. Examples of extremely low persistence include: *Astragalus tener* var. *tener*, which occurred only once (and then at < 1% cover) in the five years of observations; *Juncus leiospermus* var. *leiospermus* was found in one pool for the first two years, then was not detected again; *Legenere limosa* blinked in and out of four pools; and *Navarretia cotulifolia*, *Paronychia ahartii* and *Pogogyne floribunda* each occurred only three times.

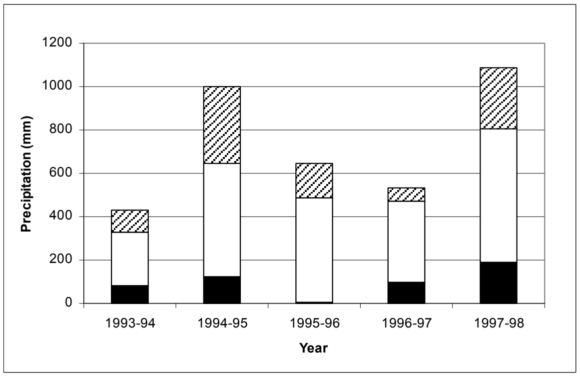

FIGURE 1. Average precipitation (mm) across ten vernal pool sites for 5 years. Total rainfall is partitioned into three seasonal components. From the bottom of each bar to the top they are: Sep-Nov, Dec-Feb and Mar-May. From Buck (2005).

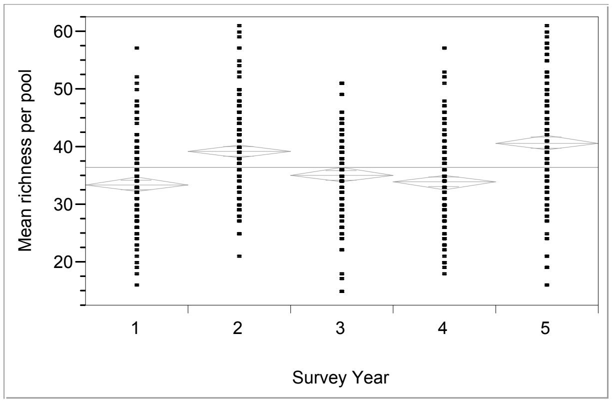

FIGURE 2. Mean species richness per pool over 5 years for 80 pools. Diamonds above the grand mean line are significantly different from those below the line. From Buck (2005).

The species identified by Barbour et al. (2003, 2005) as diagnostic elements for syntaxonomic units (class, order, alliance and association) displayed a range of persistence values. For example, at the class level (*Downingio-Lasthenietea*), six of 15 diagnostic taxa

TABLE 2. Temporal persistence (P, in percent) for diagnostic species of the class *Downingio bicornutae-Lasthenietea fremontii*, three preliminary orders within it and 11 preliminary associations within those orders. The syntaxa and their diagnostic species were defined by Barbour et al. (2003, 2005).

Diagnostic Species Name	Syntaxon	P (%)
Eryngium vaseyi	Class	99
Lasthenia fremontii	Class	95
Deschampsia danthonioides	Class	94
Pogogyne zizyphoroides	Class	92
Navarretia leucocephala ssp. *leucocephala*	Class	91
Psilocarphus brevissimus var. *brevissimus*	Class	90
Juncus bufonius var. *occidentalis*	Class	79
Crassula aquatica	Class	76
Plagiobothrys stipitatus var. *micranthus*	Class	75
Alopecurus saccatus	Class	70
Veronica peregrina ssp. *xalapensis*	Class	54
Callitriche marginata	Class	50
Isoetes orcuttii	Class	45
Pilularia americana	Class	42
Eleocharis acicularis var. *acicularis*	Class	41
Eleocharis macrostachya	Order 1	77
Lasthenia glaberrima	Order 1	60
Trifolium depauperatum	Order 2	86
Erodium botrys	Order 2	85
Hypochaeris glabra	Order 2	81
Limnanthes douglasii ssp. *rosea*	Order 2	76
Plagiobothrys greenei	Order 2	74
Hemizonia fitchii	Order 2	73
Blennosperma nanum var. *nanum*	Order 2	71
Lepidium nitidum var. *nitidum*	Order 2	65
Bromus hordeaceus	Order 2	63
Cicendia quadrangularis	Order 2	60
Vulpia bromoides	Order 2	51
Downingia insignis	Order 3	100
Cressa truxillensis	Order 3	58
Plantago elongata	Order 3	49
Cotula coronopifolia	Order 3	48
Myosurus minimus	Order 3	32
Crypsis schoenoides	Order 3	15
Pleuropogon californicus	Assn 2, 8	78
Isoetes howellii	Assn 4	31
Castilleja campestris	Assn 6	69
Mimulus tricolor	Assn 9	73
Hesperevax caulescens	Assn 9	53
Psilocarphus oregonus	Assn 9, 10	51
Holocarpha virgata ssp. *virgata*	Assn 9	44
Trifolium gracilentum var. *gracilentum*	Assn 9	43
Cerastium glomeratum	Assn 9	39
Trifolium variegatum	Assn 9. 13, 14	29
Medicago polymorpha	Assn 9	25
Achyrachaena mollis	Assn 10, 11, 12	76
Triphysaria eriantha ssp. *eriantha*	Assn 10, 11, 12	74
Layia fremontii	Assn 10, 11, 12	72
Phalaris lemmonii	Assn 10	70
Microseris acuminata	Assn 10, 11, 12	61
Psilocarphus tenellus var. *globiferus*	Assn 10	46
Taeniatherum caput-medusae	Assn 10, 11, 12	46
Lasthenia californica	Assn 10, 11, 12	41
Lupinus bicolor	Assn 11	43
Trifolium willdenovii	Assn 11	38
Navarretia tagetina	Assn 12	68
Chlorogalum angustifolium	Assn 12	64
Plantago erecta	Assn 12	59
Plagiobothrys austiniae	Assn 12	43
Vulpia microstachys	Assn 12	40
Navarretia pubescens	Assn 12	20
Montia fontana	Assn 13, 14	36
Mimulus guttatus	Assn 14	33
Frankenia salina	Assn 16	75

had persistence values > 90%, while five had values < 70%. If the number of diagnostic taxa were selectively reduced to those with relatively high persistence, more than ten species could be retained that had persistence > 70%. Similarly, the diagnostic taxa for two out of three orders could be selectively refined in number to include two to seven each that had persistence values > 70%. Within a preliminary order for saline vernal pools of the Central Valley, there was just one diagnostic species with > 70% persistence (but in this case, that single diagnostic species—*Downingia insignis*—had 100% persistence).

Some of the preliminary associations appeared to be problematic, because few or no diagnostic taxa existed with a high persistence. A few of these associations were poorly represented by the flora of the 80 study pools; for example, the Central Valley associations 1, 3, 5, 7 and 15 were not present in these pools (numbers refer to preliminarily defined associations, to be named upon completion of all analyses). Associations 2, 4, 6, 8 and 16 each have many diagnostic taxa, but only one taxon for each was found within the PGE study pools and releves; only two diagnostic taxa each for associations 13 and 14 were encountered. In contrast, many diagnostic taxa for associations 9, 10, 11 and 12 were present in the releves, and the degree of their persistence was mixed: association 9 had one of its eight diagnostic taxa with a P value 70% or higher; associations 10, 11 and 12 had four diagnostic taxa out of 16 with high P values; and associations 2, 8 and 16 had one

TABLE 3. Listed vernal pool taxa recognized by the California Native Plant Society (2001) that were detected among the 80 vernal pools over the 5 year period of time. Persistence (P) is expressed as a percent.

Species	Status	P
Juncus leiospermus var. *leiospermus*	1B	63
Downingia pusilla	2	61
Psilocarphus brevissimus var. *multiflorus*	4	61
Hesperevax caulescens	4	53
Navarretia cotulifolia	4	43
Pogogyne floribunda	1B	43
Navarretia leucocephala ssp. *bakeri*	1B	37
Legenere limosa	1B	29
Paronychia ahartii	1B	25
Navarretia heterandra	4	14
Astragalus tener var. *tener*	IB	14

diagnostic taxon each (out of only one each encountered) with a high P value.

The degree of correlation between species composition in a given releve and abiotic factors over time were statistically significant for some factors, but in every case the Mantel statistic (r) was low, meaning that dissimilarity over time was only weakly related to measured environmental factors (Table 4). Surprisingly, annual precipitation was not significantly related to changes in species composition. Geographic distance had more to do with floristic differences than did climate: the species composition of pools far apart are much more different, at any one time or over time, than the species composition of nearby pools or of releves within pools

DCA ordinations, overlaid with vectors that track pool composition over time, showed only stochastic changes in species composition. There was no evidence for cumulative, directional change. That is, the pools and releves exhibited random change on an annual basis, but not successional change.

Test of Resilience

A dendrogram for all 115 species encountered, created by agglomerative hierarchical cluster analysis (Figure 3), showed that the first division did not separate by any of the four treatments. Both primary clusters consisted of both natural and constructed and included burned and unburned pools. No significant difference between groups was found by a chi-square analysis. Examination of abiotic releve traits showed that Groups 1 and 2 were separated by their relative depth below the fill line, group 1 releves being lower (and hence inundated for a longer time) than group 2 releves.

TABLE 4. Mantel statistic (r) and significance of correlations between species composition within releves and abiotic variables. Asterisk signifies non-significance.

Variable	r	p-value
Habitat (landform)	0.518	0.001
Location along pipeline	0.409	0.001
Year	0.113	0.001
Season (early vs. late)	0.025	0.001
Annual precipitation	0.014	0.075*
Fall precipitation	-0.027	0.050*
Winter precipitation	0.108	0.001
Spring precipitation	0.121	0.001

The second division, within group 1, separated a cluster of unburned pools (that contained both constructed and natural pools) from unburned pools. The second division in group 2 produced three clusters: one of predominantly natural pools (burned and unburned); a second with a heterogeneous mix of treated pools; and a third with only constructed and burned pools. However, this latter grouping may be due to the close spatial proximity of those pools. Ordination of whole-pool data by NMS (Figure 4) produced a similar picture and conclusion: treatments were not tightly clustered or cleanly separated from one another, indicating the lack of community distinction.

We used indicator species analysis to search for species that might differentiate the four treatments, but only found 9 of the 115 species to have significant indicator values ($p < 0.05$): *Epilobium pygmaeum*, *Eremocarpus setigerus*, *Downingia ornatissima*, *Lythrum hyssopifolium*, *Mimulus latidens*, and *Veronica peregrina* were indicators of constructed-burned pools; *Allium amplectens* was an indicator of constructed-unburned pools; *Alopecurus saccatus* and *Brodiaea purdyi* were indicators of natural-burned pools; and *Achyrachaena mollis* was an indicator of natural-unburned pools. The influence of these nine taxa was not sufficient to separate treatments in cluster analysis or ordination.

DISCUSSION

In sum, vernal pool vegetation does exhibit resistance to annual variations in climate stress, but the degree of resistance increases with the scale of the syntaxon examined. Many of the diagnostic species for classes and orders show high persistence, such that the probability of finding them in the same pool,

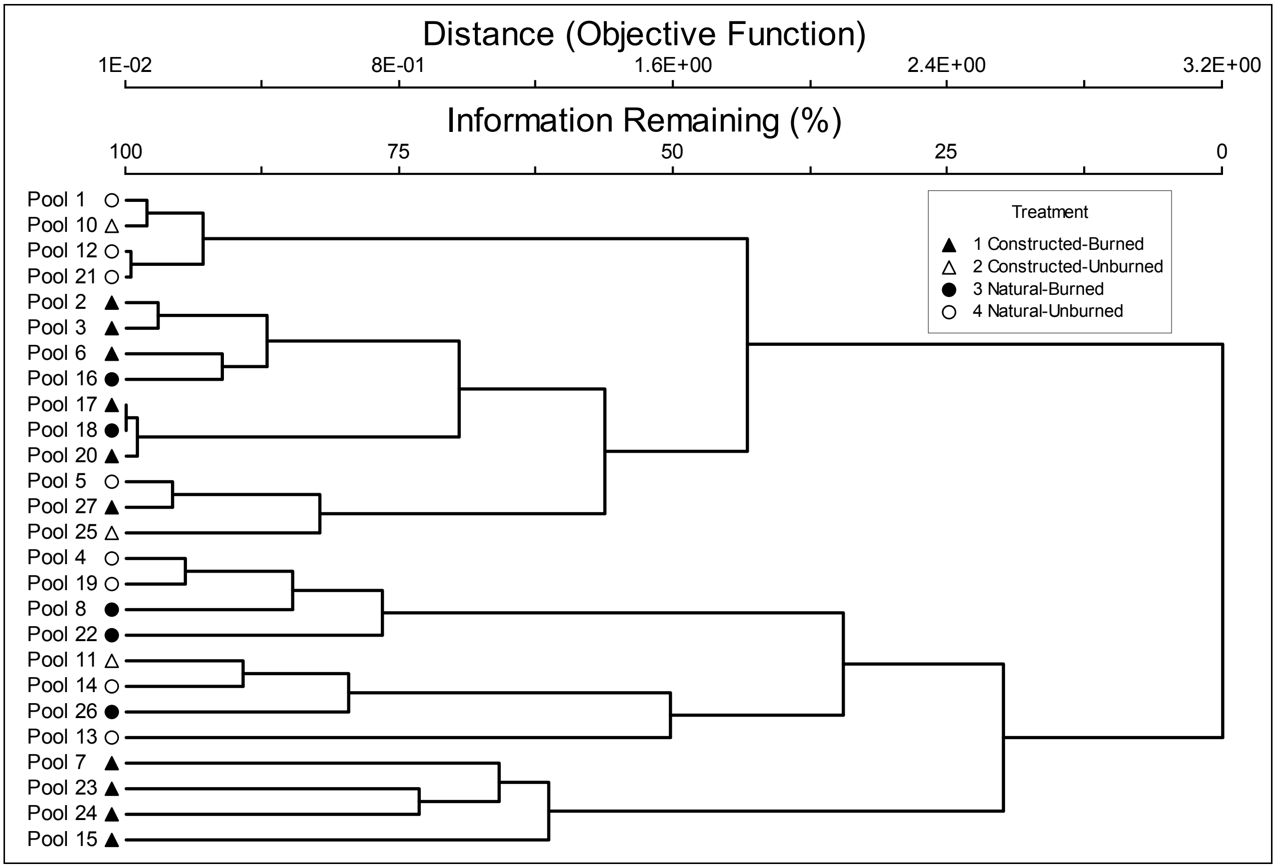

FIGURE 3. Dendrogram for all 115 species of the whole-pool data set, created by agglomerative hierarchical cluster analysis. From Starr (2004).

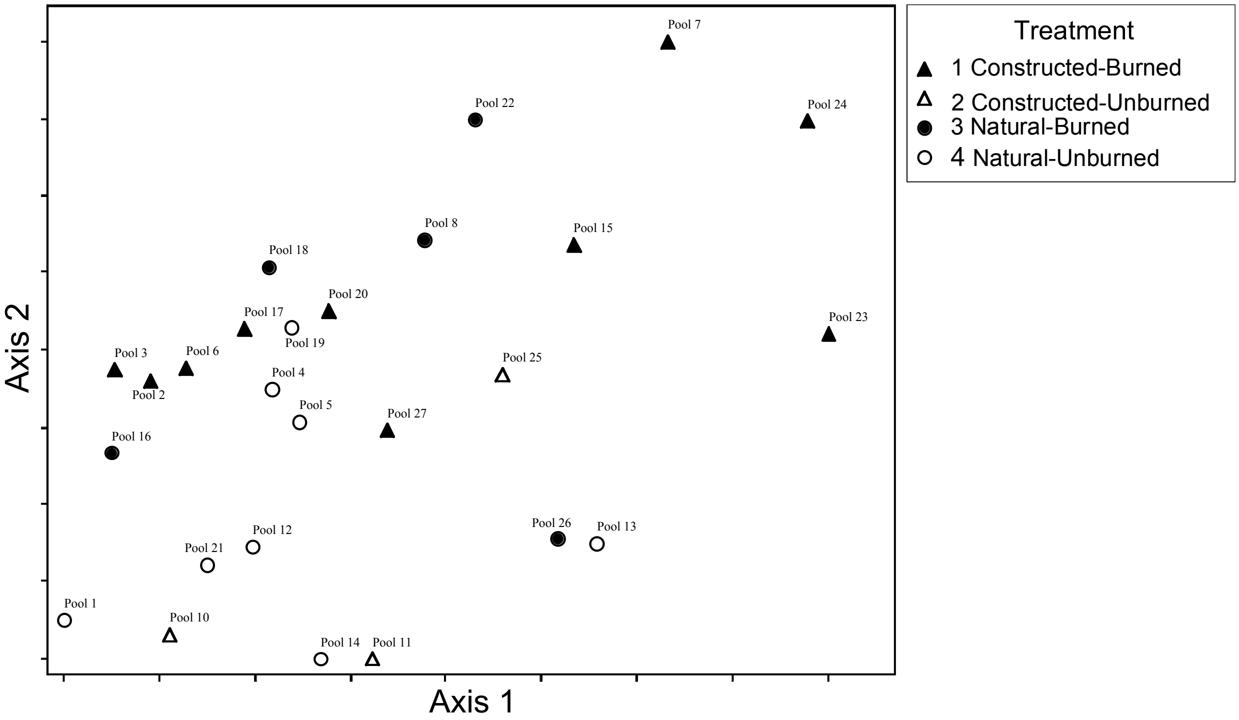

FIGURE 4. Whole-pool NMS ordination for pools within the four treatments. Tight clusters and separations between treatments are not present. From Starr (2004).

year after year, exceeds 0.7 (where 1.0 is the highest possible probability, meaning that the species is always present). Among 11 associations, however, only a minority had more than one diagnostic species with persistence probability > 0.7. This potential problem can be rectified in two ways. First of all, the classification of vernal pool plant communities has not been completed at the time of this writing, and won't be until the close of 2007. As the classification becomes more complete, the identification of the most diagnostic species will be refined. Ideally, the final selection of diagnostic species will reflect high values of persistence. Secondly, for those associations whose diagnostic taxa remain unchanged, data about persistence from this study, and others, will permit us to select a subset of diagnostic taxa that have highest persistence, relegating the others to a less critical status in terms of identifying associations.

Our analyses did not show significant differences in the species composition of constructed and natural pools at Wurlitzer Ranch. Over the course of 7-8 years (and perhaps sooner), plant species in constructed pools had become aggregated and associated into communities that closely imitated those of natural pools. Given careful planning and design of constructed pools, placing them in a habitat that already supports natural pools, and inoculating them with topsoil from adjacent or nearby pools, vernal pool associations do show the capacity to be highly resilient, although the speed of this resiliency may be such that half a dozen years or more are required. We do emphasize the caveat, that the literature indicates many vernal pool creation projects have been failures; therefore resilience depends upon the setting, the care and the ecological understanding with which the mitigation was attempted. Results from one location are not credible enough to say that pool construction can be a consistently successful mitigation option.

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