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# Plant community patterns in California oak woodlands

## Patrones en las comunidades vegetales de los pastizales de roble de California

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ABSTRACT

To identify and characterize plant communities in California oak woodlands we sampled 455 100-m transects, both in the Coast Range (CR) and the Sierra Nevada Foothills (SNF). Sampling points were established at 5-m intervals. Woody and herbaceous species were used to analyze vegetation structure and diversity. Of the 455 transects 257 included woody plants. Of a total of 53 woody and 254 understory species only 14 woody and 60 understory species were present in at least 3% of the transects. We performed a Permutational MANOVA with these species to analyze similarities. Ordination was performed using non-metric multidimensional scaling (NMDS). Manhattan distance was used to obtain dissimilarity matrices. Monte Carlo tests using randomized versions of the data sets were used as null models. Observation scores of the NMDS axes were used to perform cluster analyses. Our results indicate significant differences (P<0.05) in the vegetation between CR and SNF. Differences in herbaceous composition are also significant (P<0.05) when comparing grasslands and woodlands. Woody species richness is higher in the CR than in SNF, and herbaceous species richness is higher in woodlands than grasslands. The highest alpha diversity is found in the woodlands of the CR. NMDS indicates that the assemblage of species in California oak woodlands is not random. The 257 transects with woody and herbaceous species were grouped in 15 clusters based on the species composition. The clusters represent 11 oak subseries.

**RESUMEN**

Para identificar y caracterizar las comunidades vegetales de los pastizales de roble de California se muestrearon 455 transectos de 100 m, tanto en la Cordillera de la Costa (CR) como en el piedemonte de la Sierra Nevada (SNF). De los 455 transectos, 257 incluyeron plantas leñosas. De un total de 53 especies leñosas y 254 especies herbáceas, sólo 14 leñosas y 60 herbáceas estuvieron presentes en un 3% de los transectos. Con esas especies se realizó un ANDEVA multivariado con permutaciones para analizar similitudes. El ordenamiento se realizó utilizando escalamiento multidimensional no-métrico (NMDS) y distancia Manhattan. Pruebas Montecarlo con versiones aleatorias de los datos se utilizaron como modelos nulos. Puntajes del NMDS fueron utilizados para el análisis de conglomerados. Nuestros resultados indican diferencias significativas (P<0.05) entre la vegetación de CR y SNF. Las diferencias en la composición herbácea entre praderas arboladas y sin árboles también son significativas (P<0.05). La riqueza de especies leñosas es mayor en CR que en SNF y la de especies herbáceas es mayor en praderas arboladas que en las sin árboles. La mayor diversidad alfa se encuentra en los pastizales arbolados de CR. El NMDS indica que el ensamblaje de especies en los pastizales de roble de California no es aleatorio. De acuerdo a su composición botánica, los 257 transectos con especies leñosas y herbáceas se clasificaron en 15 grupos, que representan 11 sub-series de roble.

*Palabras clave*: Biodiversidad, canopia, composición, praderas, transecto, sotobosque.

## INTRODUCTION

### California Oak Woodlands

California oak woodlands or hardwood rangelands, a very distinctive component of California landscapes, cover nearly 4 million hectares in California. They occur in 52 of the state's 58 counties, and span eight degrees of latitude west of the Sierra Nevada (Mayer *et al.*, 1986). Oak woodlands seldom form a continuous cover over large areas. They are a major component in a landscape mosaic which includes annual dominated grassland, chaparral and strips of riparian forest (Griffin, 1988). Beyond its aesthetic value, this mosaic constitutes an important wildlife habitat, since many species rely on one community for food and on another for cover and breeding (Plant and Vayssieres, 2000). As part of this mosaic, oak woodlands constitute habitat for more than

300 vertebrate, 5000 invertebrate, and 2000 plant species, and are an important determinant of water quality and wildfire risk (Standiford, 2002).

Typically, oak woodlands are dominated by one or more species of oak (*Quercus* spp.) and several other native trees and shrubs. Local surveys indicate that the understory of oak woodlands and the associated annual grasslands are dominated by introduced annual grasses and forbs but also include native grasses and forbs (Talbot *et al.*, 1939; Bentley and Talbot, 1951; Heady, 1958; White, 1966). However, few surveys have included numerous locations along the length of the Sierra Nevada foothills and the Coast Range. A complete study carried out by Barry (1972), reported species composition for only 40 sites.

Since the 80's, recognition of potential ecological and environmental impacts associated with the conversion of wildlands to urban or agricultural uses, as well as concerns about wildfires, water quality, biological invasions and diseases have focused public attention on California oak woodlands, motivating studies to characterize these ecosystems (George and Alonso, 2008) and assess their health (Waddell and Barrett, 2005).

### Non-metric Multidimensional Scaling

Nonmetric multidimensional scaling (NMDS) is the most generally effective ordination method for ecological community data and should be the method of choice, unless a specific analytical goal demands another method (McCune and Grace, 2002). NMDS was proposed by Shepard (1962a, b) and refined by Kruskal (1964a, b). Descriptions of the method and examples of its application are elsewhere (Kruskal, 1969; Mather, 1976; Fasham, 1977; Kruskal and Wish, 1978; Kenkel and Orloci, 1986; Minchin, 1987a; Minchin, 1987b; Clarke, 1993; McCune, 1994;Ter Braak, 1995; McCune and Grace, 2002). However, to date there are very few studies that use NMDS for the ordination of plant communities on rangelands. Good examples are Seymour and Dean (1999), Kunst *et al.* (2006) and Allen *et al.* (2013).

Thus, this study aims at describing large scale geographic patterns of composition and diversity of oak woodland plant communities in California, using NMDS as the basis for their ordination and classification.

## MATERIALS AND METHODS

### Vegetation Survey

We sampled 455 transects in two Major Land Resources Areas (MLRA; Natural Resources Conservation Service, 2006) during the growing seasons of 2004 and 2005. 294 transects were located in the Coast Range (MLRA 15) and 161 transects in the Sierra Nevada Foothills (MLRA 18; Figure 1). Sites for transects were selected to be representative of the landscape associated with the main soil series on both MLRA's.

Transects were 100-m long and were used to estimate woody and herbaceous botanical composition. Sampling points were established at 5-m intervals along transects for a total of 20 points per transect. The number of times the vertical canopy projection of each woody species was intercepted was used as a measure of woody species composition. The herbaceous botanical composition was estimated using the dry-weight rank method (Mannetje and Haydock, 1963; Jones and Hargreaves, 1979).

### Data Analysis

We segregated transects by MLRA and ecosystem type: Woodland or grassland. The species composition, frequency, abundance and distribution of each subset was analyzed. We determined species richness and the three types of biodiversity on the groups using Whittaker (1972). Alpha diversity in each ecosystem type was calculated using the Shannon-Wiener Index (H´) with natural logarithms. Beta diversity, a measure of heterogeneity in the major subsets of data, was calculated as the ratio gamma over alpha diversity. Gamma diversity, the landscape level diversity, was calculated as exp (H´). We performed a Permutational MANOVA using distance matrices (Legendre and Anderson, 1999; McArdle and Anderson, 2000; Anderson, 2001) in R Core Team (2005) to analyze similarities between the major subsets of the data. With the species present in at least 3% of the transects we created five matrices of species abundance including: 1) woody species; 2) herbaceous species; 3) herbaceous species under canopy in woodlands; 4) herbaceous species in open grasslands; and 5) woody and herbaceous species all together. A species present in less than 3% of the transects was considered rare and not included in the analyses. We conducted a NMDS in R Core Team (2005) with the five vegetation matrices using Manhattan distance due to its probed performance when describing similarity relationships in compositional data (Legendre and Legendre, 1983; McCune, 1992; Roberts, 2005).

To determine if the vegetation matrices represent random assemblages of species or they have a structure different from random we performed Monte Carlo tests using randomized versions of the five data sets as null models. We repeated the tests 200 times to get minimum, mean, and maximum values.

We used the dimensions representing the best solutions for our data sets to perform cluster analyses in JMP® (SAS Institute Inc., 2007) to group the transects based on woody and herbaceous species composition. Finally, we associated those clusters to the oak series described by Allen *et al.* (1989) and analyzed their spatial distribution.

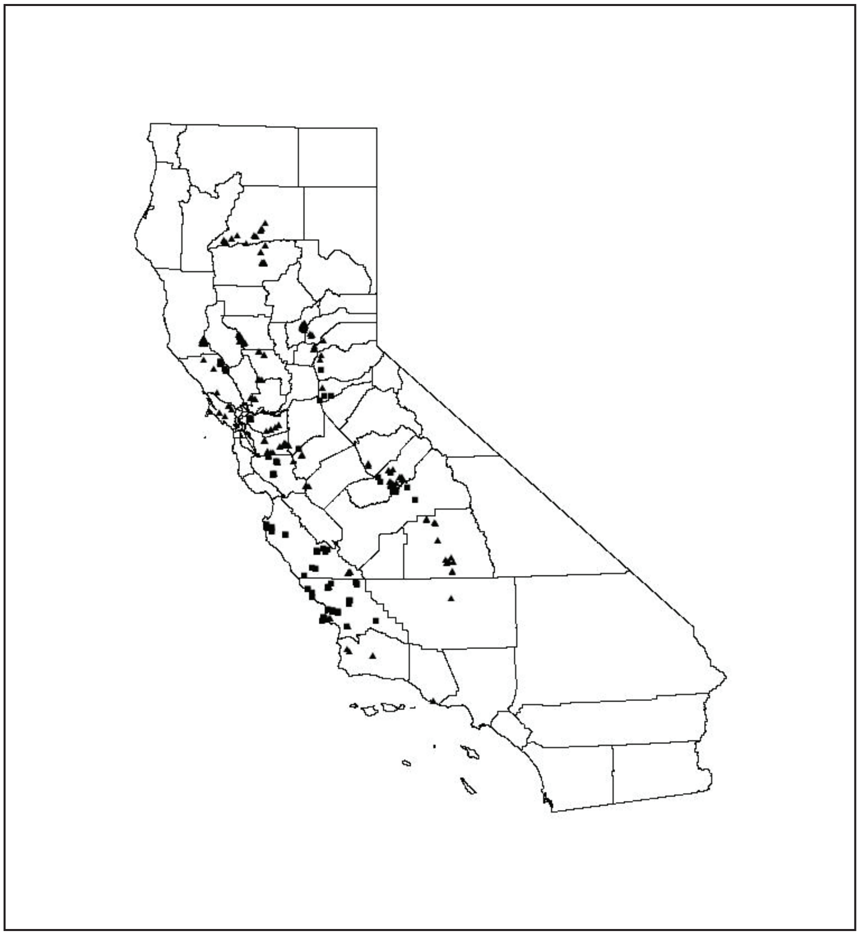

**Figure 1.** Map of the transect's location sampled in 2004 (▲) and 2005 (■)

**Figure 1.** Mapa con la ubicación de los transectos muestreados en 2004 (▲) y 2005 (■)

## RESULTS

### Species composition

The segregation of transects by MLRA and ecosystem type is shown in Table 1. Woody species were found in 257 transects (56.48%) of the 455 transects. From a total of 53 woody species, only 14 were present in at least 3% of the 257 transects (Table 2). Herbaceous species were found in all 455 transects. From a total of 254 herbaceous species, only 60 were present in at least 3% of the 455 transects (Table 3).

Results of the Permutational MANOVA using distance matrices indicated significant differences ($P<0.05$) in the vegetation between the Coast Range and the Sierra Nevada Foothill when comparing woody and herbaceous species altogether, as well as when comparing only herbaceous species. The difference in herbaceous composition was also significant ($P<0.05$) when comparing understory species in grasslands and woodlands.

### Species frequency

The Fagaceae family was the most representative among the woody species (Table 2). *Quercus douglasii* was the most frequent species, being present in 67.8% of the transects. The second most frequent species was *Quercus wislizeni* with a frequency of only 16.9%. *Pinus Sabiniana, Quercus agrifolia* and *Quercus lobata* were also present in more than 10% of the transects. The rest of the woody species were less frequent. *Umbellularia californica* and *Adenostoma fasciculatum* although not very frequent, had a high number of individuals in those transects in which they were present.

The Poaceae family was the most representative among the herbaceous species (Table 3). *Bromus hordeaceus* was present in 91.9% of the transects. The second and third most frequent herbaceous species were *Bromus diandrus* (71.6%) and *Avena* spp. (58.7%). *Lolium multiflorum*, *Erodium spp.*, *Vulpia spp.*, *Hordeum spp.*, *Bromus rubens*, *Carduus pycnocephalus* and *Trifolium hirtum* were also present in more than 25% of

**Table 1.** Segregation of transects by MLRA and ecosystem type
**Tabla 1.** Separación de transectos por MLRA y tipo de ecosistema

| MLRA | Grassland | Woodland | Total |
|---|---|---|---|
| Coast Range | 149 (32.75%) | 145 (31.87%) | 294 (64.62%) |
| Sierra Nevada Foothill | 49 (10.77%) | 112 (24.61%) | 161 (35.38%) |
| Total | 198 (43.52%) | 257 (56.48%) | 455 (100.0%) |

**Table 2.** Frequency and abundance of the 14 most common woody species in California oak woodlands
**Tabla 2.** Frecuencia y abundancia de las 14 especies leñosas más comunes en los pastizales de roble de California

| Species Symbol | Frequency[1] (%) | Abundance[2] (%) | Common Name | Scientific Name | Family |
|---|---|---|---|---|---|
| QUDO | 67.8 | 55.0 | Blue oak | *Quercus douglasii* Hook. & Arn. | Fagaceae |
| QUWI2 | 16.9 | 8.2 | Interior live oak | *Quercus wislizeni* A. DC. | Fagaceae |
| PISA2 | 11.6 | 3.9 | Foothill pine | *Pinus sabiniana* Dougl. ex Dougl. | Pinaceae |
| QUAG | 11.6 | 7.8 | Coast live oak | *Quercus agrifolia* Née | Fagaceae |
| QULO | 10.1 | 6.0 | Valley oak | *Quercus lobata* Née | Fagaceae |
| QUKE | 8.6 | 4.9 | Black oak | *Quercus kelloggii* Newberry | Fagaceae |
| AECA | 5.2 | 2.1 | California buckeye | *Aesculus californica* (Spach) Nutt. | Hippocastanaceae |
| TODI | 5.2 | 1.3 | Pacific poison oak | *Toxicodendron diversilobum* (Torr. & Gray) Greene | Anacardiaceae |
| CECU | 4.9 | 1.0 | Ceanothus | *Ceanothus cuneatus* (Hook.) Nutt. | Rhamnaceae |
| ARCTO3 | 4.5 | 0.9 | Manzanita | *Arctostaphylos Adans.* | Ericaceae |
| BAPI | 4.1 | 1.4 | Chaparral broom | *Baccharis pilularis* DC. | Asteraceae |
| QUGA4 | 3.7 | 1.9 | Oregon white oak | *Quercus garryana Dougl.* ex Hook. | Fagaceae |
| UMCA | 3.0 | 2.9 | California laurel | *Umbellularia californica* (Hook. & Arn.) Nutt. | Lauraceae |
| ADFA | 3.0 | 2.7 | Chamise | *Adenostoma fasciculatum* Hook. & Arn. | Rosaceae |

[1] Frequency in 257 transects
[2] Abundance of a total of 2,040 individuals

**Table 3.** Frequency and abundance of the 60 most common herbaceous species in California oak woodlands
**Tabla 3.** Frecuencia y abundancia de las 60 especies herbáceas más comunes en los pastizales de roble de California

| Species Symbol | Frequency[1] (%) | Abundance (%) | Common Name | Scientific Name | Family |
|---|---|---|---|---|---|
| BRHO2 | 91.9 | 22.0 | Soft chess brome | *Bromus hordeaceus* L. | Poaceae |
| BRDI3 | 71.6 | 10.1 | Ripgut brome | *Bromus diandrus* Roth | Poaceae |
| AVENA | 58.7 | 10.7 | Wild oats | *Avena spp.* L. | Poaceae |
| LOMU | 47.3 | 9.4 | Annual ryegrass | *Lolium multiflorum* Lam. | Poaceae |
| ERODI | 43.7 | 3.6 | Stork's bill | *Erodium* L'Hér. ex Ait. | Geraniaceae |
| VULPI | 42.6 | 5.1 | Annual fescue | *Vulpia* K.C. Gmel. | Poaceae |
| HORDE | 37.1 | 2.7 | Barley | *Hordeum spp.* L. | Poaceae |

**Table 3 cont.** Frequency and abundance of the 60 most common herbaceous species in California oak woodlands
**Tabla 3 cont.** Frecuencia y abundancia de las 60 especies herbáceas más comunes en los pastizales de roble de California

| Species Symbol | Frequency[1] (%) | Abundance[2] (%) | Common Name | Scientific Name | Family |
|---|---|---|---|---|---|
| BRRU2 | 28.1 | 3.0 | Red brome | *Bromus rubens* L. | Poaceae |
| CAPY2 | 26.6 | 2.0 | Italian thistle | *Carduus pycnocephalus* L. | Asteraceae |
| TRHI4 | 26.4 | 1.9 | Rose clover | *Trifolium hirtum* All. | Fabaceae |
| TACA8 | 20.4 | 2.4 | Medusa head | *Taeniatherum caput-medusae* (L.) Nevski | Poaceae |
| HEMIZ | 19.1 | 1.1 | Tarweed[N] | *Hemizonia spp.* DC. | Asteraceae |
| NAPU4 | 17.8 | 1.1 | Purple needlegrass[NP] | *Nassella pulchra* (A.S. Hitchc.) Barkworth | Poaceae |
| BRDI2 | 17.4 | 3.6 | Purple false brome | *Brachypodium distachyon* (L.) Beauv. | Poaceae |
| CYEC | 17.4 | 2.1 | Bristly dogs tail grass | *Cynosurus echinatus* L. | Poaceae |
| MEPO3 | 16.9 | 1.7 | Bur clover | *Medicago polymorpha* L. | Fabaceae |
| AVFA | 13.4 | 2.1 | Wild oats | *Avena fatua* L. | Poaceae |
| AICA | 13.2 | 0.7 | Silver hair grass | *Aira caryophyllea* L. | Poaceae |
| TOAR | 12.5 | 0.6 | Spreading hedge parsley | *Torilis arvensis* (Huds.) Link | Apiaceae |
| VUMY | 12.3 | 1.2 | Rat-tail fescue | *Vulpia myuros* (L.) K.C. Gmel. | Poaceae |
| AMSIN | 11.4 | 0.3 | Fiddle neck[N] | *Amsinckia Lehm.* | Boraginaceae |
| BRMA | 10.8 | 1.4 | Big quaking grass | *Briza maxima* L. | Poaceae |
| LOTUS | 10.8 | 0.7 | Trefoil | *Lotus spp.* L. | Fabaceae |
| LUPIN | 10.3 | 0.4 | Lupine[N] | *Lupinus spp.*L. | Fabaceae |
| TRSU3 | 10.3 | 0.6 | Subterranean clover | *Trifolium subterraneum* L. | Fabaceae |
| ERCI6 | 10.1 | 1.0 | Red stem stork's bill | *Erodium cicutarium* (L.) L'Hér. ex Ait. | Geraniaceae |
| GALIU | 9.9 | 0.4 | Bedstraw[NP] | *Galium spp.* L. | Rubiaceae |
| AETR | 9.0 | 1.6 | Barbed goat grass | *Aegilops triuncialis* L. | Poaceae |
| CESO3 | 8.8 | 0.5 | Yellow star-thistle | *Centaurea solstitialis* L. | Asteraceae |
| VICIA | 8.6 | 0.4 | Vetch | *Vicia spp.* L. | Fabaceae |
| HYGL2 | 8.4 | 0.3 | Smooth cat's ear | *Hypochaeris glabra* L. | Asteraceae |
| TRIFO | 8.4 | 0.3 | Clover | *Trifolium spp.* L. | Fabaceae |
| BRODI | 7.5 | 0.1 | Brodiaea[N] | *Brodiaea spp.* Sm. | Liliaceae |
| PLER3 | 7.3 | 0.5 | Dot seed plantain[N] | *Plantago erecta* Morris | Plantaginaceae |
| GERAN | 7.0 | 0.2 | Geranium[N] | *Geranium spp.* L. | Geraniaceae |
| VISA | 7.0 | 0.3 | Common vetch | *Vicia sativa* L. | Fabaceae |
| PLAGI | 6.8 | 0.2 | Popcorn flower[N] | *Plagiobothrys spp.* Fisch. & C.A. Mey. | Boraginaceae |
| HYPOC | 5.9 | 0.2 | Cat'sear | *Hypochaeris spp.* L. | Asteraceae |
| PLANT | 5.9 | 0.3 | Plantain | *Plantago spp.* L. | Plantaginaceae |
| RACA2 | 5.9 | 0.2 | California buttercup[N] | *Ranunculus californicus* Benth. | Ranunculaceae |

[1]Frequency in 455 transects
[N] Native plant
[NP] Native perennial plant

**Table 3 cont.** Frequency and abundance of the 60 most common herbaceous species in California oak woodlands
**Tabla 3 cont.** Frecuencia y abundancia de las 60 especies herbáceas más comunes en los pastizales de roble de California

| Species Symbol | Frequency (%) | Abundance (%) | Common Name | Scientific Name | Family |
|---|---|---|---|---|---|
| ACMO2 | 5.5 | 0.1 | Soft blowwives[N] | *Achyrachaena mollis* Schauer | Asteraceae |
| BRMI2 | 5.5 | 0.1 | Little quaking grass | *Briza minor* L. | Poaceae |
| CLARK | 5.5 | 0.1 | Clarkia [N] | *Clarkia spp.*Pursh | Onagraceae |
| ELGL | 5.5 | 0.5 | Blue wild rye[NP] | *Elymus glaucus* Buckl. | Poaceae |
| BRASS | 4.8 | 0.1 | Mustard | *Brassica spp.* L. | Brassicaceae |
| LOPU3 | 4.8 | 0.3 | Spanish clover[N] | *Lotus purshianus* F.E. & E.G. Clem. | Fabaceae |
| CEME2 | 4.0 | 0.2 | Maltese star-thistle | *Centaurea melitensis* L. | Asteraceae |
| MICA | 4.0 | 0.2 | Q-tips[N] | *Micropus californicus* Fisch. & C.A. Mey. | Asteraceae |
| TAOF | 4.0 | 0.2 | Common dandelion | *Taraxacum officinale* G.H. Weber ex Wiggers | Asteraceae |
| ACMI2 | 3.7 | 0.1 | Common yarrow[N] | *Achillea millefolium* L. | Asteraceae |
| CHPO3 | 3.7 | 0.2 | Wavy leaf soap plant[N] | *Chlorogalum pomeridianum* (DC.) Kunth | Liliaceae |
| GAVE3 | 3.7 | 0.1 | Nit grass | *Gastridium phleoides* (Nees & Meyen) C.E. Hubb. | Poaceae |
| BRCA5 | 3.5 | 0.1 | California brome[NP] | *Bromus carinatus* Hook. & Arn. | Poaceae |
| CLPE | 3.5 | 0.1 | Miner's lettuce[N] | *Claytonia perfoliata* Donn ex Willd. | Portulacaceae |
| ANAR | 3.3 | 0.1 | Pimpernel | *Anagallis arvensis* L. | Primulaceae |
| BRMA3 | 3.3 | 0.2 | Spanish brome | *Bromus madritensis* L. | Poaceae |
| ERBO | 3.3 | 0.2 | Long beak stork's bill | *Erodium botrys* (Cav.) Bertol. | Geraniaceae |
| MECA2 | 3.3 | 0.2 | California melic grass[NP] | *Melica californica* Scribn. | Poaceae |
| ERSE3 | 3.1 | 0.1 | Turkey mullein[N] | *Croton setigerus* (Hook.) | Euphorbiaceae |
| RUAC3 | 3.1 | 0.1 | Common sheep sorrel[N] | *Rumex acetosella* L. | Polygonaceae |

[1] Frequency in 455 transects
[N] Native plant
[NP] Native perennial plant

the transects. A point of concern was the presence of noxious weeds *Taeniatherum caput-medusae* and *Centaurea solstitialis* in 20.4% and 8.79% of the transects respectively.

The frequency of herbaceous species differs when comparing species under canopy versus in open grasslands. The coincidence of the 15 most frequent species (25% of the 60 herbaceous species) is 73% among these two different types of ecosystem. While *Medicago polymorpha* and *Vulpia myuros* were more frequent in grasslands, *C. pycnocephalus*, *Cynosorus echinatus* and *Torilis arvensis* were more frequent in woodlands.

## Species abundance

The most abundant woody species were *Q. douglasii* (55%), *Q. wislizeni* (8.19%), *Q. agrifolia* (7.79%) and *Q. lobata* (5.98%). The rest of the woody species represented less than 5% of abundance each (Table 2).

*B. hordeaceus* was the most abundant herbaceous species in woodlands (24%) and grasslands (19.1%). In grasslands, *B. hordeaceus, L. multiflorum* and *Avena spp*. accounted for 45.8% of the herbaceous vegetation (Table 3). In woodlands, *B. hordeaceus* and *B. diandrus* accounted for 36.1% of the understory species.

The coincidence of the 15 most abundant herbaceous species among woodlands and grasslands was 80%. However, while *Aegilops triuncialis*, *M. polymorpha* and *V. myuros* were more abundant in grasslands, *Briza maxima*, *C. pycnocephalus*, and *C. echinatus* were more abundant in woodlands.

## Species richness and biodiversity

Woody species richness and biodiversity were higher in the Coast Range than in the Sierra Nevada Foothill (Table 4). Herbaceous species richness was higher in woodlands than grasslands in both MLRA's. When comparing MLRA´s and ecosystem types, the highest value of biodiversity was found in the woodlands of the Coast Range.

**Species distribution**

When analyzing the spatial distribution of woody species we noticed that *Q. douglasii* was homogeneously distributed in both MLRA's. The same was true for *Q. wislizeni, P. sabiniana, Toxicodendron diversilobum* and *Ceanothus cuneatus. Q. agrifolia, Q. garryana, U. californica* and *Baccharis pilularis* were not present in the Sierra Nevada Foothills. *Q. lobata* and *Q. kelloggii* although present in both MLRA's were mostly located in the Coast Range. *Arctostaphylos adans* was more frequent in Northern California and *Adenostoma fasciculatum* was more common in the South.

*Bromus madritensis, Erodium botrys,* and *Micropus californicus* were not present in grasslands at the Coast Range. *Achyrachaena mollis, A. triuncialis, Anagallis arvensis, Elymus glaucus, Rumex acetosella* and *Vicia sativa* were absent in Sierra Nevada woodlands. *Achillea millefolium, A. mollis, A. arvensis, Brassica spp., Bromus carinatus, B. madritensis, Centaurea melitensis, Claytonia perfoliata*, *E. glaucus, Gastridium phleoides, Geranium spp., Melica californica*, *R. acetosella, Taraxacum officinale* and *V. sativa* were not present in grasslands at the Sierra Nevada Foothills.

**Non-metric Multidimensional Scaling**

NMDS extracted stronger axes (lower stress values) than expected by chance (NMDS of a random matrix) for both woody and herbaceous species, indicating that the assemblage of species is not random (Table 5). We concluded that 4 dimensions represented the best solution for the data sets including woody species and 6 dimensions represented the best solution for the data sets of herbaceous species.

**Table 4.** Species richness, alpha, beta and gamma diversity of California oak woodlands by MLRA and ecosystem type. CR = Coast Range; SNF = Sierra Nevada Foothill

**Tabla 4.** Riqueza de especies, alfa, beta y gama diversidad de los pastizales de roble de California según MLRA y tipo de ecosistema. CR = Cordillera de la Costa; SNF = Piedemonte de la Sierra Nevada

| MLRA | Ecosystem Type | Number of Transects | Woody species | Herbaceous species | Species Richness | Alpha Diversity | Beta Diversity | Gamma Diversity |
|---|---|---|---|---|---|---|---|---|
| CR | Woodland | 145 | 42 | 177 | 219 | 6.41 | 94.55 | 605.76 |
| CR | Grassland | 149 | 0 | 151 | 151 | 4.02 | 13.81 | 55.48 |
| SNF | Woodland | 112 | 26 | 126 | 152 | 4.99 | 29.40 | 146.64 |
| SNF | Grassland | 49 | 0 | 77 | 77 | 3.66 | 10.63 | 38.91 |
| CR+SNF | W+G[1] | 455 | 53 | 254 | 307 | 6.36 | 90.78 | 577.19 |

[1] Woodland and grassland

**Table 5.** Stress values for the vegetation matrices (NMDS) and the 200 runs of randomized data sets (RNMDS) through a Monte Carlo analysis

**Table 5.** Valores de estrés de las matrices de vegetación (NMDS) y de las 200 simulaciones con set de datos aleatorios (RNMDS) mediante análisis Monte Carlo

| | Woody species | Herbaceous species | Herbaceous species in woodlands | Herbaceous species in grasslands | Woody and herbaceous species |
|---|---|---|---|---|---|
| Dimensions | 4 | 6 | 6 | 6 | 4 |
| NMDS | 8.76 | 10.38 | 10.07 | 9.69 | 9.44 |
| RNMDSmin | 14.94 | 24.35 | 24.13 | 22.64 | 17.15 |
| RNMDSmean | 16.44 | 25.66 | 25.86 | 24.75 | 19.28 |
| RNMDSmax | 18.31 | 26.98 | 27.69 | 26.68 | 20.86 |

**Table 6.** Number of transects and individuals of woody species in the clusters of woody and understory species. Herbaceous species are not shown by space constraints.

**Tabla 6.** Número de transectos e individuos de especies leñosas en los grupos de especies leñosas y herbáceas. Especies herbáceas no se muestran por restricciones de espacio.

| Cluster | Number of Transects | Total of Individuals | QUDO | QUWI2 | PISA2 | QUAG | QULO | QUKE | AECA | TODI | CECU | ARCTO3 | BAPI | QUGA4 | UMCA | ADFA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 42 | 367 | 363 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 2 | 110 | 362 | 275 | 22 | 30 | 5 | 5 | 0 | 3 | 0 | 6 | 7 | 7 | 0 | 0 | 2 |
| 3 | 12 | 77 | 6 | 3 | 1 | 3 | 0 | 32 | 1 | 0 | 1 | 6 | 0 | 23 | 0 | 1 |
| 4 | 10 | 162 | 0 | 7 | 1 | 91 | 1 | 0 | 1 | 7 | 0 | 0 | 0 | 3 | 51 | 0 |
| 5 | 14 | 141 | 38 | 71 | 18 | 0 | 2 | 0 | 2 | 6 | 1 | 1 | 0 | 0 | 2 | 0 |
| 6 | 13 | 55 | 5 | 0 | 0 | 1 | 47 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 | 14 | 113 | 23 | 1 | 11 | 0 | 0 | 0 | 14 | 4 | 10 | 1 | 22 | 0 | 0 | 27 |
| 8 | 2 | 48 | 0 | 0 | 0 | 0 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 |
| 9 | 5 | 88 | 0 | 0 | 0 | 10 | 65 | 2 | 7 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| 10 | 14 | 89 | 14 | 0 | 1 | 41 | 2 | 11 | 5 | 3 | 0 | 0 | 0 | 10 | 2 | 0 |
| 11 | 16 | 262 | 251 | 5 | 2 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| 12 | 1 | 24 | 4 | 2 | 0 | 8 | 0 | 7 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 |
| 13 | 6 | 117 | 79 | 25 | 4 | 0 | 0 | 0 | 7 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 6 | 83 | 54 | 2 | 0 | 0 | 0 | 24 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| 15 | 2 | 52 | 10 | 27 | 11 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |

### Cluster Analysis

The 257 transects with both, woody and herbaceous species were grouped in 15 clusters (Table 6). Clusters were diverse. Clusters 2, 3 and 5 have a wide variety of species, whereas clusters 1 and 8 were essentially mono-specific. On the other hand, clusters 1 and 2 group a large number of transects but clusters 8, 12 and 15 include only a few.

Based on the species composition, the 15 clusters were classified into 11 oak subseries (Table 7) described by Allen *et al.* (1989): 1) Blue Oak/Grass; 2) Blue Oak-Interior Live Oak/Grass; 3) Blue Oak-Foothill Pine/Manzanita/Grass; 4) Blue Oak-Valley Oak/Grass; 5) Interior Live Oak-Blue Oak-Foothill Pine; 6) Black Oak/Green leaf Manzanita; 7) Black Oak-Valley Oak/ Grass; 8) Valley Oak-Coast Live Oak/Grass; 9) Coast Live Oak/Grass; 10) Mixed Oak/Grass and 11) Mixed Oak-California Buckeye/Grass.

Based on the oak subseries, six of the seven series of hardwood rangelands were represented in this study: 1) Blue Oak; 2) Black Oak; 3) Coast Live Oak; 4) Interior Live Oak; 5) Valley Oak; and 6) Mixed Oak. None of the transects was classified into the Scrub Oak series.

## DISCUSSION

The sites sampled are representative of the landscape associated with the main 144 soil series in 30 Counties and 2 MLRA's, but were taken during two consecutive growing seasons (2004 & 2005) and correspond to a static description of California oak woodlands. Studies accounting for the dynamic replacement of species on the long term in oak woodlands are still required.

Only 56.48% of transects include woody species, so the other 43.52% of the samples represent grasslands. The fact that oak woodlands are a major component in a landscape mosaic which includes grassland, chaparral and strips of riparian forest (Griffin, 1988) and the evidence of cyclical succession between woodlands, grasslands, chaparral and coast sage scrub (Callaway and Davis, 1993) suggest the need for studies integrating the different vegetation types in the "grassland-forest continuum".

Like in earlier studies (Talbot *et al.*, 1939; Bentley and Talbot, 1951; Heady, 1958; White, 1966), this survey of species composition along 455 transects in the foothills of the Sierra Nevada Mountains and the Coast Range found that introduced annual grasses including

**Table 7.** Clusters and transects in each oak subseries when considering woody and understory species altogether
**Tabla 7.** Grupos y transectos en cada subserie de roble considerando las especies leñosas y herbáceas

| Oak Subseries | Cluster | Number of Transects |
|---|---|---|
| Blue Oak/Grass | 10 | 3 |
| Blue Oak-Interior Live Oak/Grass | 1, 9 & 12 | 74 |
| Blue Oak-Valley Oak/Grass | 11 | 13 |
| Interior Live Oak-Blue Oak-Foothill Pine | 3 | 14 |
| Black Oak/Green Leaf Manzanita | 14 | 6 |
| Black Oak-Valley Oak/Grass | 6 | 4 |
| Valley Oak-Coast Live Oak/Grass | 15 | 1 |
| Coast Live Oak/Grass | 4 | 10 |
| Mixed Oak/Grass | 5 & 13 | 7 |
| Blue Oak-Foothill Pine/Manzanita/Grass | 8 | 8 |
| Mixed Oak-California Buckeye/Grass | 2 & 7 | 117 |
| TOTAL | 15 | 257 |

*B. hordeaceus*, *B. diandrus*, *Avena* spp., *L. multiflorum* and *Vulpia* spp. dominate the understory of oak woodlands and annual grasslands (Table 3). Forbs add to the diversity of these communities with one-third of the species being native, mostly annual forbs. Additionally, native perennial grasses are more prevalent than reported in earlier local surveys. Nearly 20% of the transects contained *Nassella pulchra*, *E. glaucus*, *B. carinatus* and *M. californica* in frequencies of 3 to 5%. The noxious weeds *C. pycnocephalus* and *T. caput-medusae* occurred at frequencies greater than 20%, while *C. solstitialis* and *A. triuncialis* had frequencies just under 10%. The 14 common woody species used in the analyses are native to California.

## CONCLUSIONS

For the purposes of this study NMDS has demonstrated to be a method that yields an objective ordination and constitutes a good basis for the classification of hardwood rangelands.

When comparing the stress values of the NMDS for the vegetation matrices versus the randomized version of each data set as a null model in Monte Carlo tests our results indicated that the plant community associations in California oak woodlands are not random assemblages of species, supporting the community-unit concept of organization.

Our results also demonstrate that differences in the herbaceous composition under canopy and in open grasslands are significant in oak woodlands, and that the presence of woody species increases the biodiversity of the herbaceous strata. However, although grasslands in the Sierra Nevada Foothill have the smallest values of species richness and biodiversity, this could be a result of the small number of transects of this type studied in this survey.

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