Distribution of vegetation in a California desert grassland
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INTRODUCTION

No Californian grasslands support native species exclusively (D'Antonio et al. 2007, Bartolome et al. 2008). Instead, they are mosaics of California natives and exotics from the Old World. Even those grasslands celebrated for their nativeness support alien species (Hopkinson et al. 2009). Understanding the site preferences of natives and exotics can help grassland managers whose management goals include the conservation and enhancement of native species populations.

The invasion of Old World grasses and forbs is usually attributed to human transport of propagules to the New World and the introduction of domestic livestock, as well as secondary factors such as changes in fire regime and cultivation (Bartolome et al. 2008). The degree of invasion varies from nearly complete exotic dominance in Valley grassland, through native and exotic co-dominance in coastal prairie and western Mojave grasslands, to continued native dominance on serpentine and vernal pool sites. These observations are necessarily quite general because associations and alliances in this complex vegetation type are as yet poorly described (Sawyer et al. 2009).

Change over space and time in California grasslands is best described as non-equilibrium (*sensu* Wiens 1984) because it is predominantly driven by environmental site factors such as weather and soils (Jackson and Bartolome 2002). Consequently, although California's grasslands are complex ecosystems in which physical features and management activities are highly inter-dependent, environmental site characteristics are the most reliable indicators of natives in the grassland landscape (Gea-Izquierdo et al. 2007, Jackson and Bartolome 2007). Identifying the causes underlying changes in grassland structure will require much better identification of ecological sites (Brown 2010) and a better understanding of how ecological sites respond to variation in environmental drivers. As more information is obtained about the variety of grassland associations, different drivers of change are likely to become apparent.

Agriculture is one major driver of change from native to exotic dominance. Tillage has eradicated and prevented the recolonization of native perennial bunchgrasses in many parts of California. In areas with soils and climate hospitable to native bunchgrass dominance, a history of crop farming is regularly associated with bunchgrass absence and exotic annual grass abundance (Stromberg and Griffin 1996, Robertson 2004, D'Antonio et al. 2007).

Variation in soil fertility is also a strong control on the distribution of alien species invasion in the California grassland landscape. As soil nitrogen increases so do invasive grasses in serpentine grasslands (Huenneke et al. 1990, Weiss 1999, Gram et al. 2004) and coastal prairie (Maron and Connors 1996). In contrast, low fertility sites have been slower to change to exotic dominance. For example, in Valley grassland in the Diablo Range of central California, Gea-Izquierdo et al. (2007) found that sandy soils low in phosphorus were islands of the native bunchgrass, *Nassella pulchra*, within a sea of alien grasses and that native forb species richness was highest in low nitrogen soils. In another study, sandy hummocks with low cation exchange capacity were found to have the highest native forb richness in a serpentine grassland (Seabloom et al. 2003a).

In more arid grassland environments like the western Mojave, water availability is a primary determinant of the type of vegetation a site can support. A site's aspect, slope, erosional versus depositional position on the landscape, soil texture, and organic matter are primary controls on soil water availability (Duniway et al. 2010).

Bromus madritensis ssp. *rubens* (red brome) and *Erodium cicutarium* (redstem filaree) are common exotic species in the Mojave Desert (Brooks 1999a, Brooks 1999b, Brooks 2003). Despite the success of the exotics, native herbaceous species persist in high numbers in the western Mojave Desert compared with grasslands statewide. Further investigation is necessary to determine why native species are thriving here (Keeler-Wolf 2007). We went to the Mojave Desert side of the legendary Tejon Ranch to investigate spatial patterns of this native-exotic vegetation mosaic.

In this paper, our first goal is a data-driven, quantitative description of the vegetation of a western Mojave Desert grassland. Secondly, we attempt to isolate spatial relationships of vegetation and environmental site factors, with a special focus on sites that support native species.

STUDY SITE

We studied the Mojave Desert grasslands of Tejon Ranch. The 1093-km^2 ranch, a vestige of the Mexican-California Rancho land ownership system, is the largest contiguous privately owned property in California. Four distinct ecological regions converge on Tejon Ranch: Great Central Valley, Southwestern California, Sierra Nevada, and Mojave Desert (Hickman 1993). The study site lies on the southeastern side of the Ranch, in the Antelope Valley, the wedge-shaped western border of the Mojave Desert. Forty plots were randomly sited in 37.48 km^2 of grasslands that span 900-1200 m above sea level in an area circumscribed by approximately 34.48°N-34.53°N, 118.44°W-118.35°W. Grasslands cover all aspects, northeast through southwest (Figure 1).

Climate

The Mojave is a rainshadow desert. The orographic effect increases toward the east in the Antelope Valley (Soil Survey Staff, 1970). Our study site is influenced by the Mediterranean climate from the area to the west (Keeler-Wolf et al. 2007), but a desert climate regime predominates (Western Regional Climate Center 2011a). A multi-decadal rainfall pattern in the Mojave Desert was detected by Hereford et al. (2006): 1900 to 1946, rainfall was relatively high; 1947-1976 was a drought; 1977-1998, rainfall was relatively high; and 1998 to 2006 was a drought. This 30-year historical cycle suggests the current drought, which began in 1999, will continue until about 2030 (Brooks and Minnich 2006).

The closest weather station is in Neenach (34.48°N 118.35°W, 881 m above sea level), but available data are historical only. In 1893-1963, annual average rainfall from August 1-July 31 was 21.6 cm, with 93% falling between October and April. On average 18.8 cm of snow fell in

November through April Average temperatures were 4.9° C in January and 27.3°C in July. (Western Regional Climate Center 2011b). Sixty six km to the southeast, the Palmdale Irrigation District weather station (34.35°N 118.6°W, 791 m above sea level) provides data from 1951 to the present. The Palmdale station does not differentiate rain and snow. Average precipitation 1951-2011 from August 1- July 31 was 18.5 cm with 90% falling between October and April. 1.7 cm fell in October and November, and 16.6 cm fell in December through April.

In the year of our study, August 2009-July 2010, total rainfall in Palmdale was 22.1 cm, 120% of the 1951-2011 60-year average. Ninety two percent of the rain fell between December and April with only 0.1 cm rain falling in October and November (UC IPM 2011). The 2009-2010 rains could be characterized as heavy and late, with an isolated pulse of early rain.

Geomorphology, geology and soils

The Antelope Valley is bordered by the Tehachapi Mountains to the north and the Transverse Ranges to the south. The strike-slip, left-lateral Garlock Fault runs through the Tehachapis, and the right-lateral San Andreas Fault runs through the base of the Transverse Ranges. Additional strike-slip faults – Pastoria, Pinyon Hill, and North Oso Canyon – dot the southern face of the Tehachapis in our study site (Dibblee 2008, Keller et al. 1987).

Prior to the Pleistocene, the Antelope Valley sloped and drained to the west. Since the uplift of the Transverse Ranges in the upper Pleistocene, Tehachapi and Transverse mountain streams travel east and terminate in the Rogers and Rosamond Playas in the eastern Antelope Valley (Ponti 1985). Accordingly, streams originating in the Tehachapis trend northwest to southeast.

Alluvial fans and bajadas of Holocene alluvial silt, sand and gravels, and Pleistocene alluvial sand and gravels are the most common topographic features in the study area (Figure 2). Median grain size, age, and slope of the alluvial deposits decrease with distance from the Tehachapi Mountains (Dibblee 2008). Adjacent to the mountains, the alluvial deposits are Pleistocene, elevated, and dissected. The dissection results in rolling topography with convex terrace escarpments separated by concave valleys (Figure 3). The terrace escarpments exceed 10 meters in height with moderate slopes (10%-32%). Toward the middle of the Antelope Valley basin, the alluvial deposits are undissected with gentle slopes (1%-13%).

The grasslands reach north into the foothills of the Tehachapi Mountains, on Jurassic/Cretaceous granitic and dioritic basement rock with pendants of Paleozoic/Mesozoic metasedimentary limestone and schist of the Bean Canyon Formation (Wiese and Fine 1950, Dibblee 2008, Figure 3).

Several beds of Pliocene lake sediments lie between the Tehachapi foothills and the alluvial fan-bajada complex (Wiese and Fine 1950, Dibblee 2008). Dibblee (2008) named these fine grained sediments the Meeke Mine Formation (map symbol Tmm on Figure 3). The lacustrine beds are overlain by Pleistocene gravels, in some parts thickly (Wiese and Fine 1950). Cores 21 meters deep revealed the material is mostly clay with localized deposits of sand from weathered granite (Keller et al. 1987). The Formation is visible as low, gently sloping hills with cobbles of mixed origin on the surface.

Metasedimentary Bean Canyon Formation pendants are situated at higher elevations northwest of the Meeke Mine Formation. Northwest-southeast trending streams originating in the Tehachapis carry alluvium from the granitic mountains, the calcareous pendants, and the lakebeds to the bajada complex at lower elevations. For example, see the streams that cut through Cottonwood Canyon and Little Sycamore Canyon in Figure 2.

Soils underlying the grasslands are mapped as Ayar (Typic Haploxererts); Hanford (Typic Xerorthents); Lebec (Calcic Haploxerolls); Oak Glen (Pachic Haploxerolls), Oakdale (Mollic Haploxeralfs), Ramona (Typic Haploxeralfs), Terrace escarpments, and Vernalis loam (Calcic Haploxerepts) (Soil Survey Staff 1970). We investigated soil characteristics on a spatial scale much smaller than the soil mapping units.

Biotic features

Vegetation is a mosaic of native and exotic grasses and forbs, composite shrubs *Chrysothamnus nauseosus* and *Ericameria linearifolia*, and *Yucca brevifolia* (Joshua trees). California ground squirrels and gophers are common, and occasionally a pronghorn antelope herd can be observed.

The human population increased by 350% between 1970 and 1990 in the Mojave Desert (Berry et al. 2006), and as civilization spread, so did exotic grasses and forbs (Brooks 1999). *Bromus madritensis* ssp. *rubens* and *Erodium cicutarium* have invaded a wide variety of growing conditions in the western Mojave and are common in our study site. Biomass of both species increases with soil nitrogen, phosphorus, and water, but *Erodium cicutarium* is also successful in dry, nutrient poor sites (Brooks 1999b). Their success is attributed to the speed and efficiency with which their seedlings use soil nutrients across varying conditions of nitrogen availability, plant density, and soil climate (Defalco et al. 2003, Blackshaw 1992). Both species are native to the Mediterranean and Northern Africa, but *E. cicutarium*'s native habitat is more arid than that of *B. madritensis ssp. rubens* (Brooks 2000, Sauer 1988). Accordingly, *B. madritensis* ssp. *rubens* is a widespread invasive annual grass in the wetter 1000-2000 m middle elevations of the Mojave Desert (Brooks and Minnich 2006), while *E. cicutarium* is more common at drier lower elevations below 800-1000 m (Brooks and Berry 2006).

First observed in California in 1848, *B. madritensis* spp. *rubens* was common in the Mojave by the 1950s (Brooks 2000). Its abundance increased dramatically in the 1970s-1990s (Brooks and Minnich 2006), during a period of high rainfall (Hereford et al. 2006) and human population growth (Berry et al. 2006). Pollen data show that *E. cicutarium* became established around the Santa Barbara area between 1750 and 1765. It predates California's first Spanish mission and livestock grazing, and likely arrived via birds and mammals from Baja, California (Mensing and Byrne 1998). It has been in the Mojave since the 1800s (Brooks 1999b).

Quantitative reconstruction of prehistoric fire regimes in the Mojave is elusive, because the typical fire history markers like trees and active lakebeds are missing from the landscape (Brooks and Matchett 2006). Fuel continuity and fuel type are first order controls on fire recurrence in California's deserts (Brooks and Minnich 2006), so grasses and shrubs at high cover and densities would likely have carried fires beyond ignition points. These fires were likely moderate-severity and stand-replacing, but with fire return intervals exceeding 100 years (Brooks and Matchett 2006).

In recent decades, fire size and frequency have increased, and the majority of wildfires in the Mojave have occurred in middle elevation grasslands and shrublands, following years of high rainfall. *Bromus madritensis* ssp. *rubens* is the most widespread exotic grass at this elevation zone, and there is concern that the shorter fire return interval and increased fire size are due to the fine, continuous fuels it produces between shrubs (Brooks and Matchett 2006).

The study area has been grazed by sheep or cattle more or less continuously since 1843, when livestock were first introduced to the area in large numbers. Number and class have varied. Today the grazing regime is primarily stockers who lightly graze the entire area. Unpaved ranch roads, electricity wires, and other ranch infrastructure are visible from almost all study plots. A portion of the study area was farmed in the 1950s and 1960s.

METHODS

Field research

Forty study plots were selected in the study area. Thirteen plots were on alluvial fans (<4% slope), thirteen were on bajadas (≥4% slope), seven were on terrace escarpments underlain by alluvium, five were in concave drainage valleys between the escarpments, and two were in the Tehachapi foothills on Bean Canyon Formation pendants (Figure 2). Plots were randomly sited and stratified by landform in order to incorporate a variety of soil depths, slopes, aspects, and erosional and depositional processes into our study. The number of plots per landform was dictated by relative area of the landform in the study area, which was determined using Kern County topographical maps and digital elevation models (USDA/NRCS National Cartography & Geospatial Center 2010) in ArcGIS, Version 9.0 (ESRI 2004).

All plots were in herbaceous species-dominated patches of 100 m^2 or more. To identify plots that were on soils that were farmed in the past, we overlaid a GIS shapefile of our plots on geoeferenced aerial photographs taken in 1950s and 1960s in which evidence of cultivation could be discerned. Based on this photographic evidence, seven of the forty plots were in areas previously under crop or hay cultivation. Agriculture may have been more extensive before the photographs were taken, but we designated only those seven plots as definitively historically farmed.

Study plots were 50 cm by 50 cm squares (0.25 m^2). At each plot we characterized cover by recording 50 ground cover "hits" using a 50-point frame. We lowered one point, recorded the first item the point encountered in space (plant, soil, rock, litter, or feces), and then lowered the next point, recorded the item, and so forth.

After sampling the ground cover at each plot, we used a 15 cm long x 5 cm diameter auger to collect a shallow (0-15 cm) and deep (30-45 cm) soil sample from the plot center. We collected both samples to capture any depth trends that may be differentially affecting deep-rooted bunchgrasses and shallow-rooted annual grasses. Annual grass roots extend, on average, 30 cm with the majority of the roots concentrated above 20 cm, and California native perennial grass roots generally extend to at least 60 cm, with the majority concentrated above 35 cm (Holmes and Rice 1996, Hull and Muller 1977, Savelle 1977, Hunter and Wu 2005). Sampling below 30 cm should provide information about resources that annual species cannot access, but perennial grasses can.

By pounding a sharpened steel rod into the ground, stopping when we hit saprolite, and marking and measuring the rod, we recorded soil depth (see Reynolds et al. 1997, Kolb et al. 2002, Tesfa et al. 2008). The depth measurement was verified in several plots by digging holes. The rod was 200 cm long, and if we did not hit saprolite or bedrock, depth was recorded as >200 cm.

We recorded slope and aspect of the area in a 10-m radius around the plot using a compass and clinometer. We assessed disturbance by small mammals and cattle as none, light, moderate or heavy within a 5-m radius of the plot. The cattle use assessment was limited to the time since break of season 2009. Major indicators of cattle use were herbivory, defecation, trampling, and presence on plot. The major indicator of small mammal use was burrowing in the plot.

The UC Davis Analytical Lab tested the 40 shallow and 40 deep soil samples for total nitrogen and carbon (flash combustion method); bioavailable phosphate (Olsen et al. 1954); plant available sulfate (CaP extract); exchangeable potassium, sodium, calcium, and magnesium; and particle size content (suspension by hydrometer). We tested pH in the lab by mixing 15 g sieved soil with 30 mL deionized water, mixing the sample, and swirling the slurry and supernatant solution while taking the reading using a handheld pH meter (Robertson et al. 1999).

It is common practice to use the Bray phosphorus test (Bray and Kurtz 1945) on acidic soils and the Olsen phosphorus test (Olsen et al. 1954) on neutral to basic soils, although Olsen-P can give reliable results on acidic soils (Fixen and Grove 1990; Elrashidi 2010). We elected to use Olsen-P for all samples even though six had pH less than 6. To verify that Olsen-P was accurate, we tested the six pH<6 soils with both the Bray and Olsen methods. The test result data were highly correlated ($R^2 = 0.974$), supporting our decision to use Olsen-P on all samples regardless of pH.

Plot 20 was on a Bean Canyon metasedimentary pendant. Its soil was so rocky and shallow, we could not extract a deep sample. We substituted the plot's shallow texture and chemistry values for the missing deep values in our analysis.

Statistical analyses

Grassland community structure

We used Detrended Correspondence Analysis (DCA) in PC-ORD (McCune and Mefford 2006) to isolate vegetation types in the relative cover data of the 40 plots. Relative cover was the proportion of the "hits" of a particular species in relation to all plant "hits" per plot. DCA locates plots and species in ordination space, typically on two or three axes. Greater distance between plots in ordination space reflects a lower similarity in composite variables. Plots that are close together may represent significant community affinities.

Three plots were strongly correlated as a distinct community type and were significant outliers from the rest of the plots. They were removed and a subsequent analysis was performed on the remaining 37 plots. After removing the three outlying plots, parts of the ordination graph exhibited only subtle plot separation, so we used TWINSPAN to further guide classification (McCune and Mefford 2006). DCA clustering, TWINSPAN, dominance, and affinity were considered in the vegetation classification. We designated vegetation types as native if they had 20% or greater relative cover of native species.

Spatial patterns in vegetation and site factors

We used General Linear Mixed Modeling (GLMM) to investigate two frequently occurring native communities, *Phacelia ciliata-Monolopia lanceolata* (Great Valley phacelia-common monolopia) and *Lupinus bicolor-Vulpia microstachys* (miniature lupine-small fescue), and the most common alien species, *Erodium cicutarium* and *Bromus madritensis ssp. rubens*. We selected the following independent variables for the analysis: Olsen-P, total nitrogen, pH, percent clay, landform, and heat load. Heat load is a 0-1 index in which zero represents the coolest heat load (northeast facing aspect) and one represents the warmest heat load (southwest facing aspect) (McCune and Grace 2002). Soil data were from the shallow (0-15 cm) soils.

We checked for potential correlations between independent variables using Spearman Rank correlation coefficients to minimize the effect of small sample sizes, and we used the variance inflation factor of full models with all covariates for each species and alliance. We analyzed the relationship between relative cover and covariates with the logistic link function for proportional data (number of hits of the species as a proportion of the total vegetation hits) and a binomial error distribution fitted using Laplace approximation. We estimated parameters using Maximum Likelihood and the glmer function in the lme4 package in R 2.12.1 (R Development Core Team 2009) following recommendations in Bolker et al. (2008) and Zuur et al. (2009). Landform and plot ID were included as random effects terms. Landform was included to account for potential autocorrelation between plots collected in the same type of landform. Plot ID was included to account for overdispersion in our dataset.

We compared models using Akaike's Information Criteria corrected for small sample sizes (AIC_c). Because the number of covariates was small, we fit all possible combinations of models, which created nine possible models for the *Lupinus bicolor-Vulpia microstachys* community, *Erodium cicutarium*, and *Bromus madtriensis* ssp. *rubens* and five possible models for the *Phacelia ciliata-Monolopia lanceolata* community. We began by comparing two models with all possible fixed effects covariates with and without the random effects term landform. We then selected the best fitting of these two models and proceeded to compare models varying fixed effects terms following guidelines in Zuur et al. (2009). The best fitting model was the one with the lowest AIC_c and the highest Akaike weight (w_i) or the weight of evidence for each model, given the data, from a set of candidate models (Burnham and Anderson 2002). We used the Akaike weight (w_i) of each model (i) to select a 95% confidence set of models that together account for 95% of the total weight of all models (Burnham and Anderson 2002). We calculated the importance weight (w^+) for each covariate by summing the Akaike weights of all models in which that variable appeared and the model averaged coefficient values for each parameter across all models by summing the product of the Akaike weights (w_i) and coefficient values for each model across all models. We calculated unconditional model standard errors following guidelines in Burnham and Anderson (2002). We checked the goodness of fit of our models by inspecting the partial residual plots of residuals and covariates following recommendations in Zuur et al. (2009) and by checking the departure in deviance for models in the 95% confidence set from a null model including only the random effect term plot ID and an intercept.

Finally, we created a DCA biplot with vegetation data as the main matrix and categorical variables representing degree of cattle use, small mammal use, and infrastructure as the second matrix to isolate site factors driving vegetation groupings (McCune and Mefford 2006).

RESULTS

Grassland community structure

Of 2000 point hits (50 points per plot, 40 plots), 1517 were plants. Remaining hits were soil, rocks, litter, and feces. We observed 53 species, 11 exotic and 42 native to California. The two most species rich plots had eight and ten species (plot 34 and 36, respectively). While only 20% of the species were exotic, they accounted for 65% of overall relative cover; similar composition is the norm in other Mojave Desert grassland studies (Brooks and Berry 2006).

The vegetation split into ten types (Table 1, Figure 4). We arbitrarily defined a native community type as one with greater than 20% relative native cover. Twenty-seven of the forty plots were native vegetation types.

Table 2 displays the species with the highest overall relative cover. *Erodium cicutarium* was found in 39 of 40 plots and had the highest overall relative cover, at 48%. Because *E. cicutarium* was essentially ubiquitous, it had negligible effect on plot separation or clustering in ordination space.

The native forb assemblage *Phacelia ciliata-Monolopia lanceolata*, on plots 2, 4, and 5, was the most distinct vegetation type. The three plots were outliers on an ordination axis which explained 46% of the variability in the relative cover data (R^2=0.455). Native forbs *Caulanthus anceps* (Lemmon’s mustard) and *Erodium macrophyllum* (large leaved filaree) were found only in this plant community and the native *Astragalus didymocarpus* (common dwarf milkvetch) had high affinity with this community. Plot 2 was the only plot where *Erodium cicutarium* was absent.

Lupinus bicolor-Vulpia microstachys, Exotic annual grassland, and *Trifolium albopurpureum* (Indian clover) types were clearly separated by an axis with R^2=0.434. *Lupinus bicolor-Vulpia microstachys* was the most frequent community. It defined 16 of the 40 plots. *Lasthenia californica* (goldfields) was found only in this type at relative cover ranging from 3-27%.

The *Trifolium alborpurpureum* community defined five plots. The relative cover of native species ranged from 14% to 30% in these plots, but the community was designated as non-native because, overall, it did not fall within our ≥ 20% relative cover cut-off.

California native perennial bunchgrasses *Achnatherum speciosum* (desert needlegrass), *Nassella cernua* (nodding needle grass), and *Poa secunda* (pine bluegrass) were found in nine of the forty plots, all in the *Lotus wrangelianus-Nassella cernua* (calf lotus-needle grass), *Lupinus bicolor-Vulpia microstachys, Trifolium albopurpureum,* or *Trifolium albopurpureum-Vulpia microstachys* communities. *Poa secunda* was the most frequent and abundant native perennial bunchgrass, in five plots. It accounted for 40% of the relative cover in plot 35, which was in the *Poa secunda* community. *Nassella cernua* was in three plots (max cover = x%) and *Achnatherum speciosum* in two (max cover = y%).

Site factors: soils, geology, and geomorphology

Shallow soils in plots 2, 4, 5, 18, 20, 23 had values of clay; exchangeable K^+, Na^+, Ca^{2+}, and Mg^{2+}; and total nitrogen and total carbon that exceeded two standard deviations from their respective means (Table 3), causing distributions of these variables to be non-normal and skewed right. These plots were on the Bean Canyon Formation or downstream of both the Bean Canyon Formation and Meeke Mine Formation. Plot 7, 9, 15, and 16 were also downstream of both formations (Figure 2), but shallow soils in these plots had chemical and textural levels closer to the system mean. Soils in plots further removed from the Bean Canyon and Meeke Mine formations also had chemical and textural values closer to study area means (?).

Plot 26 had shallow soil with sulfate greater than two standard deviations from the system mean, which caused the distribution of sulfate to be non-normal and skewed right.

Soil pH and phosphate were approximately normally distributed across the 40 plots with no significant outliers. Sand and clay were inversely correlated, and silt mediated the two particle size classes. pH and sand in deep soils were weakly inversely correlated (R^2=0.526). Soils with the lowest *and* highest pH were on or downstream of Meeke Mine deposits.

Depth of soils ranged from 21 cm to greater than 200 cm. Aside from shallow soils on the summits of the Tehachapi foothills (plot 20 was 21 cm deep and plot 23 was 76 cm deep), depth did not follow the expected pattern of increasing from ridgetop to hillslope to valley bottom (Heimsath et al. 1997).

Heat loads of plots ranged from 0.07 to 0.995.

Plots in areas of past cultivation were on alluvial fans with soils exceeding 130 cm in depth and pH ranging between 6.12-7.18. Shallow soils in four of the six cultivated plots had phosphate levels higher than the 40-plot mean of 10.725 ppm.

Spatial patterns in vegetation and site factors

We found the *Phacelia ciliata-Monolopia lanceolata* community in plots 2, 4, and 5, adjacent to streams carrying materials from the Bean Canyon and Meeke Mine Formations. Relative cover of this community was strongly associated with the percentage of clay and weakly associated with pH (Akaike weights w^+= 0.770 and 0.45, respectively, Table 4; Table 5). These three plots, along with plot 18, had the highest clay levels in the study, with percent clay ranging from 44%

to 57% (mean shallow clay = 18%, n=40; Figure 5a). Along with plot 23, which supported the *Lotus wrangelianus-Nassella cernua* community and was on the limestone Bean Canyon Formation, these three plots had the highest pH levels in the study. The four plots' pH ranged from 7.82 to 8.15 (mean pH = 6.6, n=40; Figure 5a).

The *Trifolium alborpurpureum* vegetation type was also clustered around the Meeke Mine Formation, on soils with high calcium and nitrogen levels. The aforementioned clay-rich plot 18 was in the *Trifolium albopurpureum* community. It was the only plot beside the three *Phacelia ciliata-Monolopia lanceolata* plots with the native forb *Astragalus didymocarpus*.

Relative cover of the *Lupinus bicolor-Vulpia microstachys* community was strongly associated with percent clay and weakly associated with soil pH and total nitrogen (w^+ = 0.959, 0.452, 0.299, respectively, Table 4; Table 5). This community preferred soils low in clay, nitrogen, and pH, and declined to less than 10% relative cover at sites with greater than 30% clay (Figure 5b).

Erodium cicutarium was strongly associated with percent clay and weakly associated with nitrogen and heat load (w^+ = 0.948, 0.448, and 0.289, respectively, Table 4; Table 5). It declined to less than 10% relative cover at sites with greater than 30% clay, but overall the species succeeded in varying conditions of heat load and percent total nitrogen (Figure 5c).

Bromus madritensis ssp. *rubens* was strongly associated with heat load and weakly associated with total nitrogen and Olsen-P (w^+=0.914, 0.45, 0.278, respectively Table 4; Table 5). Its highest relative cover was on northeast-facing sites with heat load less than 0.5 (Figure 5d). It was absent from eleven plots, which all had heat loads exceeding 0.9.

Achnatherum speciosum, Nassella cernua, and *Poa secunda* were absent from plots that had been farmed historically. Soils in the five plots with *Nassella cernua* and/or *Achnatherum speciosum* were relatively shallow (48-82 cm) with phosphorus levels well below the mean and clay that increased with depth.

Plot 37, in the *Coreopsis bigelovii-Lupinus nanus-Eschscholzia californica* community, had soil with the lowest nitrogen, lowest calcium, and highest sand of all soils in the study. The two *Lupinus concinnus* (bajada lupine) plots were also very sandy and had the highest heat loads and elevations in the study.

Our DCA biplot indicated that cattle use, small mammal use, and ranch infrastructure had little to no effect on the structure of vegetation. Of the seven plots that had been farmed in the past, five supported the native *Lupinus bicolor-Vulpia microstachys* community, one supported the native *Amsinckia menziesii var. intermedia* Herbaceous Alliance community, and one supported Exotic annual grassland (Figure 4).

Models including landform such as alluvial fan and terrace escarpment as covariates did not perform well. They only appeared in the 95% confidence set of models for *Erodium cicutarium* and *Bromus madritensis* ssp. *rubens* and were never the best fitting models (w_i =0.03 and 0.065 respectively, Table 5).

DISCUSSION AND CONCLUSIONS

Vegetation alliances and associations

We found ten grassland communities in the western Mojave on Tejon Ranch. Two were consistent with alliances described by the California Native Plant Society (CNPS) in the Manual of California Vegetation (Sawyer et al. 2009). Our *Amsinckia menziesii var. intermedia* Herbaceous Alliance follows the membership rules of the CNPS *Amsinckia* (*menziesii, tessellata*) Herbaceous Alliance. Also, CNPS' *Poa secunda* Herbaceous Alliance is defined by >50% relative cover; our *Poa secunda* type had ≥40% relative cover *Poa secunda* (Sawyer et al. 2009).

Our Exotic annual grassland type is similar to CNPS' *Bromus rubens-Schismus (arabicus, barbatus)* Semi-Natural Herbaceous Stands in the Mojave Desert (According to Calflora, *Bromus madritensis* ssp. *rubens* is undergoing a name change and will soon be called *Bromus rubens*). *Bromus rubens* accounts for >80% relative cover in the CNPS alliance (Sawyer et al. 2009), however, the type we found had lower *B. madritensis* ssp. *rubens* (*B. rubens*) cover, at 40% or less.

Our *Lupinus bicolor-Vulpia microstachys* type largely falls within CNPS' *Lasthenia californica-Plantago erecta-Vulpia microstachys* Herbaceous Alliance (Jennifer Buck, CNPS, pers. comm., June 2, 2011). We propose that the Mojave Desert Region description of this alliance - "Stands occur with *L. californica* and *P. erecta* but lack *V. microstachys* in the Antelope Valley and adjacent areas as far north as Inyokern" - be amended (Sawyer et al. 2009). Based on our findings, the Mojave Desert description or a newly described association should include both *V. microstachys* and *L. bicolor*.

We found extensive cover of *Trifolium albopurpureum* and *Phacelia ciliata*, yet neither is in alliances or associations described by Sawyer et al. (2009). We propose that these species are included, at least at the association level.

Monolopia lanceolata is included as part of the *Eschscholzia californica* Herbaceous Alliance on well-drained soils in the western Mojave Desert (Sawyer et al. 2009), but we observed an opposite trend, with *M. lanceolata* on clay-rich soils with poor drainage.

Site factors driving community distribution

Native herbaceous communities are succeeding among the multitudes of *Bromus madritensis* ssp. *rubens* and *Erodium cicutarium* in our study site. The high spatial correlation of these native communities with environmental site factors in our small plots, in which vegetation and sites factors are closely linked, coupled with the lack of evidence that cattle and small mammal herbivory affect vegetation distribution, indicate that our study site is likely driven by non-equilibrium system processes: environmental site factors are the primary drivers of vegetation abundance and distribution.

Clay

The proportion of clay-sized particles in the soil near the surface is the strongest control on vegetation distribution. In turn, the geology likely controls distribution of clay. In the spring of 2010, clay was strongly positively related to the distribution of the most distinct vegetation type in our ordination, *Phacelia ciliata-Monolopia lanceolata*; strongly negatively correlated with the most frequent and widespread vegetation type, *Lupinus bicolor-Vulpia microstachys* and strongly negatively correlated with the species with the highest frequency and overall relative cover, *Erodium cicutarium*. Based on those results, we modeled the relative cover of these important communities and species as functions of clay (Figure 6). In this model, as clay increases, *Phacelia ciliata-Monolopia lanceolata* increases and *Lupinus bicolor-Vulpia microstachys* decreases. *Erodium cicutarium* decreases *slightly* as clay increases, but its cover never reaches zero.

Low fertility and natives

Like grassland ecologists in Diablo Range, serpentine, and Coastal Prairie ecosystems (Gea-Izquierdo et al. 2007, Huenneke et al. 1990, Weiss 1999, Gram et al. 2004, Maron and Connors 1996), we observed native species occurring more frequently in low fertility soils. *Lupinus bicolor-Vulpia microstachys*, *Coreopsis bigelovii-Lupinus nanus-Eschscholzia californica*, and *Lupinus concinnus* communities, and native perennial bunchgrasses *Nassella cernua* and *Achnatherum speciosum* were found on low fertility sites. On the other end of the spectrum, sites supersaturated with nutrients were also hospitable to natives, as evinced by the *Phacelia ciliata-Monolopia lanceolata* and *Lotus wrangelianus-Nassella cernua* communities. These findings echo general trends in California grasslands: natives tend to be relegated to marginal sites with difficult growing conditions (Bartolome et al. 2007).

Plots supporting *Nassella cernua* and *Achnatherum speciosum*, which had low phosphorus soils in which clay increased with depth, also warrant further investigation. It is possible the deeper roots of the perennials may have a competitive advantage over the shallower roots of the exotic annuals (Gea-Izquierdo et al. 2007), and they are accessing nutrients and water retained by the deeper, more clay-rich soils. Also, the deeper perennial roots may have the ability to store phosphate for later use whereas annuals cannot (Jeffrey 1987).

Climate and exotics

Erodium cicutarium and/or *Bromus madritensis* ssp. *rubens* were present in all environmental conditions we measured. In the southwest facing, high heat load plots where *Bromus madritensis* ssp. *rubens* was absent, *Erodium cicutarium* had high relative cover. *Bromus madritensis* ssp. *rubens* hails from more mesic native environments than *Erodium cicutarium* (Brooks 2000, Sauer 1988), and where conditions are too arid for this alien grass, the alien forb dominates. Likewise, *Erodium cicutarium* cover declines in soils with plentiful clay, which might be expected from a species with arid origins, but clay was not a deterring factor for the *Bromus madritensis* ssp. *rubens* whose mesic home is presumably clay-rich.

Implications for restoration

In past agricultural sites, native perennial bunchgrasses were absent, but native annuals were abundant. Because previous studies have found that past agricultural sites are not hospitable to native species, this result was a surprise and may be of interest to grassland ecologists and restorationists statewide.

California desert grassland managers planning native annual restoration projects should consider choosing the appropriate species for the environments identified by this study. Seeds of *Phacelia ciliata, Monolopia lanceolata*, *Trifolium albopurpureum*, *Lupinus bicolor,* and *Vulpia microstachys* are sold for restoration projects (California Native Plant Link Exchange 2011). For *Phacelia ciliata* and *Monolopia lanceolata*, soils high in clay and pH appear to be the most appropriate. For *Trifolium albopurpureum*, clay rich, high nitrogen, high calcium soils may yield successful restoration outcomes. For *Lupinus bicolor* and *Vulpia microstachys*, sandy, low nutrient sites and even old agricultural sites would be promising. Control efforts for *Erodium cicutarium* may be more successful on clay rich soils, while control efforts for *B. madritensis* ssp. *rubens* may be more successful on warmer aspects.

Further research

More investigation is needed to understand the nutrient contributions of the mixed alluvium parent material to both the soils and the vegetation on and downstream of the Pliocene lacustrine Meeke Mine Formation and Paleozoic/Mesozoic Bean Canyon Formation. Several of these plots supported native communities, yet others supported Exotic annual grassland. Similarly, several plots had extremely high levels of total nitrogen, potassium, sodium, calcium, magnesium, and clay, yet others had nutrient levels closer to the system mean. Perplexingly, soils with the lowest *and* highest pH were on or downstream of Meeke Mine deposits. We hypothesize that alluvial parent material from these formations is the primary reason that some soils have extreme nutrient and clay values, and that soils with low pH and non-extreme chemical and textural values likely formed where Pleistocene gravels were deposited thickly. Future attention should be paid to dominance patterns of the communities that occur on these soil types: *Trifolium alborpurpureum* and *Phacelia ciliata-Monolopia lanceolata*.

In this paper, we described the vegetation of the study area using data-driven, quantitative methods. We isolated soils, geomorphology, and geology that were hospitable to native species in a year when rains were largely heavy and late. Temporal and spatial variation is extremely high in California grasslands, and multiple-year studies are often necessary to characterize ecological dynamics (Bartolome et al. 2007). For example, in the western Mojave, exotics tend to flourish in dry years, possibly because they germinate prodigiously with little rainfall whereas native annual seeds "wait" for more favorable conditions (Brooks 1999b). Conversely, during wet years, annual native species populations have spiked at the expense of exotic annual populations (Brooks 1999b, Brooks and Berry 2006). Also, the timing and amount of rains can lead to dominance of either grasses, *Erodium*, or *Trifolium* (Pitt and Heady 1978). When we collected our data in the spring of 2010, forbs were in great abundance in the western Antelope Valley. A quick pulse of rain fell in October 2009, and then the site received little to no rain until December, when rains fell heavily. This study illustrated that native annual species succeeded in certain site types under these specific weather conditions. We designed this study to illuminate spatial patterns in environmental sites and vegetation in a snapshot in time, but capturing interannual variability in the vegetation will be essential to further understanding why native grasses and forbs are able to persist in the western Mojave.

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Table 1: Ten grassland community types with membership rules. We designated vegetation types as native if they had 20% or greater relative cover of native species. California Native Plant Society (CNPS) information is from Sawyer et al. 2009.

Vegetation type	**Membership rules**	**Native cover**	**Native type?**	**# of plots**
Amsinckia menziesii var. intermedia Herbaceous Alliance	≥10% relative cover of *Amsinckia menziesii var. intermedia*. Same as alliance described by CNPS.	28%	Yes	1
Coreopsis bigelovii-Lupinus nanus-Eschscholzia californica	≥10% relative cover of each of the species.	45%	Yes	1
Phacelia ciliata- Monolopia lanceolata	>20% relative cover of *Monolopia lanceolata*, *Phacelia ciliata*, with *Caulanthus anceps* and *Erodium macrophyllum.*	>50%	Yes	3
Lotus wrangelianus-Nassella cernua	≥10% relative cover *Lotus wrangelianus*, ≥6% cover *Nassella cernua*.	25%	Yes	1
Lupinus bicolor-Vulpia microstachys	≥10% relative cover of *Lupinus bicolor*, *Vulpia microstachys*, with *Lasthenia californica.*	≥22%	Yes	16
Exotic annual grassland	>80% relative cover of exotic herbaceous species commonly observed in California annual grassland. Similar to CNPS *Bromus rubens-Schismus (arabicus, barbatus)* Semi-Natural Herbaceous Stands.	<20%	No	8
Lupinus concinnus	≥10% relative cover *Lupinus concinnus*.	≥20%	Yes	2
Poa secunda	≥40% relative cover *Poa secunda*. Similar to CNPS *Poa secunda* Herbaceous Alliance.	44%	Yes	1
Trifolium albopurpureum	≥3% relative cover *Trifolium albopurpureum.*	≥14%	No	5
Trifolium albopurpureum-Vulpia microstachys	≥10% relative cover *Trifolium albopurpureum*, *Vulpia microstachys*.	≥28%	Yes	2

Table 2. Eight species with the highest total relative cover.

Species	**Species origin**	**Total relative cover**
Erodium cicutarium	Exotic	47.9%
Bromus madritensis ssp. *rubens*	Exotic	10.6%
Lupinus bicolor	Native	8.7%
Vulpia microstachys	Native	6.1%
Monolopia lanceolata	Native	2.8%
Phacelia ciliata	Native	2.4%
Bromus tectorum	Exotic	2.4%
Poa secunda	Native	1.3%

Table 3: Chemical and textural properties of shallow soils with measures of central tendency, variability, and range, and the plots with soil property values greater than two standard deviations from the mean.

Soil Property	**Median**	**Mean**	**std dev**	**Minimum**	**Maximum**	**Plots > 2 std. dev. from mean**
Calcium (meq/100 g)	6.98	12.583	12.14	2.95	47.9	23, 2, 4, 5
Clay (%)	13	18	12.176	8	57	18, 2, 5, 4 > 3 std dev
Magnesium (meq/100 g)	1.235	1.954	1.731	0.47	9.48	4
Potassium (meq/100 g)	0.35	0.53	0.434	0.07	1.84	2, 5, 4
Sodium (meq/100 g)	0.02	0.12	0.378	<0.01	2.28	5
Sulfate (ppm)	2.4	2.5	1.309	1.1	8.7	26
Total Carbon (%)	0.595	1.032	1.253	0.15	7.38	23, 20 > 5 std dev
Total Nitrogen (%)	0.0565	0.068	0.039	0.01	0.193	18, 23

Table 4. Relative support for fixed effect covariates from models of the relative cover of species and communities. *N* is the number of models in which the covariate occurs and w^+ is the cumulative Akaike importance weight for all models sharing a given covariate. Coefficient values are model averaged estimates from all models in the 95% confidence set with unconditional model averaged standard error estimates in parentheses.

	Covariate	*N*	w^+	Coefficient
Lupinus bicolor-Vulpia microstachys				
	Clay	5	0.959	-0.128 (0.02)
	pH	5	0.452	-0.241 (0.226)
	Nitrogen	5	0.299	-1.730 (3.255)
Phacelia ciliata-Monolopia lanceolata				
	Clay	3	0.77	0.149 (0.097)
	pH	3	0.45	3.676 (3.308)
Erodium cicutarium				
	Clay	5	0.948	-0.020 (0.008)
	N	5	0.448	1.57 (1.427)
	Heat	5	0.289	0.058 (0.042)
Bromus rubens				
	Heat load	5	0.914	-1.540 (0.631)
	Nitrogen	5	0.45	2.556 (2.478)
	Phosphorus	5	0.278	0.002 (0.005)

Table 5. AIC_c results for models fitted to vegetation relative cover data collected from 40 plots in the western Mojave in 2010. Models show fixed effect covariates included in the 95% confidence set of models.

Model	*K*	ΔAIC_c	w_i
Lupinus bicolor and Vulpia microstachys			
Clay	3	0	0.398
pH + Clay	4	0.551	0.302
Clay + N	4	2.104	0.139
pH + Clay + N	5	2.843	0.096
Lakebed			
pH + Clay	4	0	0.396
Clay	3	0.791	0.267
pH	3	1.202	0.217
Erodium cicutarium			
Clay	3	0	0.397
N + Clay	4	0.721	0.277
N + Heat load + Clay	5	2.303	0.125
Clay + Heat load	4	2.411	0.119
N + Heat load + Clay*	6	5.192	0.030
Bromus rubens			
Heat load	3	0	0.407
N + Heat load	4	1.049	0.241
P + Heat load	4	2.328	0.127
N + P + Heat load	5	3.430	0.073
N + P + Heat load*	6	3.668	0.065

***** Denotes the model also includes landform as a random effect term. All other models include only plot ID. *K* is the number of parameters for each model. ΔAIC_c is the difference in AIC_c relative to the best model and w_i is the Akaike weight.

Figure 1. 40 study plots on varying landforms and aspects. Plot numbers correspond to latitude, with 1 being the southernmost plot.

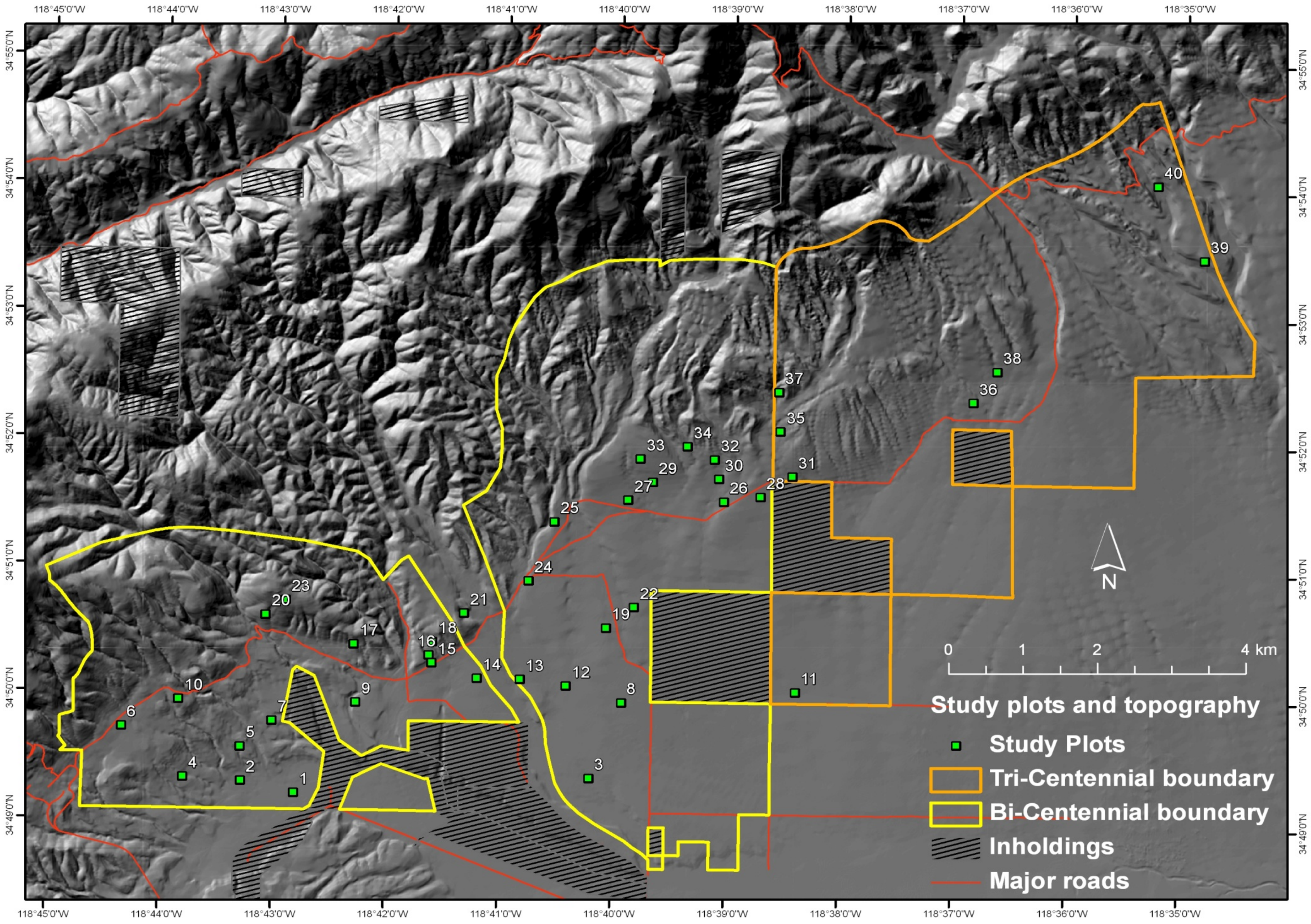
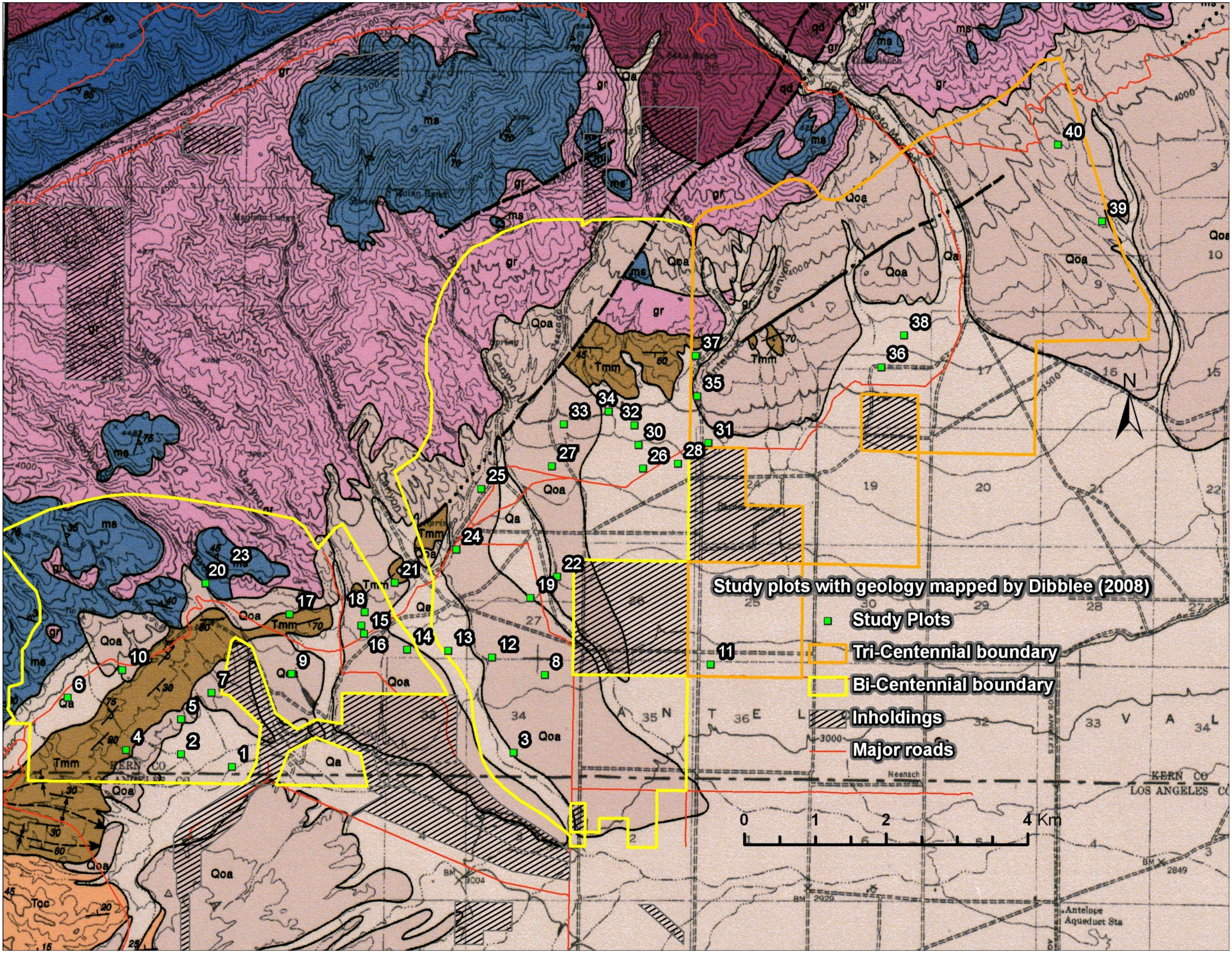


Figure 2: Geology of study area (Dibblee 2008) with study plots. Northwest-southeast trending streams carry alluvium from granitic Tehachapis, calcareous metasedimentary pendants, and Pliocene lakebeds from high elevations to the bajada-alluvial fan complex in the middle of the basin.

Geology key:

- Blue: Bean Canyon formation. Metasedimentary sequence, unfossilferous, occurs as pendants in granitic rocks of Tehachapi Mountains, intruded by Cretaceous rocks; age, probably late Paleozoic
  - ms - schist, dark gray to nearly black, platy, varies to phullite, hornfels, and argillite, with faint to conspicuous bedding
  - ml – limestone, in large part recrystallized to marble, of mainly calcite and some dolomite, white with some bluish gray veins, with coards and fine layers intercalated.
- Qoa-Older Surficial Sediments. Loose to weakly consolidated, dissected where elevated; age, presumably Pleistocene. Alluvial gravel and sand of unsorted detritus, poorly bedded.
- Qa - Surficial Sediments. Unconsolidated, undissected alluvial sediments. Alluvial silt, sand and gravel of valley areas.
- Tmm (brown) - Meeke Mine Formation. Terrestrial fluviatile gravels; age late Pliocene or early Pleistocene. Alluvial gravel, weakly consolidated, composed of subangluar to rounded pebbles and cobbles of granite rock, hornfels, black schist, quartzite, and marble in a matrix of gray-brown loamy gritty sand.
- gr (pink) - Granitic and dioritic rocks. Plutonic crystalline basement complex of Tehachapi Mountains , Antelope Buttes, and Willow Springs Mountain; age, Jurassic or Cretaceous. Granite, white to cream white, massive, of quartz and feldspar, with numerous white dikes and apophyses of fine-grained aplite to coarse-grained pegmatite.



Study plots with geology mapped by Dibblee (2008)

Figure 3. Rolling topography of terrace escarpments and valleys in the background and gently sloping bajadas in the foreground.

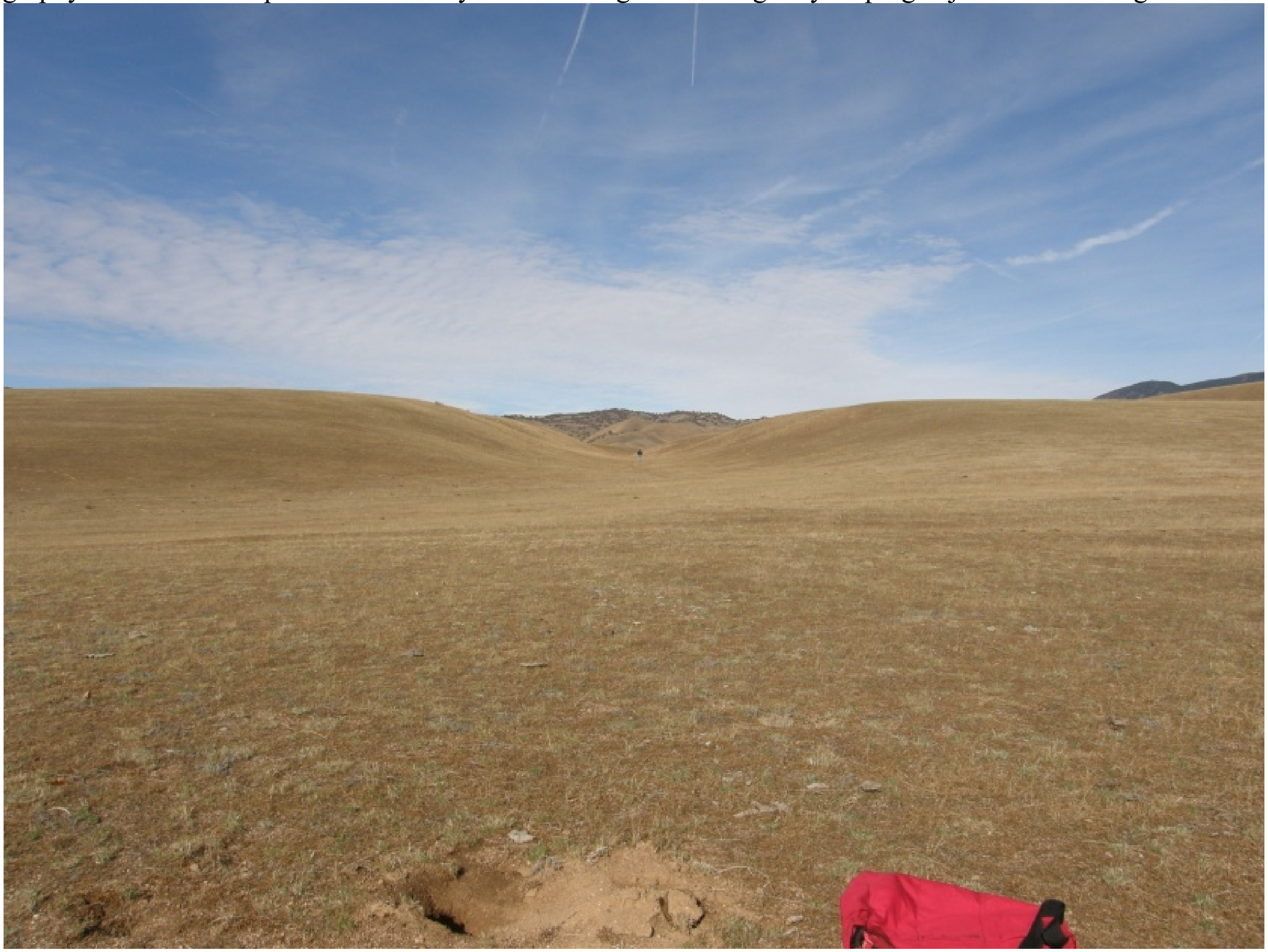


Figure 4. Ten vegetation types in 40 plots with topography and historically farmed areas.

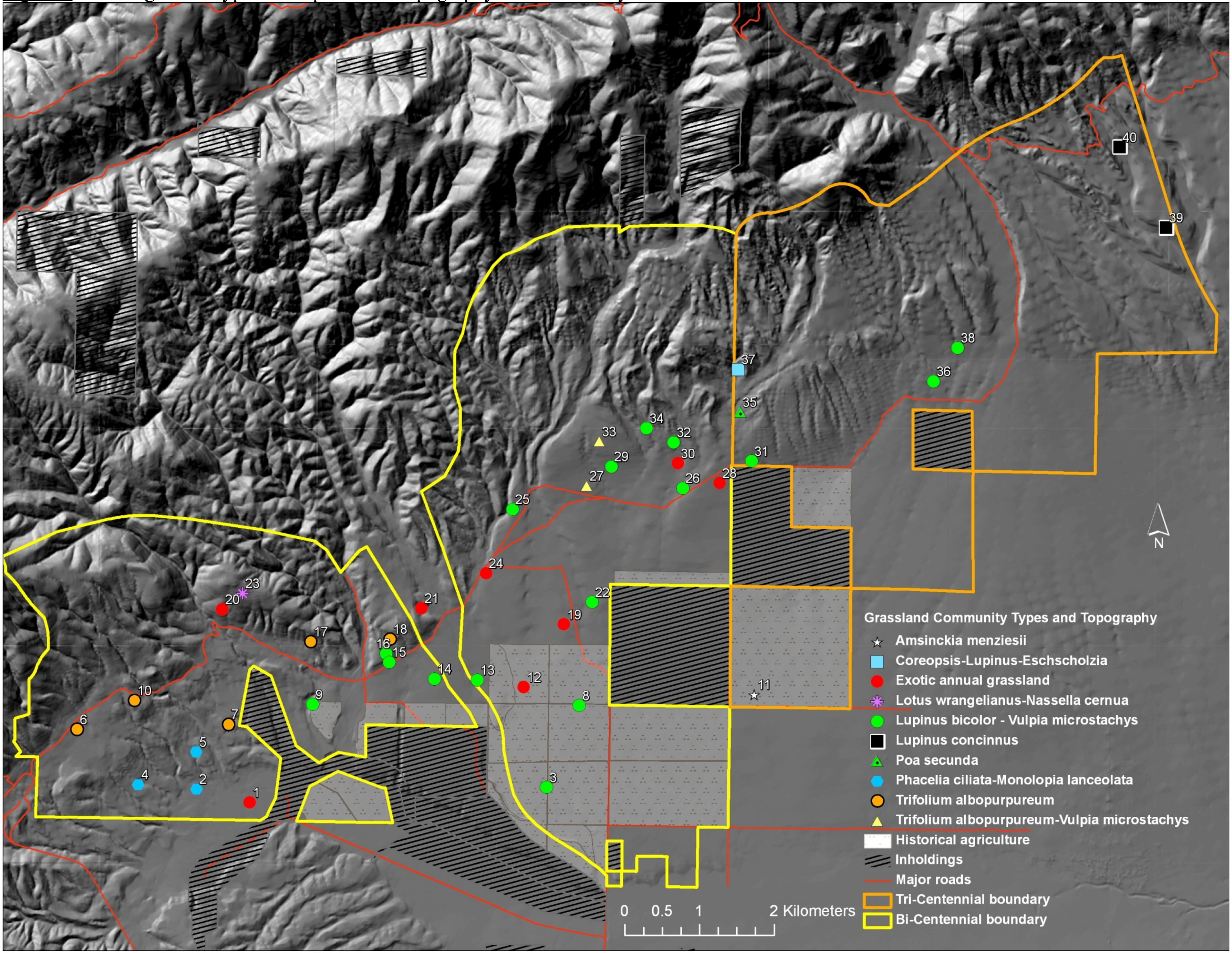
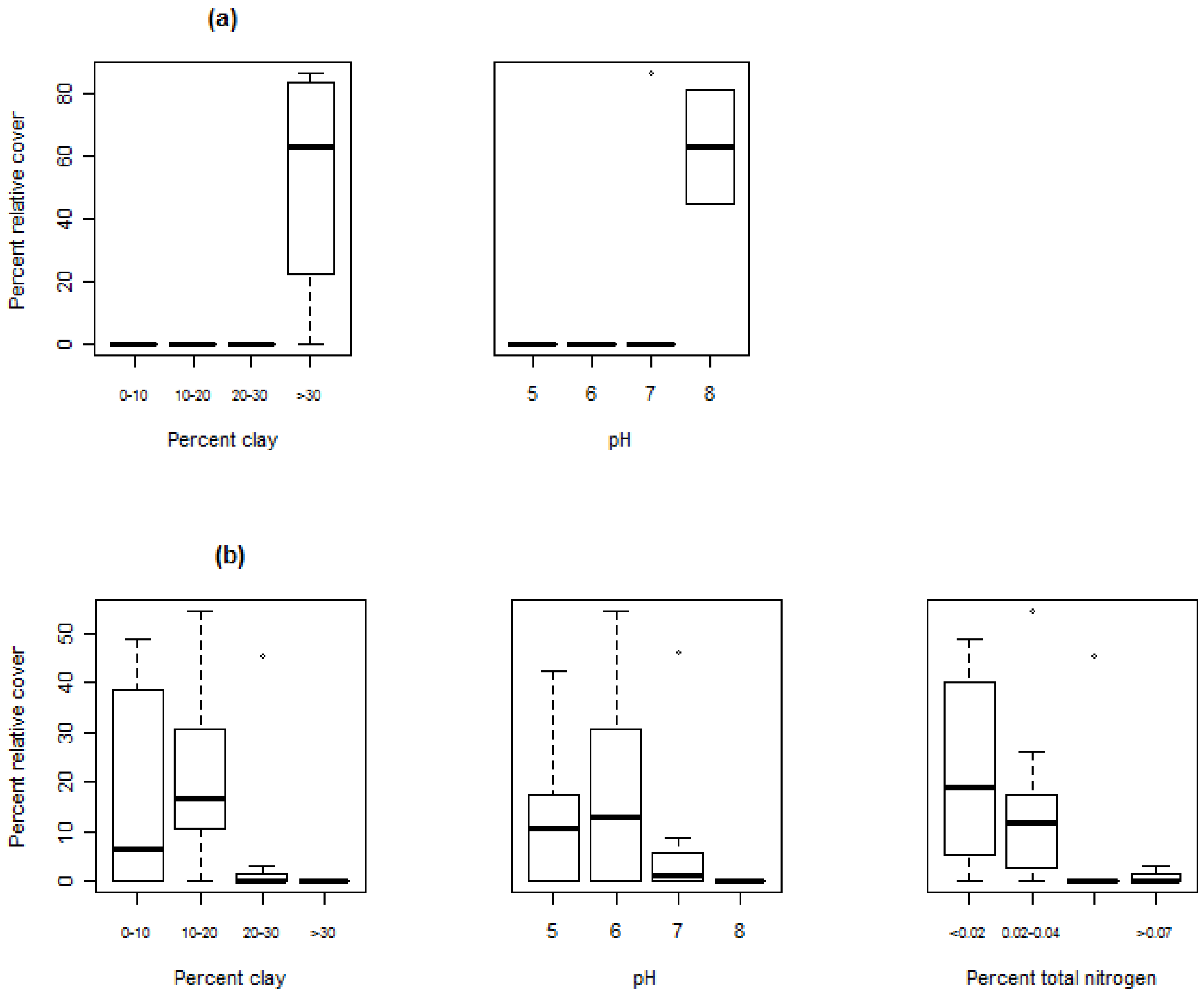
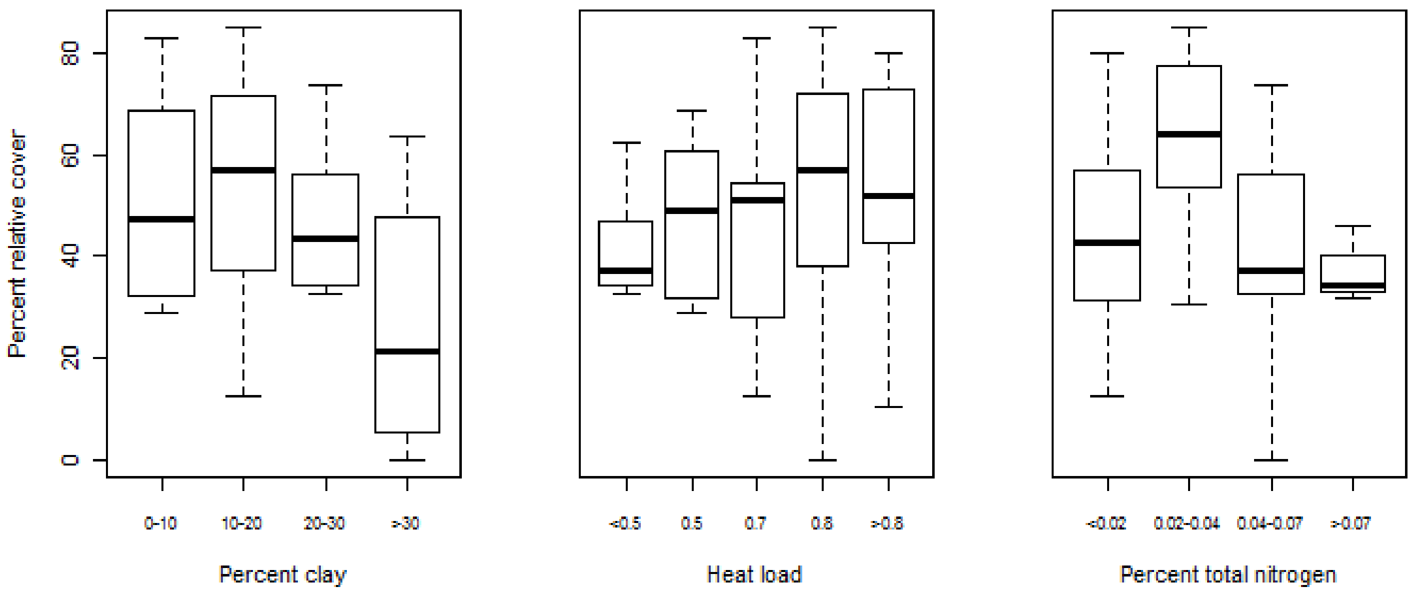


Figure 5. Relationships between common exotics and vegetation types and soil covariates included in analysis of factors determining relative cover. a) *Phacelia ciliata-Monolopia lanceolata* b) *Lupinus bicolor-Vulpia microstachys* c) *Erodium cicutarium*, d) *Bromus madritensis* ssp. *rubens*



(c)


Percent relative cover
0
20
40
60
80
0-10
10-20
20-30
>30
Percent clay
<0.5
0.5
0.7
0.8
>0.8
Heat load
<0.02
0.02-0.04
0.04-0.07
>0.07
Percent total nitrogen

(d)

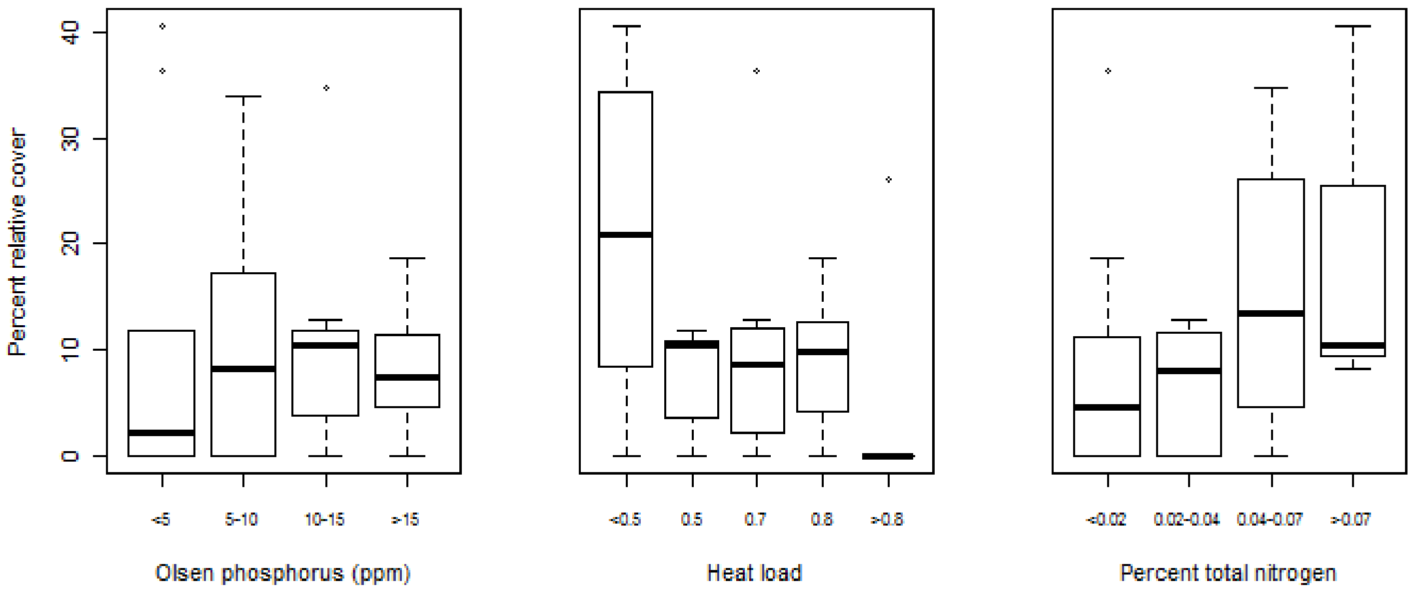

Percent relative cover
0
10
20
30
40
<5
5-10
10-15
>15
Olsen phosphorus (ppm)
<0.5
0.5
0.7
0.8
>0.8
Heat load
<0.02
0.02-0.04
0.04-0.07
>0.07
Percent total nitrogen

Figure 6. Estimated relative cover of common exotics and vegetation types as a function of clay. Results were obtained via model averaging across the 95% confidence set of models.