Taxonomic, phylogenetic, and functional diversity of a Sierra Nevada subalpine meadow community along soil hydrological gradient

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Abstract

Mountain meadows occupy about 2% of the Sierra Nevada Range but house many narrow endemic and imperiled species. In this study, we investigated plant community structure and assessed species, phylogenetic, and functional diversity of Dog Valley Meadow, a subalpine meadow in the northern Sierra Nevada Range, California. Variation in groundwater level creates three distinct meadow-type habitats – hydric, mesic, and xeric types – making it an excellent system to investigate plant community structure at local scale along a hydrological gradient, while providing a complete floristic baseline data for conservation management and research. We estimated plant presence and cover or abundance in 341 1 m^2 plots within 27 line transects separated by 10 m across the entire meadow. We computed several species, phylogenetic, and functional alpha diversity at plot and meadow type levels, as well as species and functional beta diversity measures along a soil hydrological gradient. The phylogenetic diversity calculations were based on a pruned chronogram phylogeny. We also conducted nonmetric multidimensional scaling (NMDS) to visualize species beta diversity and determined the local site and species contributions to beta diversity. Furthermore, we conducted indicator species analysis to investigate ecological fidelity of plants to meadow types, and assessed nonrandom species co-occurrences. We assessed the species nativity, growth form, conservation status, and response to grazing, and conducted a census of coniferous species in the meadow. We recorded 80 species across 23 plant families in the meadow, including 67 plants in the hydric, 55 in xeric, and 53 in the mesic habitats. Asteraceae and Poaceae were the most represented families in the meadow. The meadow community is dominated by native herbaceous and graminoid plants, only four of which are of conservation concern. The xeric habitats have the highest plot-level species diversity, phylogenetic diversity, and functional divergence. Hydric meadow communities have the highest and significant species dissimilarity from other meadow types, while mesic habitats have the highest functional beta diversity. A total of 37 indicator species indicates strong ecological fidelity across the three meadow types, and this drives 23% nonrandom species co-occurrences. The phylogenetic and functional diversity measures show that the meadow community is driven by phylogenetic clustering coupled with high functional divergence to facilitate resource partitioning. A roughly even representation of decreasers, increasers, and invaders in the meadow highlight post-disturbance vegetative recovery after historical grazing. We recorded about 300 conifer saplings and juveniles mostly in the mesic and xeric meadows, indicating recent encroachment associated with lower groundwater levels, driven by regional aridification. This baseline biodiversity data can support conservation and restoration efforts and facilitate future monitoring efforts in the meadow.

Keywords: species diversity, phylogenetic diversity, functional diversity, Dog Valley Meadow, hydric meadow, xeric meadow, mesic meadow.

Introduction

The Sierra Nevada Range, running north-south for over 600 km, is among the largest and longest mountain ranges in North America (Wolf and Cooper 2015). Alpine and subalpine meadows found on Sierra Nevada range in elevations from 280 m to 3,935 m, and between 0.4 and ~1900 ha in land area coverage (Allen 1987; Fryjoff-Hung and Viers 2012). Over 18,000 mountain meadows occur in the Sierra Nevada Range occupying about 2% of the total area, but housing over 1400 vascular plants including 170 species of conservation concern, and over 500 obligate meadow plants (Roche et al. 2012; Merrill and Jurjavcic 2018). These meadows are dominated by herbs and/or graminoids growing on fine-textured soils supported by shallow groundwater level on impermeable bedrocks (Weixelman et al. 2011). Therefore, Sierra Nevada meadows and their communities are controlled by soil hydrology, receiving their water from groundwater recharge, seasonal precipitation, recharge from nearby creeks, surface runoffs, springs, and underground seeps (Loheide et al. 2009; Weixelman et al. 2011). The meadows are groundwater reservoirs and recharges, they support biodiversity through summer water releases, prevent winter and spring soil erosion, and act as carbon sinks (Weixelman et al. 2011; Purdy et al. 2012; Norton et al. 2011, 2014). The Sierra Nevada meadows also continue to be a vital summer habitat for native birds, amphibians, and fishes (Erman 1996; Kattelmann and Embury 1996; Siegel and DeSante 1999).

Paleobiological studies show that most of the contemporary meadows in the Sierra Nevada appeared between 4000 and 3000 years ago under wetter climatic conditions and increased snowpack, while groundwater level rises may have excluded the alpine trees and created the forest gaps (Anderson 1987; Anderson and Smith 1994; Parker 2002). Therefore, meadow plant communities in the northern Sierra Nevada Range, especially those on the eastern slopes, are vulnerable to climate change due to groundwater table reduction resulting from precipitation fluctuations, decrease in snowpack, early spring snowmelt, and increasing evapotranspiration (Viers et al. 2013; Drexler et al. 2013; Hauptfeld et al. 2014; Goulden and Bales 2014; Albano et al. 2019); however, climatic vulnerability is also dependent on edaphic factors, topographic positioning, and underlying geology (Vivoni et al. 2008; Weixelman et al. 2011; Lundquist & Loheide 2011; Kitlasten and Fogg 2015). Given that the hydrology of meadows is influenced by precipitation seasonality, principally, winter snow, climate change, characterized by warm and wet winters and early snowmelt will have profound impacts on meadow recharge and consequently on meadow community plant composition. Therefore, long-term monitoring allows us to understand how climate change directly or indirectly impacts meadow plant communities and assess their ecological stability over time.

Plant community structure in a meadow is primarily driven by groundwater level. On one end, there are perennially wet meadows with shallow water levels and are called hydric type meadows; they support dense vegetation of water-loving plants, some of which form organic soils and peatland (Dwire et al. 2006; Lowry et al. 2011; Weixelman et al. 2011). On the other end, meadows with deeper groundwater levels are dominated by xeric type vegetation (Dwire et al. 2006; Lowry et al. 2011; Weixelman et al. 2011). Moreover, mesic meadow types are seasonally wet meadows with intermediate conditions between xeric and hydric habitats. Most meadows in the Sierra Nevada are classified as having one meadow type, but the Dog Valley meadow, a large subalpine meadow (71.58 acres) located at 1834.7 m elevation on the northern Sierra Nevada Range, is exceptional having distinct hydric, mesic, and xeric habitats in the same meadow. Based on meadow classification key, the Dog Valley Meadow could be classified as dry meadow with mosaics of groundwater seepages and springs flowing downhill through small channels into the nearby Dog Creek (Weixelman et al. 2011). The xeric meadow is dry by midsummer and is dominated by perennial dryland grasses, sedges, and herbs. The hydric meadow portion includes discharge slopes (seeps and channels), the adjacent Dog Creek into which the seeps and channels empty, and the surrounding riparian vegetation. Mesic meadow is a seasonally wet transitional vegetation zone between the xeric and hydric habitats. The meadow inhabits four species of conservation concern including the federally threatened *Ivesia webberi* and the narrow endemic congeneric, *I. aperta* var. *canina*. Additionally, the meadow has biocultural significance, having historically been part of the California trail. Among 10 surveyed sites that inhabit the federally threatened *I. webberi*, the Dog Valley meadow has the highest species richness and diversity (Borokini et al. 2021).

This study investigated alpha taxonomic, phylogenetic, and functional diversity, and taxonomic and functional beta diversity along the soil hydrological gradient in the Dog Valley meadow. Many similar studies have investigated species diversity in different meadows that are geographically distinct, thus adding potential spatial autocorrelation confounding factors (e.g., Moore et al., 2013; Freitas et al., 2014). In this study, we focused on a single large meadow with three distinct habitat types along the soil hydrological gradient, thus offering an opportunity to disentangle the local effects of soil hydrology on meadow plant communities. We used this study to answer the following questions: (a) Is there significant difference in species, functional, and phylogenetic diversity along the soil hydrological gradient? (b) Is there a phylogenetic and functional community structure for plants in the meadow? (c) Is beta diversity structured along a hydrological gradient in the meadow? (d) Are species distributions and co-occurrences within the meadow nonrandom, and are they structured along hydrological gradients? (e) What is the spatial pattern of distribution of woody species in the meadow? Despite its management by the U.S. Forest Service as part of the Humboldt-Toiyabe National Forest, the botanical knowledge of the Dog Valley meadow is incomplete, thus we provide baseline biodiversity data for immediate conservation management and policy use and future monitoring under climate change.

Materials and Methods

Field surveys

We laid out 27 line transects across the entire Dog Valley meadow in the west-northwest direction to capture all three meadow types. Each transect was approximately 10 m apart, and along each transect, we established 1 m^2 sampling units (plots) which were 10 m apart. Within each plot, we identified all taxa to the species-level and estimated their abundance. Field-identifications were confirmed by taxonomic expert at the University of Nevada Reno herbarium. In total, we surveyed 341 1 m^2

plots, distributed in 113 hydric, 131 mesic, and 97 xeric plots between June 13 and 28, 2024. We also recorded elevation and coordinates (WGS84 reference system) for all surveyed plots using Garmin GPS eTrex 64. Voucher specimens collected during the surveys were deposited at the Natural History Museum of Truckee Meadows Community College, Reno, Nevada. Additionally, we counted all coniferous species in the meadow and recorded their GPS coordinates and described the location within the meadows. We used estimated heights of the conifer species to categorize them into age classes: saplings (<1.5 m), small juveniles (1.5-4.5 m), large juveniles (4.5-15.0 m), and matured trees (>15 m), based on standard classifications (Gucker 2007).

Data curation

The raw plant sampling data was formatted into a species by site matrix containing species composition and abundance for all surveyed plots. We standardized the species names, compiled their growth forms, and native status based on the Kew's Plants of the World Online (https://powo.science.kew.org/), and determined their national and global conservation status using the NatureServe explorer (https://explorer.natureserve.org/) and the IUCN Red List of Threatened Species (https://www.iucnredlist.org/), respectively. We also categorized the species into decreasers, increasers, and invaders, based on literature that associated the overrepresentation of these categories with overgrazing (Stoddart et al. 1975; Weeden 1981; Ratliff 1985). Decreasers are highly palatable forage plants that indicate healthy climax vegetation which reduce their abundance under heavy grazing; increasers are less palatable or grazing-tolerant plants in grazed communities, therefore their density increases as decreasers shrink under grazing (Ksiksi et al. 2005). Invaders are minimal or absent in climax communities, but become opportunistic invaders which colonize heavily degraded and disturbed vegetation (Ksiksi et al. 2005).

Data analysis

Species-based analyses: We assessed several plot-level alpha diversity measures including species richness, Shannon-Weiner *H′* diversity index, and Hill's numbers for the 341 1 m^2 plots using functions in vegan R package 2.7-3 (Oksanen et al. 2026). Hill's numbers represent the exponential conversion of the Shannon-Weiner *H′* diversity index into natural number for ecological interpretation and comparison across sampling units (Jost 2007). We computed the beta diversity across the three meadow types using the Hellinger distance in adespatial R package 0.3-29 (Dray et al. 2026). Additionally, we used the beta.div function in adespatial R package to decompose Hellinger-based beta diversity into total sum of squares (SS_{total}) and total beta dissimilarity (BD_{total}), as well as the local site and species contributions to beta diversity (LCBD and SCBD, respectively) across hydrological gradients in the meadow (Legendre and De Cáceres 2013). Statistical significance of the LCBD and SCBD values were tested using 1,000 permutations with Holm corrections for the p values. SCBD illustrates the relative contribution of each species, while LCBD describes the effects of microsite conditions to the overall beta diversity, which could highlight the hydrological gradients in the meadow plant community (Legendre and De Cáceres 2013; Hill et al. 2021). We ran a Bray-Curtis dissimilarity-based non-metric multidimensional scaling (NMDS) on Hellinger-transformed plant community data for the meadow using the metaMDS()

function in vegan R package. The NMDS was visualized in a biplot with 95% confidence ellipses around each of the three meadow types.

We also conducted a probabilistic species co-occurrence analysis to investigate if there are nonrandom associations of the surveyed species along hydrological gradients in the meadow (Griffith et al. 2016). This analysis could provide insight into whether species assemblages in each of the three meadow types is random or nonrandom and identify what biotic interactions drive plant communities in these meadow types (Veech 2014). We conducted the co-occurrence analysis in cooccur R package version 1.3 (Griffith et al. 2016). Additionally, we conducted indicator species analysis to investigate what species have ecological fidelity to each of the three meadow types; this analysis is based on the relative frequency and abundance of species in each of the three meadows (Dufrêne and Legendre 1997).

Phylogenetic analysis: We pruned the chronogram megaphylogeny (n=123,189 tips) published in Carruthers et al. (2026). This phylogeny is a supertree constructed using DNA sequences deposited in GenBank and other open and published sources (Carruthers et al. 2026). The pruned tree (Figure S1) was used to calculate several plot-level and total phylogenetic diversity measures across the three habitat types using functions in picante R package version 1.8.2 (Kembel et al. 2010). The calculated alpha phylogenetic measures include Faith's phylogenetic diversity (PD), mean pairwise distance (MPD), and mean nearest-pairwise distance (MNTD), as well as standardized effect sizes with 1,000 randomizations to obtain net relatedness index (NRI) and nearest taxon index (NTI) from MPD and MNTD, respectively. Because of anticipated high correlation between species richness and PD, we conducted SES on the PD, using "taxa.labels" null model to investigate if observed PD would be different than random (Pavoine et al. 2013; Swenson 2014; Jarzyna et al. 2021). Significant deviation from null assemblages is obtained when SES values are < -1.96 or > 1.96 (Lazzaro et al. 2020). Positive NRI or NTI (> 0.5) values indicate phylogenetic clustering, negative values (NRI or NTI < -0.5) suggest phylogenetic overdispersion, while values close to zero are interpreted as random assemblages (Webb et al. 2006; Gundersen and Vadstein 2024). We also estimated divergence time, that is, the evolutionary age of the surveyed species from the phylogeny.

Functional diversity (FD) analyses: We downloaded available data of the four most represented functional traits for the surveyed species from the Botanical Information and Ecology Network (BIEN) trait database (Enquist et al. 2026) using the BIEN R package version 1.2.8 (Maitner 2026). These traits – leaf area, leaf biomass, seed mass, and whole plant height – represent a mixture of vegetative and reproductive stages of plants. Because of low floristic representation (n=10 species) in the trait data, we imputed trait data from the mean trait values at genus level for other species, which increased our sample size to 29 species. The trait data were z-score standardized to minimize bias due to different measurement scales. We then used the dbFD() function in the FD R package version 1.0-12.5 (Laliberte et al. 2026) to calculate various functional diversity measures including functional richness, functional evenness, functional divergence, functional dispersion, and functional group richness (see Table 2 for definitions and interpretations). Functional group richness was assessed from discrete trait groups (total of 3 groups or clusters) into which each of the species was assigned based on hierarchical clustering using Ward’s minimum variance method. We conducted standardized effect size analysis (1,000 randomizations) on the four functional diversity measures to determine their statistical significance for each of the 1 m^2 plots. SES values < -1.96 indicate significantly low FD values and is interpreted as functional convergence, SES values > 1.96 represent significantly high FD values, interpreted as functional divergence, while SES values close to zero are interpreted as random assemblages in trait space. Finally, we calculated Jaccard-based functional beta diversity among the three meadow types using functions in mFD R package version 1.0.7 (Magneville et al. 2022). Functional beta diversity was computed as overlap between convex hulls of pairwise meadow types in trait space, decomposing it into functional turnover and nestedness (Baselga 2012; Villéger et al. 2013). Convex hulls were constructed based on principal coordinates analysis (PCoA) on the four functional traits and aggregated species abundances in the three meadow types using the Euclidean distance metric.

Finally, we used Pearson correlation tests to investigate relationships among the several taxonomic, phylogenetic, and functional diversity measures, and also tested if these diversity measures were significantly different across the three meadow types. We used summary statistics to describe the variability of conservation status, plant family, biogeography and growth form of the surveyed plant species. Additionally, we used a chi-squared test to investigate the spatial distribution of the coniferous species along the hydrological gradients in the meadow.

Results

Species richness and distributions along moisture gradient

We recorded gamma richness of 80 species and overall Hill numbers of 21.39 across the entire meadow; these species were distributed across 23 plant families with Asteraceae having the highest floristic representation (n=19 species), followed by Poaceae (n=12 species) and Brassicaceae (n=7 species) (Table S1). These species comprise 69 native plants and nine introduced species, as well as two unknown species that could not be identified to the species level (Figure 1a, Table S1); about 75% of the recorded species were herbaceous plants (Figure 1b, Table S1). A vast majority (67.5%) of the species belong to G5 indicating low extinction risk; however, four of the species were classified as G2 or G3, indicating imperiled and vulnerable conservation status, respectively (Figure 1c, Table S1). The xeric meadow recorded the highest (n=8 species) invasive species richness but the lowest total invasive species abundance, mesic meadows have the least invasive species richness (n=5 species), while the total abundance of invasive species was the highest in hydric meadows, primarily driven by the extensive *Bromus inermis* cover. Among the 80 recorded species, *Poa secunda* (n=255), *Epilobium brachycarpum* (n=248), *Artemisia arbuscula* (n=221), *Balsamorhiza hookeri* (n=210), and *P. bulbosa* (n=209) had the highest frequencies across the 341 1 m^2 plots, indicating high abundance in the meadow. Moreover, total abundance for *P. secunda*, *E. brachycarpum*, and *Bromus inermis* were the highest among all surveyed species. In contrast, species of conservation concern such as *Primula tetrandra*, *Trifolium lemmonii, Ivesia webberi*, and *I. aperta* var. *canina* were recorded in 4, 51, 81, and 108 plots, respectively. Most of the surveyed species were relatively phylogenetically young, with evolutionary age ranging from 3.46 mya for *Antennaria luzuloides* and *A. dimorpha* to 422.83 mya for *Pinus jeffreyi*. The species contributions to beta diversity (SCBD) values ranged from <0.001 in *Ericameria nauseosa* to 0.24 in *Bromus inermis* (Table S1). The recorded flora in the meadow comprises 31 decreasers, 38 increasers, and 11 invaders (Figure 1d) illustrating a plant community undergoing post-disturbance succession.

Species, phylogenetic, and functional diversity

Alpha species diversity was statistically different across all meadow habitat types: the total species richness (SR) was the highest in hydric meadow, while mean species richness was higher for both xeric and mesic (Kruskal-Wallis $X^2 = 11.33$, df = 2, p = 0.004; Figure 2a). Species diversity index (Kruskal-Wallis $X^2 = 11.06$, df = 2, p = 0.004; Figure 2b) and Hill's numbers (Kruskal-Wallis $X^2 = 11.06$, df = 2, p = 0.004; Figure 2c) were the highest in the xeric habitat, closely followed by mesic meadows (Table 2).

The pruned chronogram phylogeny contained 57 of the 80 surveyed plants in the entire study area, representing 46 xeric, 36 mesic, and 46 hydric meadow species (Figure S1). Both the habitat-type level and plot-level phylogenetic diversity (PD) plots were the highest in xeric habitat (Kruskal-Wallis $X^2 = 18.31$, df = 2, $p < 0.001$; Figure 2d). PD significance was recorded in 16 mesic, 16 hydric, and 10 xeric meadow plots, but most of these plots have low observed PD indicating phylogenetic clustering. While mean pairwise distance (MPD), mean nearest-taxon distance (MNTD), and net relatedness index (NRI) were slightly higher in xeric meadows and nearest taxon index (NTI) was the highest in mesic habitat, the differences were not significant (Table 2). Similar to PD, plot-level MPD was generally low, and low MPD significance ($SES < -1.96$) was obtained in 33 plots (9 mesic, 14 hydric, and 10 xeric meadow plots) indicating phylogenetic clustering in these plots. Likewise, low MNTD significance ($SES < -1.96$), observed 12 plots each in mesic and hydric habitats and nine xeric meadows, indicates phylogenetic clustering (Table 2). A total of 221 (64.8%) of the 341 plots have positive NRI values (≥ 1.0) indicating phylogenetic clustering, another 116 (34%) plots represent random assemblages, while four plots have negative NRI values, suggesting phylogenetic overdispersion (Table 2). Likewise, NTI produced 14 and 212 plots with negative and positive NTI, respectively, while another 115 plots have NTI close to zero and are considered random assemblages.

Overall, functional richness (FRic) was low across all survey plots indicating low trait variability and small trait space occupation; however, FRic was significantly the highest in hydric meadow (Kruskal-Wallis $X^2 = 15.25$, df = 2, $p < 0.001$; Figure 2e). Moderate values (0.4-0.7) of functional evenness (FEve) were more frequently distributed across the three meadow types (hydric = 49 plots, xeric = 43 plots, mesic = 72 plots), followed by low FEve values (0.0-0.4) distributed in 22 mesic, 26 xeric, and 32 hydric plots, while 67 plots with high FEve (0.7-1.0) were located in 20 xeric, 22 hydric, and 25 mesic plots. Overall, mean FEve was the highest in mesic habitat but the difference was not significant (Table S2). Functional divergence (FDiv) > 0.6, indicating highly differentiated trait assemblages, was recorded in 228 of the 341 1 m^2 plots, including 65 hydric, 74 xeric, and 89 mesic plots, however, FDiv was significantly the highest in xeric habitats (Kruskal-Wallis $X^2 = 14.53$, df = 2, $p < 0.001$; Figure 2f). In this study, functional dispersion (FDis) < 0.5 was considered low, indicating an over-representation of certain traits in the community. We recorded low FDis in 30 mesic, 34 hydric, and 18 xeric communities, but the difference in FDis was not significant across meadow types (Table 2). The standardized effect size (SES) analysis produced random trait assemblages based on the FRic and FDis (SES close to zero), while significantly low FD values (SES < -1.96) were obtained in six 1 m^2 plots for FDiv (2 hydric, 3 mesic, and 1 xeric plots) and five plots for FEve (2 mesic and 3 hydric plots). Finally, functional group richness (FGR) ranged from one to three across the surveyed plots, but mean FGR was the highest in mesic meadows, but this measure was not significantly different across the three meadow habitats (Table 2). The dendrogram, illustrating the classification of the species based on their functional traits and upon which the FGR was computed, is plotted in Figure S2. Owing to the statistical implementation of FD, plots that have less than three species or more trait data than species richness did not produce functional diversity measures and were designated NA.

Relationships among alpha species, phylogenetic, and functional diversity

Overall, PD was significantly correlated with SR, justifying the PD SES calculation, but PD was moderately related with Hill's numbers. MPD was positively correlated with PD and MNTD but negatively related with NRI and NTI (Figure 3). Further, FRic was moderately correlated with PD, but not with SR and Hill's numbers. FDis is positively, moderately, and significantly correlated with all species and functional diversity measures, and PD, but not with other phylogenetic measures (Figure 3).

Species and functional beta diversity among meadow types

The xeric plant community was less dissimilar to mesic (D=0.38) but highly dissimilar to the hydric assemblage (D=0.66), while mesic was moderately dissimilar to hydric community (D=0.49). Total beta diversity computed based on aggregate species richness and gamma diversity per habitat showed that hydric plant community was the most dissimilar meadow (D=7.21), followed by xeric communities (D=5.04) and mesic (D=4.82); total sum of squares (SS_{total}) was 0.27, while the overall beta diversity (BD_{total}) in the meadow is 0.14. The local contributions of the meadow types to beta diversity were significantly higher for hydric (0.50; adjusted p=0.009), but low and statistically nonsignificant for xeric (0.38, adjusted p>0.05) and mesic (0.13, adjusted p>0.05). The NMDS ordination (stress = 0.02) and biplot shows that xeric habitat is mostly nested within the mesic type, while hydric meadow is largely dissimilar (Figure 4).

Contrary to the species beta diversity patterns, functional beta diversity was the highest in the mesic meadow, having the highest dissimilarity with xeric meadow (D=0.94) and with hydric sites (D=0.94), while hydric and xeric meadows were functionally more similar (D=0.25). Functional nestedness was high between mesic and xeric site (D=0.58) and between mesic and hydric meadows (D=0.48), while we obtained moderate functional turnover among meadow pairs (mesic-xeric: 0.37, mesic-hydric: 0.47), but functional nestedness and turnover measures were low between hydric and xeric meadows (D=0.12 and 0.13, respectively).

Species associations and Indicator species analysis

The co-occurrence analysis considered 30.4% (n=961 pairs) of the possible 3160 floristic pairwise combinations that met the statistical requirement (expected co-occurrence value ≥ 1) among the 80 species across the meadow. The co-occurrence analysis of the 961 pairs produced 110 positive, 107 negative, and 744 random floristic pair associations, indicating 22.6% non-random species co-occurrences in the meadow (Figure 5, Table S2). Additionally, 37 of the 80 surveyed plants were identified as indicator species; the 37 indicator species comprise six, 13, and 18 species with high and significant ecological fidelity in mesic, xeric, and hydric habitats, respectively (Table 1).

Woody species distribution and expansion

We counted 296 stands of three woody species comprising 294 *Pinus jeffreyi* stands, and one stand each of *Cercocarpus ledifolius* and *Juniperus* sp. in the meadow. The 294 *P. jeffreyi* stands include 193 saplings, 74 small juveniles and 27 large juveniles, of which 119 stands occur in the mesic meadow while the remaining 175 stands (59%) were observed in the xeric habitat. We observed a random ($p>0.05$) distribution of the three life stages of the woody species between the mesic and xeric meadow habitats.

Discussion

Understanding plant community structure and underlying drivers must go beyond species-level diversity assessment and integrate both ecological and evolutionary mechanisms. In this study, we quantified both alpha and beta species, phylogenetic, and functional diversity along soil hydrological gradients of a large subalpine meadow plant community in the northern Sierra Nevada range, California. As expected, alpha and beta diversity differed among hydric, mesic, and xeric meadow habitats. Despite limited water availability, the xeric meadows have the highest species diversity, Hill's numbers, phylogenetic diversity, mean pairwise distance, mean nearest-pairwise distance, nearest relatedness index, functional divergence and dispersion. Mesic habitats have the highest functional evenness and functional group richness and share the highest mean species richness and diversity index with xeric habitats, while hydric meadows have the highest total species richness, but also the lowest species and phylogenetic diversity and functional divergence. We recorded 80 species in the meadow, comprising native forbs, grasses, and herbaceous plants with about 300 tree saplings and juveniles scattered in the xeric and mesic habitats. Asteraceae was over-represented in the meadow while native *Poa secunda* and *Epilobium brachycarpum* were among the most abundant species in the meadow. We recorded nine invasive species mostly concentrated in the xeric meadow habitat.

Community assemblage and structure in the Dog Valley meadow complex is driven by phylogenetic clustering. This is supported by overall low plot-level PD, MPD, and MNTD values as well as high frequency of plots with positive NRI and NTI values. SES analyses on these phylogenetic measures resulted in fewer than 50 plots with significant deviation from null expectations, which could be attributed to the small plot-level floristic richness. This result underscores the contribution of regional species pool with shared evolutionary history to the local meadow community, since previous studies have demonstrated low PD significance of plants in western North America (Qian et al. 2013; Mishler et al. 2020), consistent with the niche conservatism hypothesis (Vamosi et al. 2009; Hawkins et al. 2014; Weigelt et al. 2015; Ma et al. 2016). Phylogenetic clustering in this meadow may also reflect the strength of environmental filtering as a driver of community assemblage due to an interplay of regional arid climatic conditions and local soil hydrological gradient in the meadow. A fair amount of the surveyed plots exhibits random assemblages which conforms to the neutral theory that predicts equal chances of all species of colonizing and establishing in a community with little to no fitness advantage from species functional traits (Hubbell 2001; Rosindell et al. 2012; Peterson et al. 2021). Neutrality in relatively closed systems like a subalpine meadow located within an extensive conifer forest is to be expected because the Dog Valley meadow complex mimics a hypothetical island system where species that colonize and persist are those that are able to reach the meadow and adapt to the marginal soil hydrological conditions (MacArthur and Wilson 1967; Peterson et al. 2021). This result shows that the Dog Valley meadow plant community is influenced by both niche and neutral processes, highlighting previous studies that explained that community assemblages are often driven by a balance between mechanistic and stochastic processes (Hubbell 2005; Alonso et al. 2006).

All functional diversity (FD) measures, except functional evenness, have no or weak relationships with species and phylogenetic diversity measures, while functional beta diversity showed striking contrasting patterns from species dissimilarity indices; these are evidence that FD measures reflect different processes driving community assemblage in the Dog Valley meadow than species and phylogenetic diversities. Weak or no FD-PD relationship is reported in several studies (Swenson and Enquist 2009; Bernard-Verdier et al. 2013). While functional richness is low, it is significantly different across meadow types; however, high functional divergence (FDiv > 0.6) observed in

66.8% of the plots especially in xeric habitats indicates assemblages driven by resource partitioning. Coupled with inferred phylogenetic clustering, we describe this study area as an assemblage of closely related plants with high trait variability to ensure resource partitioning to avoid water-induced competition (Westoby et al. 2002; Bernard-Verdier et al. 2012). Successful coexistence, facilitated by functional divergence, is further supported by about 23% nonrandom plant co-occurrence among obligates in each meadow type. Lack of relationship between PD and FD may support growing empirical evidence that phylogenetic similarity does not necessarily equates to ecological similarity (Wiens et al. 2010; Mazel et al. 2017). However, the observed weak FD-PD relationship could also be due to low species representations (n=29 of 80 species) and trait data limitations (Tucker et al. 2018). High functional dissimilarity and turnover is evident of strong habitat sorting and preference of the species among the three meadow types.

Species assemblage along these moisture gradients shows striking patterns of floristic alpha and beta diversity. Hydric meadows have the highest meadow-type level species richness but the lowest plot-level species, functional, and phylogenetic diversity, indicating high abundance and dominance of water-loving and functionally similar species in the habitat. Perennially wet meadows are often characterized by the dominance of water-loving plants facilitated by steady water availability from groundwater and adjacent creek recharges (Freitas et al. 2014), but this results in decreased plant diversity (Dwire et al. 2004, 2006; McIlroy and Allen-Diaz 2012; Freitas et al. 2014). Many of these hydric plants are summer flowering while the xeric meadow plants are late spring to early summer bloomers, indicating adaptations to temporal resource availability and use and avoidance of extreme dry summer conditions. Furthermore, species beta diversity and the NMDS plot illustrate high floristic dissimilarity in hydric meadow compared to the mesic and xeric sites, and this was supported by significantly high local contributions to beta diversity for hydric habitats. Therefore, relatively high ecological fidelity of species to hydric and xeric meadow (27% and 23%, respectively) compared to 11% floristic affinities with mesic meadow as well as high functional divergence and dissimilarity support strong habitat preferences by these surveyed plants.

Sierra Nevada meadows have been severely degraded since the 1860s by unregulated sheep and cattle grazing and grazing-related wildfires to promote herbaceous regrowth (McKelvey and Johnston 1992; Kinney 1996). Climax communities are expected to have a higher concentration of decreasers which are palatable native forage species, therefore deviation from this expectation is an indicator of historical or current grazing; in contrast, high richness of increasers and invaders in the meadow suggest historical grazing occurred in the meadow (Dyksterhius 1949; Vesk and Westoby 2001). Moreover, the meadow was part of the historical California Trail during the gold rush period that brought thousands of people to California. The historical disturbance as caravans passed through the meadow, opportunistic grazing by their livestock, and subsequent logging and reforestation efforts have left anthropogenic imprints on the community structure of the Dog Valley Meadow. An overwhelming majority of reviewed papers showed negative effects of grazing on the ecology of Sierra

Nevada meadows (Vernon et al. 2022) with many studies reporting reduced native plant diversity and an increase in nonnative species (Dull 1999; Oles et al. 2017; DeRose 2019). However, high richness of decreasers indicate that the meadow may be undergoing post-grazing succession, which may be due to its protection within the Humboldt-Toiyabe National Forest and the designation of critical habitat for species of conservation concern, thus allowing for passive restoration. However, natural restoration to climax community may be impeded by biological invasions (Richardson et al. 2007; Gaertner et al. 2012). In this meadow, we recorded nine invasive species but with relatively high abundance, especially in the hydric habitat. Previous studies have warned that increasing global temperatures and propagule movement via recreation will increase future invasion risks (D'Antonio et al. 2004; Hellmann et al. 2008). This is particularly important since numerous active recreational campsites are adjacent to the meadow.

Post-grazing passive recovery and progressive succession towards climax communities may also be hampered by climate change which drives extreme drought events and aridification. The age classes of the ~300 recorded coniferous species point to recent coniferous expansion which is indicative of reducing groundwater levels associated with aridification of the western U.S. (Overpeck and Udall 2020; Carroll et al. 2024; Ryu et al. 2025). It is anticipated that increasing dryness in the region will facilitate expansion of the coniferous species in the meadow, as it did over 10,000 years ago when groundwater level dropped and meadows faced drought (Koehler and Anderson 1994; Gruell 2001). The invasion of conifer species into meadows can reduce the amount of open meadow conditions, alter light and moisture availability and biogeochemical cycles, and cause shifts in species composition and productivity (Ratliff 1985; Norman and Taylor 2005; Darrouzet-Nardi et al. 2006). Meadow microhabitats have been reported to change spatiotemporally in response to soil hydrological changes (Fites-Kaufman et al. 2007). While xeric meadow plant communities may be resilient to arid conditions due to plant pre-adaptation, woody shrub and conifer encroachment will likely increase in this habitat type, causing a shift of shade-intolerant xeric species into mesic meadow types as groundwater levels drop (Bartolome et al. 1990; Gruell 2001). Groundwater level drop may also shrink the mesic meadow and the mesic floristic obligates may face competition from the migrating xeric plants, which will result in localized species losses. However, we anticipate that continuous recharge from the adjacent Dog Valley Creek will ensure the ecological stability and resilience of the hydric meadow plant communities under climate change.

The Dog Valley Meadow complex is going through post-grazing succession modulated by spatiotemporal changes in groundwater levels, driven by climate change. Continuous aridification in western U.S. and extreme weather events will continue to impact this meadow resulting in plant community shifts. Therefore, this meadow is an excellent system to monitor the synergistic effect of climate change and soil hydroclimate on plant communities on a temporal scale. Therefore, we hope the high-resolution biodiversity data generated from this study will form a baseline for the periodic monitoring of this ecologically important site under future climate change. Species-based temporal beta diversity alone may not fully capture the effects of climate change in an ecosystem (Li et al. 2025; Zhu et al. 2026); therefore, we advocate for better representation of functional traits to facilitate studies that investigate functional homogenization under climate change in the western U.S.

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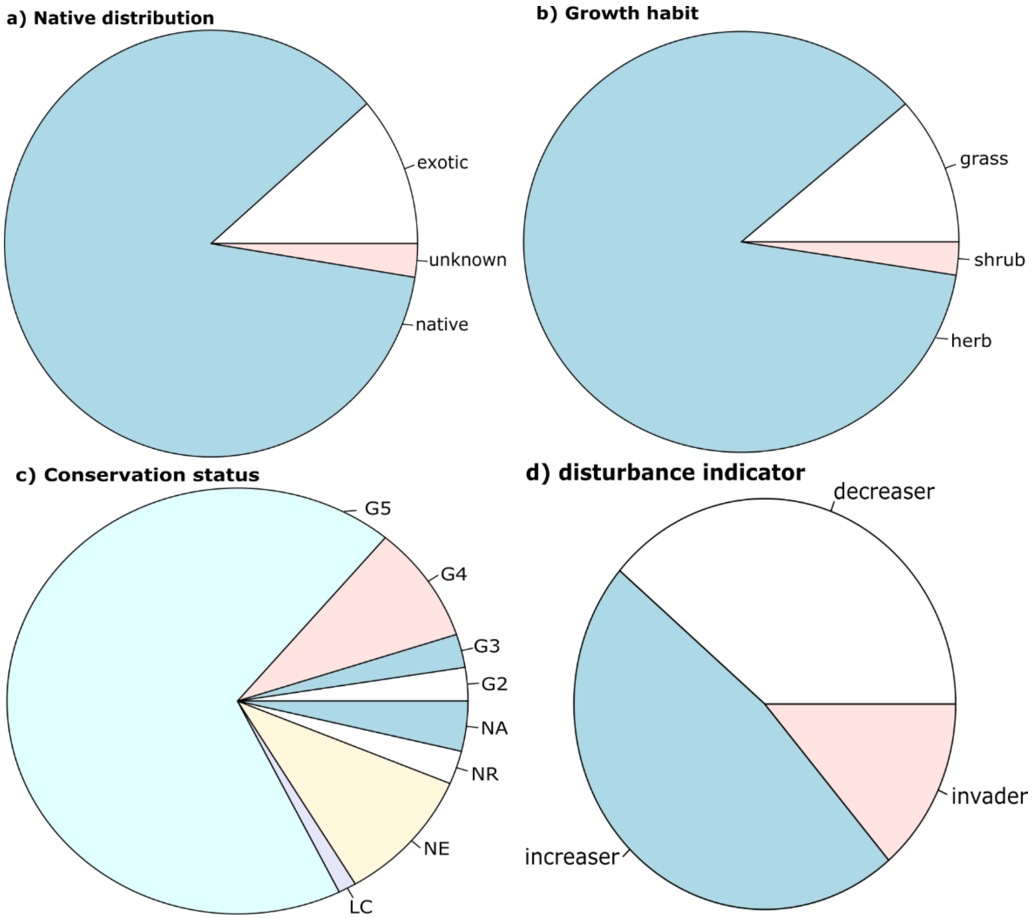

Figure 1. Pie charts describing the representation of (a) native distribution, (b) growth habit, (c) conservation status, and (d) species classification based on their responses to grazing pressure of the 80 species surveyed in Dog Valley Meadows, northern Sierra Nevada Range, California.

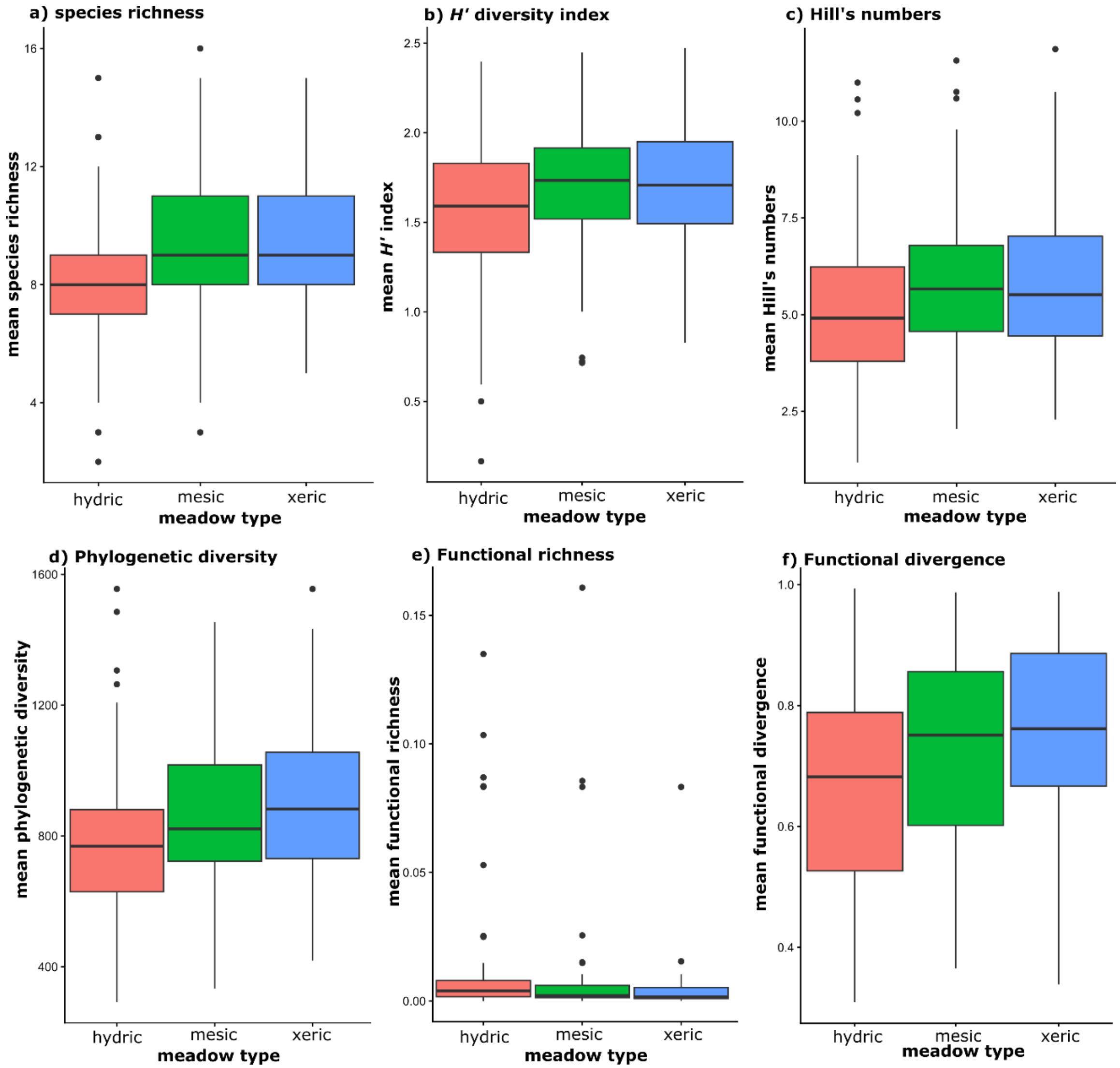

Figure 2. Boxplots illustrating the distribution of the six representative species, phylogenetic, and functional diversity across the three meadow types in Dog Valley Meadows, northern Sierra Nevada Range, California.

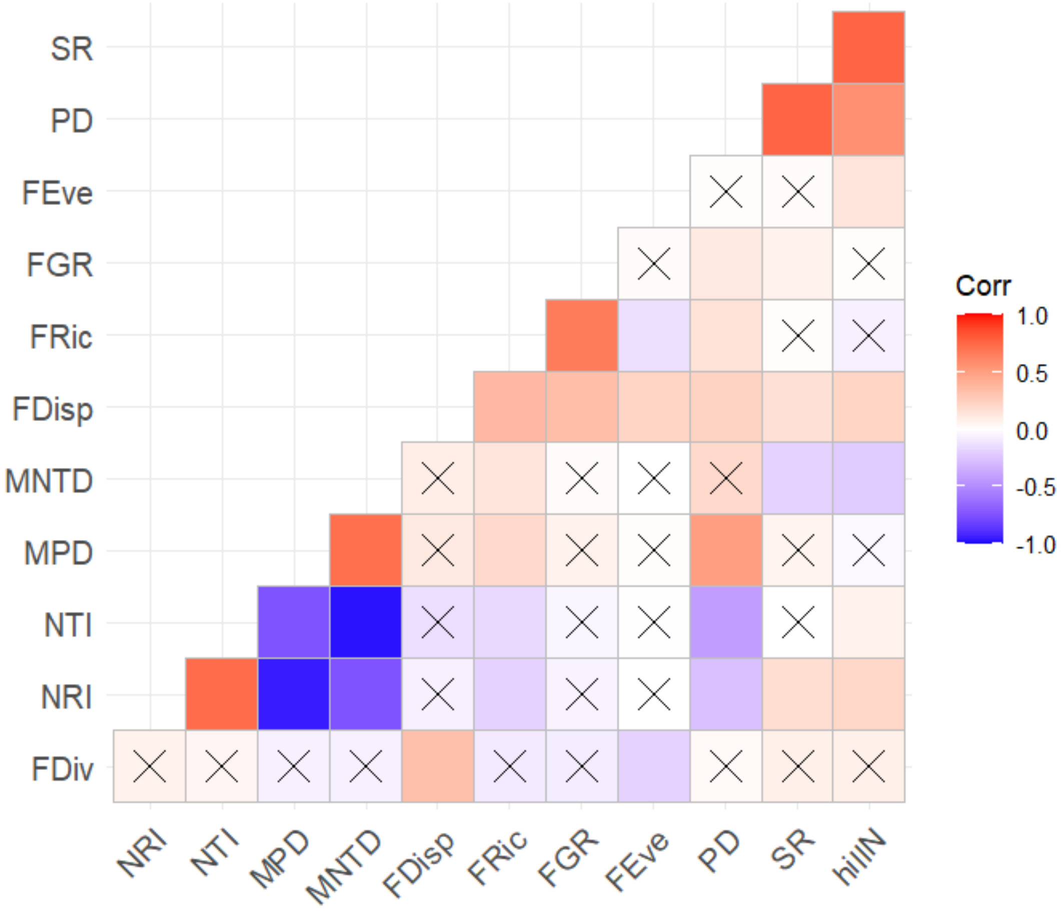

Figure 3. Correlation plot of the several species, phylogenetic, and functional diversity measures. *The × symbol indicates nonsignificant pairwise relationship. SR = Species richness, hillN = Hill's numbers, PD = phylogenetic diversity, FEve = functional evenness, FGR = functional group richness, FRic = functional richness, FDisp = functional dispersion, MNTD = Mean nearest-pairwise distance, MPD = mean pairwise distance, NTI = nearest taxon index, NRI = net relatedness index, FDiv = functional divergence.*

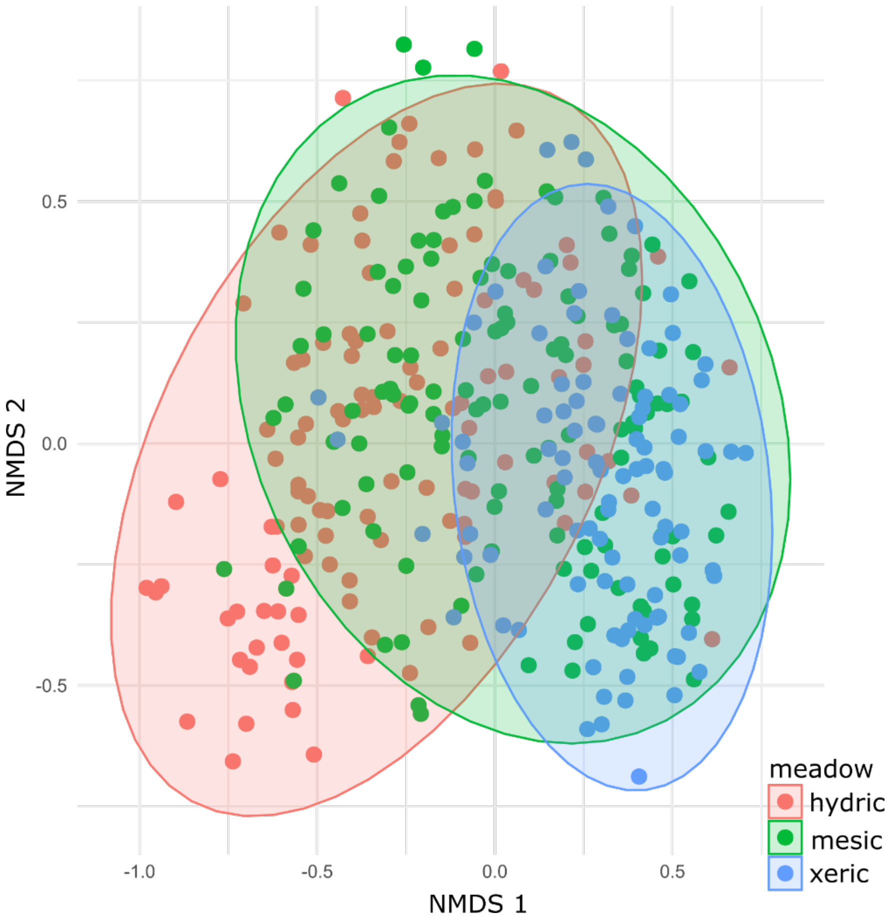

Figure 4. Nonmetric multidimensional scaling (NMDS) plot of the species composition and abundance aggregated into the three meadow types – hydric, mesic, and xeric habitats.

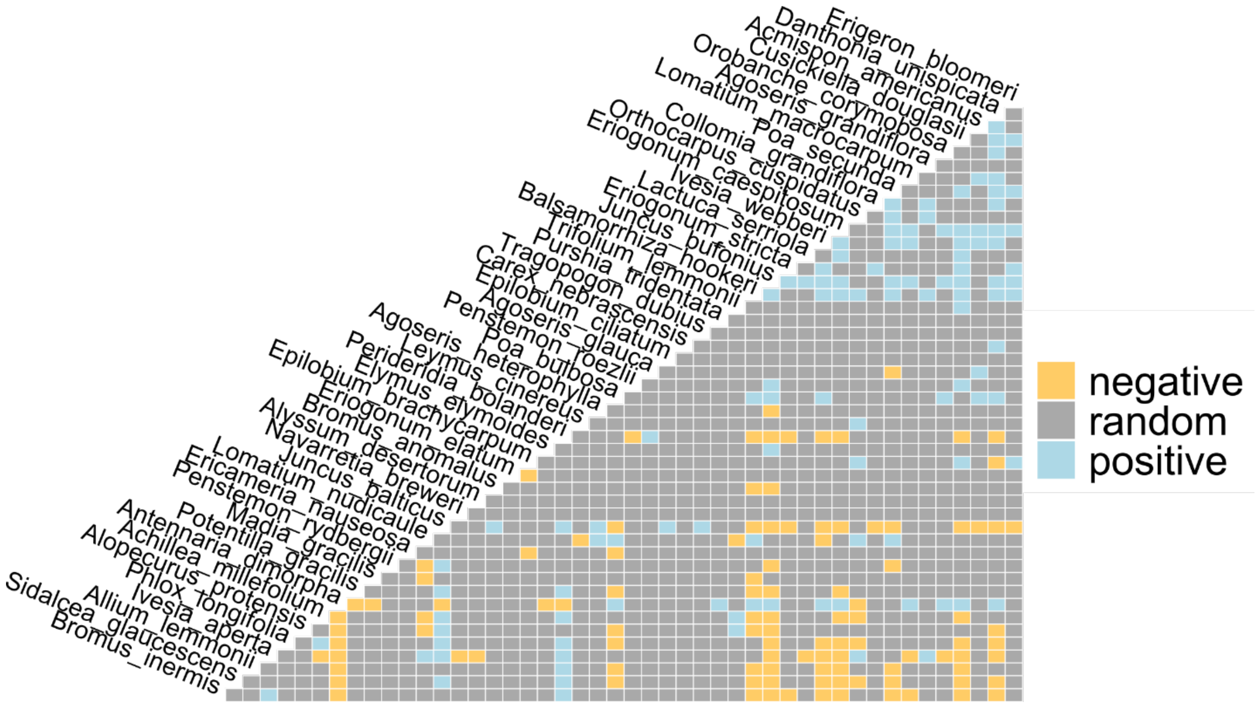

Figure 5. A matrix illustrating the random and significant nonrandom species co-occurrences across the three meadow habitats in Dog Valley Meadow, northern Sierra Nevada Range, California

Table 1. List of indicator species associated with the xeric, hydric, and mesic habitat types in the Dog Valley Meadow, northern Sierra Nevada Mountain Range, California

Species	Association value	P value	Meadow association
Juncus balticus	0.624	< 0.001	hydric
Bromus inermis	0.539	0.001	hydric
Perideridia bolanderi	0.529	0.001	hydric
Ivesia aperta var. *canina*	0.445	0.004	hydric
Agoseris grandiflora	0.375	0.04	hydric
Allium lemmonii	0.353	< 0.001	hydric
Phlox longifolia	0.343	< 0.001	hydric
Sidalcea glaucescens	0.331	< 0.001	hydric
Alopecurus pratensis	0.322	< 0.001	hydric
Potentilla gracilis var. *fastigiata*	0.286	< 0.001	hydric
Achillea millefolium	0.285	< 0.001	hydric
Madia gracilis	0.266	< 0.001	hydric
Agoseris glauca	0.253	0.02	hydric
Bromus anomalus	0.23	0.003	hydric
Navarretia breweri	0.228	0.01	hydric
Penstemon rydbergii	0.203	0.04	hydric
Wyethia mollis	0.198	0.02	hydric
Epilobium ciliatum	0.186	0.03	hydric
Artemisia arbuscula	0.619	< 0.001	mesic
Balsamorrhiza hookeri	0.53	0.04	mesic
Lomatium nudicaule	0.453	0.03	mesic
Eriogonum elatum	0.349	< 0.001	mesic
Fritillaria pudica	0.195	0.02	mesic
Phoenicaulis cheiranthoides	0.195	0.02	mesic
Eriogonum caespitosum	0.621	< 0.001	xeric
Antennaria dimorpha	0.583	< 0.001	xeric
Juncus bufonius	0.582	< 0.001	xeric
Danthonia unispicata	0.54	< 0.001	xeric
Ivesia webberi	0.489	< 0.001	xeric

Cusickiella douglasii	0.411	< 0.001	xeric
Eriogonum stricta	0.322	0.003	xeric
Purshia tridentata	0.282	< 0.001	xeric
Lactuca serriola	0.275	< 0.001	xeric
Lomatium macrocarpum	0.248	0.02	xeric
Orobanche corymobosa	0.216	0.01	xeric
Alyssum desertorum	0.212	0.03	xeric
Chrysothamnus viscidiflorus	0.176	0.02	xeric

Table 2. Suite of taxonomic, phylogenetic, and functional diversity measures calculated for the Dog Valley Meadow flora, Sierra County, California. *Phylogenetic diversity measures were calculated for xeric, mesic, and hydric portions of the meadow using 46, 36, and 46 species pruned from the tree. Functional diversity used a subset of 28 species for which four traits – leaf area, leaf biomass, seed mass, and whole plant height – was available from the Botanical Information and Ecological Network (BIEN). The diversity measures for each meadow type were represented by average and range values in parenthesis.*

Diversity metric	**Description and interpretation**	**Xeric**	**Mesic**	**Hydric**
Mean species richness	Average species richness per 1 m^2 plot in each of the three meadow types	9.11 (5-15)	9.11 (3-16)	8.16 (2-15)
Shannon-Weiner *H'* index	A statistical representation of diversity accounting for species richness and abundance. Higher values indicate high diversity	1.70 (0.83-2.47)	1.69 (0.72-2.45)	1.54 (0.17-2.40)
Hill's numbers	Also known as effective number of species. An exponential conversion of the Shannon-Weiner *H'* index into natural numbers	5.8 (2.29-11.86)	5.7 (2.05-11.57)	5.0 (1.18-10.99)
Aggregate beta diversity	Aggregate floristic dissimilarity across meadow types	5.04	4.82	7.21
Total richness per meadow	Aggregate species richness in each of the three meadow types	55	53	67
Indicator species richness	Total number of species that have significant relative frequency and abundance of species in each of the three meadow types	13	6	18
Faith's phylogenetic diversity (PD)	Total sum of branch lengths connecting plants in each 1 m^2 plot to the root of the tree. Higher PD values mean a plant community is composed of distantly related species, indicating more evolutionary diversity or phylogenetic richness. Low PD indicates phylogenetic clustering	906.32 (419.33-1555.53)	847.30 (333.99-1454.83)	770.51 (291.68-1555.66)
Mean pairwise distance (MPD)	Average evolutionary distance between all possible pairs of species in each 1 m^2 plot, averaged for each of the three meadow types. Low MPD indicates phylogenetic clustering, while high MPD represents overdispersion.	278 (213.15-452.87)	277 (222.67-421.12)	277 (193.94-446.22)
Mean nearest-pairwise distance (MNTD)	Unlike MPD which is computed including ancestral nodes, MNTD measures average distance of each species to its closest phylogenetic relative on the tips for each plot. Low MNTD indicates phylogenetic clustering while high values represent phylogenetic overdispersion.	206.17 (87.88-356.25)	204.03 (121.47-338.95)	206.05 (67.55-315.13)
Net relatedness index (NRI)	NRI compares MPD in each 1 m^2 plot with MPD of null communities. Positive NRI values (> 0.5) indicate phylogenetic clustering, negative NRI (< -0.5) means phylogenetic overdispersion, while NRI = 0 means random assemblages	0.59 (-1.90-1.15)	0.57 (-1.53-1.14)	0.55 (-1.94-1.66)

Nearest taxon index (NTI)	NTI is similar to NRI except that it is calculated based on MNTD. NTI < -0.5 indicates phylogenetic overdispersion, NTI > 0.5 illustrates phylogenetic clustering, while values between -0.5 and 0.5 represent random assemblages	0.63 (-1.97-2.68)	0.70 (-1.63-2.00)	0.74 (-1.24-3.03)
Functional richness (FRic)	Functional richness is the amount of available niche space that is occupied by species in each 1 m^2 plot based on the overall multidimensional trait space conducted in the principal coordinates analysis ordination.	0.001 (3.69e-05-8.33e-02)	0.001 (3.56e-02-1.60e-02)	0.01 (5.31e-06-1.34e-01)
Functional evenness (FEve)	Functional evenness measures the under- or over-representation of traits in trait space based on species abundance in each 1 m^2 plot. FEve values are categorized as low (0.0-0.4), moderate (0.4-0.7), or high (0.7-1.0). Low FEve means the clumping of trait cloud in functional space.	0.51 (0.04-0.98)	0.54 (0.03-0.89)	0.51 (0.03-0.97)
Functional divergence (FDiv)	Functional divergence measures the relative abundance of species with unique traits in each 1 m^2 plot. FDiv values > 0.6 are considered highly differentiated trait assemblages while low FDiv represent high trait similarity among species in a plot.	0.76 (0.34-0.99)	0.73 (0.37-0.99)	0.67 (0.31-0.99)
Functional dispersion (FDis)	Functional dispersion represents abundance-weighted variance in trait distributions of species in each 1 m^2 plot in relation to abundance-weighted centroid in trait space. Low FDis indicate over-representation of some traits. There is no standard threshold for FDis, but in this study, we consider FDis < 0.5 to be low representing over-representation of certain traits.	0.68 (0.02-1.28)	0.64 (0.00-1.25)	0.62 (0.00-1.81)
Functional group richness (FGR)	FGR is calculated posteriori for each of the 1 m^2 plots as the richness of discrete functional groups to which all species were assigned using hierarchical clustering.	1.95 (1-3)	1.97 (1-3)	1.96 (1-3)

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