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Variations in Groundwater Level and Microtopography Influence Desert Plant Communities in Shallow Aquifer Areas

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Abstract
An improved understanding of the relationships among vegetation, groundwater level, and microtopography is crucial for making well-informed management decisions in areas with shallow groundwater resources. We measured plant species abundance/composition and richness in relation to depth to groundwater (DTW) and microtopography in Owens Valley, California, particularly in areas where DTW ranged from 0 to 4 m. Sampling occurred along 67 vegetation transects across three community types. Relationships between DTW and community composition were evaluated using non-metric multidimensional scaling (NMS), while non-parametric multiplicative regression was used to relate DTW and microtopography to species abundance. The dominant gradient in species composition (NMS Axis 1) explained ~51% of variation in our distance matrix and was most strongly associated ($r = 0.55$) with DTW. The graminoids *Juncus arcticus*, *Leymus triticoides*, and *Distichlis spicata* had strong affinities toward areas with the shallowest DTW (<1.5 m). One salt-adapted species *Sporobolus airoides* and one shrub *Ericameria nauseosa* dominated areas with intermediate DTW (1.5–2.0 m), whereas the shrubs *Atriplex torreyi*, *Sarcobatus vermiculatus*, and *Artemisia tridentata* were dominant in areas with deeper DTW (>2.0 m). Variation in microtopography affected species abundance and increased species richness for vegetation communities at either extreme of the water table gradient, shallow, and deep DTW but not the intermediate DTW. Findings indicate that desert plant communities from shallow aquifers have adapted to different DTW and microtopography conditions and that considering those adaptations may be important to manage groundwater and vegetation resources in these areas.

Keywords Desert plant communities · Indicator species analyses · Microtopography · Owens Valley · Shallow aquifer · Water table depth

Introduction

Globally, groundwater aquifers support over 50% of the human population by supplying freshwater for drinking and other domestic water needs (Li et al. 2018; Adimalla et al. 2018). According to UNESCO (2012), 2.5 billion people of the world's population rely entirely on groundwater resources to meet their daily needs for water. In the United States, groundwater accounts for 25% of the freshwater used (Maupin et al. 2014). Also, because of its multiple uses, groundwater is essential for sustaining agricultural development and to maintain ecosystem integrity (Alley et al. 2002; Evans et al. 2013). Groundwater supplies approximately 40% of the world's irrigated lands and 60% within the United States (Taylor et al. 2013). However, excessive groundwater withdrawals have depleted the resource and caused side effects including lowered water tables, reduced groundwater storage, and soil deposition (Perrone et al. 2016; Musa et al. 2020). Anthropogenic groundwater alterations caused by pumping impair the ecology and ecosystem services of groundwater-dependent ecosystems (Griebler and Avramov 2015; Kath et al. 2018). Continued

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and increased demands for water resources concomitant with depleted groundwater resources in arid and semi-arid regions increasingly result in competing interests (e.g., agriculture, industry, domestic use, and ecosystem conservation) against each other for sparse resources.

Sustainable utilization of groundwater resources is crucial for the coexistence of humans and wildlands in arid and semi-arid regions (Zhou et al. 2013). The conflict between anthropogenic water uses and ecosystem conservation is increasingly clear, particularly in dry areas (Wallace et al. 2003). In shallow aquifer areas, those where groundwater is within the reach of vegetation rooting systems, it is important to understand the link between groundwater and vegetation responses to better forecast the effects of groundwater level changes on vegetation growth and community dynamics (Naumburg et al. 2005; Froend and Sommer 2010). The relationship between vegetation condition and groundwater is an active research topic in ecohydrology (Jin et al. 2007) that remains inadequately documented, in part, because of its complexity (Mata-González et al. 2012a). In arid and semi-arid areas, vegetation can be groundwater-dependent resulting in depth to the water table (DTW) being an important factor affecting vegetation cover and composition (Jin et al. 2011; Lv et al. 2013). Lowered water tables typically result in drought stress on vegetation, reduced plant cover, diversity and richness (Chen et al. 2015; Zeng et al. 2019; Huang et al. 2019), reduced plant growth, species loss, and changes to community composition (Glazer and Likens 2012). In contrast, the effect of raised water tables on individual plant growth is variable, with both decreased (Kahlown et al. 2005; Kadioglu et al. 2019; Wen et al. 2020) and increased growth being observed in different situations (Lambers et al. 2013; Epie et al. 2014; Musarika et al. 2017). Significantly rising water tables and the associated anoxic soil conditions negatively affect root exudation and respiration (Jones et al. 2009) and kill flooded roots (Huang et al. 2019).

Exploring and understanding the relationship between the biotic and environmental components of an ecosystem and especially the variation in plant communities, species diversity, and abundance along environmental gradients are key branches of ecological research (Tavili and Jafari 2009). These types of studies focused on shallow aquifer ecosystems and dependent vegetation are sorely missing. Previous research has focused on the single effect of groundwater level on plant species in the field (Pataki et al. 2008; McLendon et al. 2008; Mata-González et al. 2012a) or in controlled experiments (Abdallah et al. 2017, 2018). Nevertheless, the effect of multiple factors on plant communities, plant distribution, and species richness has been poorly explored. Our study area (Owens Valley, California, USA) is part of an arid region containing a shallow aquifer that is important for urban and agricultural use in highly populated areas in California (Naumburg et al. 2005). Thus, understanding plant relations with environmental variables in these types of areas is of high importance for groundwater management.

In this study, we used a combination of multivariate community analyses (non-metric multidimensional scaling: NMS), cluster analysis, and indicator species analysis (ISA) (Wolski and Kruk 2020) and non-parametric multiplicative regression (NPMR) to understand the relationships between plant species composition and DTW and microtopography in the Owens Valley. Our specific research objectives were to describe variation in plant community composition, explore the relationships between DTW and microphotography with vegetation community composition and plant species abundance, and evaluate the influence of variation in microtopography on species richness along a DTW gradient in the Owens Valley. We intend the results of this work to enhance our scientific understanding of vegetation responses to groundwater variation in arid environments. Such insights have value for natural resources conservation and water resources management, particularly in water-limited ecosystems.

Materials and Methods

Study Site

Our study was located in Owens Valley, a closed basin in eastern California, between the Sierra Nevada and the White/Inyo Mountains. The Owens Valley is a part of the Great Basin Desert and receives 130–170 mm of annual precipitation with 82% occurring from November to April (Mata-González et al. 2014). The climate is characterized by hot and dry summers and cold and relatively moist winters. The arid environment supports desert shrubland and grassland plant communities (Natural Resources Conservation Service 2002). The valley floor receives abundant water from snowmelt from the surrounding mountains and accumulates it in a shallow aquifer (0–4 m) that is within reach of the roots of many plant species of the area (Mata-González et al. 2012a). The study site encompassed about 100 km along the Owens Valley floor, from areas near Laws, CA in the north (Latitude 37° 24’ 03” N, Longitude 118° 20’41” W) to areas near Lone Pine, CA in the south (Latitude 36° 35’ 11” N, Longitude 118° 04’ 14” W). The elevation of the site ranges from 1264 m above sea level in the north to 1138 m in the south. The soils confirmed at the study site (valley floor) are generally deep, well drained, and nearly level on flood plains, alluvial fans, and stream terraces (Natural Resources Conservation Service 2002).

Pre-European uses of the land included incipient irrigated agriculture using the abundant water resources of the Owens Valley area (Lawton et al. 1976). It is unclear how extended this activity was through the Owens Valley and how this could have affected the microtopography of the area. Recent use of the land includes livestock grazing that is managed by different public agencies. Early overutilization of the rangeland resource may have produced changes in vegetation (Natural Resources Conservation Service 2002) of the area, but it is not clear if livestock grazing has contributed to a homogenization of the microtopography of the area.

Transect Location and Plant Evaluations

This study took place in non-riparian areas where groundwater was anticipated to be relatively shallow and where the representative plant communities of the area were present. Sampling areas were selected for the presence of the most abundant plant species of the area: *Artemisia tridentata*, *Atriplex torreyi*, *Ericameria nauseosa*, *Distichlis spicata*, *Juncus arcticus*, *Leymus triticoides*, *Sarcobatus vermiculatus*, and *Sporobolus airoides* (Mata-González et al. 2012b). This allowed us to cover most of the variation in plant communities of the area. Initial sites were selected based on historic vegetation maps and aerial photographs and then corroborated by site visits. Final site selection for the establishment of sampling transects was confirmed when plant communities (based on representative species) were evenly spread across the entire study site. In addition to looking for representativeness in plant communities, we also looked for sampling areas with less than 4 m in DTW because we wanted to avoid abnormal areas that do not represent the conditions of the valley floor. Permanent DTW monitoring wells distributed all over the Owens Valley were used to estimate DTW for the potential sites.

Following site selection, we located and sampled 67 transects (transect lengths varied from 15 to 110 m, with an average of 68 m) across the target vegetation types throughout the whole Owens Valley. The length of the transects varied because the patches of representative vegetation also varied in size. Vegetation sampling was performed during August and September. The identity of every species intercepted at 1-cm point intervals along each transect was recorded. Plant cover (total and by species) was measured at every 1-m portion of the transect by dividing the total number of 1-cm hits by 100 and subsequently calculated for the whole transect. Averages for plant species cover by transect were used in the final data analysis.

Depth to Groundwater (DTW) Measurements

DTW measurements were obtained at average intervals of 5–10 m along the sampled transects. In total, 820 DTW measurements were made along the 67 transects throughout the study area. DTW measurements were carried out in narrow test holes made with a backhoe-mounted soil auger or a hand auger powered by an electric drill connected to a portable generator (depending on equipment availability). DTW measurements were obtained by inserting an electric water sensor with sound alarm into the test holes. The measurements were made about 2 h after the test holes were finished to allow for stabilization of the water levels. For the purposes of data analysis, the DTW measurements were averaged by transect.

Microtopography Measurements

What we call microtopography in this study is represented by ground surface elevations that were recorded along the vegetation transects. Those elevations were obtained with a Nikon DTM-420 prismless total station with sub-centimeter accuracy at intervals of 1.0 m along the transects. Variations of microtopography were calculated as relative elevation, i.e., the difference in elevation of a given sampling point and the lowest point in the transect. Therefore, a point with value near zero indicated a depression, while a point with a greater value indicated a mound.

Statistical Analysis

The species matrix used for community analysis consisted of 67 rows (transects) by 28 columns (species; after deletion of rare species). Cells in the species matrix contained percent cover (number of hits for the species of interest divided by the total samples for that transect, all multiplied by 100). Species groups based on community composition were formed using cluster analysis (McCune and Mefford 2015). We used a Euclidean distance measure and Ward's method for clustering (Wishart 1969). Rare species (occurring in <5% of plots) were deleted prior to analysis because group assignment of species with few occurrences is generally unreliable (McCune et al. 2002). We relativized by plot totals (sum of cover within each row) to focus on the relative contribution of each species cover to the total cover in each plot. In order to select the optimal number of groups, we first looked for natural grouping, i.e., homogeneity within groups, by evaluating dendrogram stem lengths. Longer stem lengths indicated increased homogeneity within groups. We then balanced the percentage of information remaining (higher is preferred) with the smallest number of groups that were biologically meaningful with regard to our knowledge of the system. ISA (Dufrêne and Legendre 1997) was used to identify species with strong affinity toward groups identified using cluster analysis. ISA generates indicator values (IVs) based on relative abundance and relative frequency that indicates the strength of tendency toward a priori groups (McCune et al. 2002). Significance of IVs was determined by comparing observed values to results from 10,000 randomizations.

We used NMS (McCune and Mefford 2015) to extract the strongest community composition gradients using a Sorenson distance measure. We used the "slow and thorough" NMS autopilot setting and Kruskal's strategy 2 for penalization for ties in the distance matrix. To relate abiotic and biotic factors with community variability, a second matrix containing environmental and biotic variables was overlaid onto the ordination space, and linear correlations between those variables and the ordination axes were calculated.

Relationships between DTW and microtopography and species occurrence (presence/absence) were evaluated using NPMR (McCune and Mefford 2009). NPMR uses a multiplicative kernel smoother, requires no assumptions regarding the relationship between response and predictor variables, and automatically models interactions among predictors (McCune 2006). Over-fitting protection is provided by leave-one-out cross-validation during the model fitting process. We used a local mean estimator, Gaussian kernel, and automatic average minimum neighborhood size option in HyperNiche V. 2. 1. 3. The "aggressive" over-fitting control setting was used, up to 10% missing estimates was allowed, and we selected the minimal back-tracking option in HyperNiche. The best two predictor models were selected for each species based on the log-likelihood ratio (logB). Model quality was evaluated by comparing the likelihood of the results generated using an a priori model (average frequency of the species in the whole dataset) compared to the likelihood of results produced using the posterior models using Bayes factors (B_{12}); the likelihood results were interpreted using $\log_{10}(B_{12})$ or logB (McCune 2006; Giordani and Incerti 2008). To relate species abundance to community composition gradients, two predictor (NMS Axes 1 and 2) response surfaces (generated from the best models) were plotted for selected species onto the ordination space.

We tested the null hypothesis of no relationship between microtopography and species richness for each vegetation group (each DTW level) by comparing species accumulation curves assuming random expectation (no consideration for microtopography) of plot addition (Oksanen et al. 2020) compared to species accumulation curves generated with plots ordered by microtopography quantiles (0.01, 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.80, 0.90, 0.99, 1.00) for that group. Plots were each 1.0 m section along transects. If the rate of species accumulation, generated by plots ordered based on microtopography, differed from random expectation that provided evidence for a relationship between microtopography and species richness for that group.

Results

Plant Species and Groundwater

A total of 67 species were identified in our study area, 28 of which were considered common (occupied >5% of plots) and thus included in our multivariate and NPMR analyses (Table 1). The complete list of the 67 species is in Supplementary Table S1. The dendrogram from cluster analysis was cut at three groups (~40% of the information retained; Supplementary Fig. S1). These three vegetation groups separated clearly into different areas of the ordination space (Fig. 1).

The three-dimensional NMS ordination yielded a stable solution and represented 79.4% of the variation in the distance matrix (final stress = 14.5; randomization test $p = 0.004$; Fig. 1). Axis 1, by far, represented the dominant community gradient (explaining 51.4% of variation in the distance matrix) and was strongly related ($r = 0.55$) to DTW, with increasing DTW moving from left to right along Axis 1 (Fig. 1). The DTW gradient was concomitant with decreasing perennial vegetation cover ($r = -0.69$) and increasing cover of bare ground ($r = 0.59$) moving left to right along Axis 1. Many of the same species occurred in all three vegetation groups identified using cluster analysis (Table 2). However, species dominance shifted between groups (Fig. 1). The graminoids *D. spicata*, *L. triticoides*, and *J. arcticus* were most associated with group 1 that was located low along Axis 1, corresponding to plots with the shallowest DTW (mean DTW is less than 1.5 m) (Figs. 1 and 2 and Supplementary Table 2). Dominant species in group 2, corresponding to plots with intermediate DTW (mean DTW is between 1.5 and 2.0 m), included *S. airoides*, *E. nauseosa*, and *D. spicata* (Figs. 1 and 2 and Table 2). Group 3 that was found high on Axis 1, corresponding to plots with the greatest DTW (mean DTW is greater than 2.0 m), was most associated with *A. torreyi*, *S. vermiculatus*, *A. tridentata*, and *D. spicata* (Figs. 1 and 2 and Table 2). *Distichlis spicata*, while widely distributed and had a very strong correlation with the ordination space, did show a strong affinity (IV = 56.8) to group 1 (Table 1).

Axis 2 represented the second strongest community gradient (explaining 15.2% of variation in the distance matrix) and was most associated with *S. airoides* ($r = 0.78$) and *E. nauseosa* ($r = 0.34$) abundance (Fig. 1). Depth to water ($r = 0.213$), East (0.205), and North (–0.180) were the most correlated environmental factors with Axis 2 indicating that plots higher on Axis 2 corresponded to those in the south east with greater depth to water and plots lower on Axis 2 tended to be those in the northwest with shallower DTW.

NPMR revealed that dominant species had nonlinear responses to the ordination space (Fig. 2). Contour plots

Table 1 Species abundance information

Species	Code	Freq	% of plots occupied	Average cover (%) plots occupied	Standard deviation (SD)	Group tendency	IV
Distichlis spicata	DISP	61	91.0	18.10	18.10	1	**56.8**
Sporobolus airoides	SPAI	50	74.6	10.20	10.31	2	**77.5**
Juncus arcticus	JUAR	38	56.7	14.15	6.23	1	**81.6**
Ericameria nauseosa	ERNAN3	36	53.7	9.22	7.99	2	**47.2**
Atriplex torreyi	ATTO	34	50.7	7.82	7.83	3	**51.8**
Leymus triticoides	LETR5	26	38.8	6.01	10.21	1	**50.9**
Bassia hyssopifolia	BAHY	24	35.8	6.88	1.73	1	**29.9**
Glycyrrhiza lepidota	GLLE3	23	34.3	9.53	1.62	2	19.8
Sarcobatus vermiculatus	SAVE4	20	29.9	8.72	4.53	3	**50.1**
Pyrrocoma racemosa	PYRA	17	25.4	1.99	0.84	1	**35.6**
Atriplex truncata	ATTR	15	22.4	1.74	0.34	1	**30.4**
Helianthus annuus	HEAN3	12	17.9	2.20	1.49	1	11.9
Artemisia tridentata	ARTR2	11	16.4	1.88	4.22	3	**50.1**
Suaeda moquinii	SUMO	11	16.4	2.18	1.17	3	14.8
Carex spp.	CAREX	10	14.9	0.88	0.33	1	15.0
Cordylanthus maritimus	COMAC	10	14.9	1.31	0.84	2	10.8
Atriplex confertifolia	ATCO	8	11.9	1.65	0.40	3	**28.6**
Cordylanthus ramosus	CORA5	8	11.9	0.99	0.87	3	**36.8**
Stephanomeria exigua	STEX	6	9.0	0.47	0.03	3	9.0
Nicolletia occidentalis	NIOC	6	9.0	0.69	0.28	1	12.0
Iva axillaris	IVAX	6	9.0	1.58	0.62	2	6.5
Cleomella plocasperma	CLPL2	6	9.0	1.48	0.07	1	9.0
Anemopsis californica canadensis	ANCA	6	9.0	0.68	3.91	1	5.4
Malvella leprosa	MALE3	6	9.0	0.92	0.07	1	3.8
Poa secunda	POSE	6	9.0	0.45	0.08	1	4.4
Polypogon monspeliensis	POMO5	6	9.0	1.29	0.16	1	9.2
Atriplex serenana	ATSE2	4	6.0	0.75	0.28	3	9.4
Salix exigua	SAEX	4	6.0	0.82	0.06	2	3.2

Group affinity from ISA analysis along with indicator values IV is depicted for the 28 species included in the ordination species matrix. The whole list of species can be found in the Appendix. Bold indicates significant ($p > 0.05$) IVs

show that high probability of occurrence for dominant species including *D. spicata*, *J. arcticus*, *E. nauseosa*, *S. airoides*, *A. tridentata*, and *S. vermiculatus* was concentrated in specific areas of the ordination space. For example, high abundances of *D. spicata* are located low to moderate along Axis 1 but decrease low along Axis 2 corresponding to areas of high *J. arcticus* abundance. *Ericameria nauseosa* and *S. vermiculatus* had somewhat contrasting distributions along Axis 2 with *E. nauseosa* concentrated mostly at the top of Axis 2, and midway along Axis 1 while high abundance of *S. vermiculatus* was at the very bottom of Axis 2 and high along Axis 2. *A. tridentata* was only abundant at the extreme right side of Axis 1 (depth to water gradient) and declined rapidly moving left toward lower Axis 1 scores (shallower DTW).

Species Distribution as Affected by Groundwater and Microtopography

Depth to water and microtopography were strongly ($\mathrm{logB} > 10$) related to most species (Table 3). DTW and microtopography were fairly comparable in terms of their importance (sensitivity) as predictors of occurrence for most species in our study area (Table 3). DTW and microtopography were most strongly related to *J. arcticus* ($\mathrm{logB} = 168.9$), *D. spicata* (147.1), *L. triticoides* (93.9), and *A. tridentata* (92.9; Table 3). DTW was the most important predictor for *D. spicata* ($\text{sensitivity} = 1.44$) and *J. arcticus* (1.16). Microtopography was a slightly better predictor for the occurrence of *D. spicata* ($\text{sensitivity} = 1.59$) and *L. triticoides* (1.23) and a much better predictor (0.33) for the occurrence of *A. tridentata* compared to DTW (0.15).

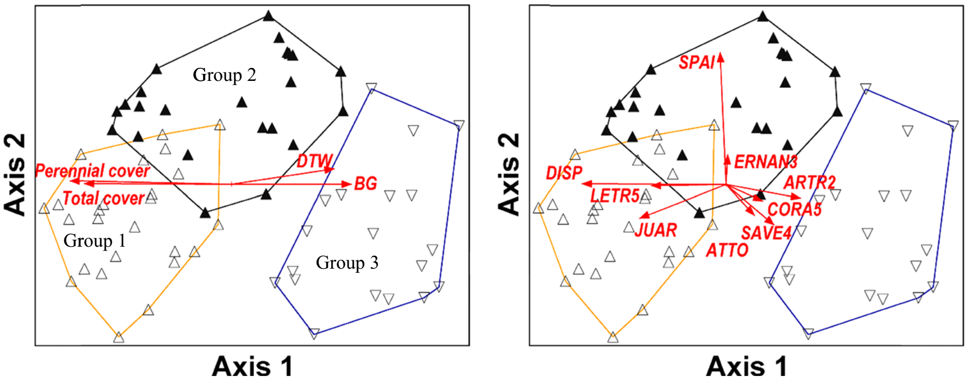


Fig. 1 NMS ordination of Owen's Valley plots in species space. Vectors show linear correlations between the ordination space and environmental variables (left) and species (right). Direction of correlation is indicated by the arrow and vector length represents strength of correlation. Axis 1 was mainly correlated with depth to groundwater (DTW) with increasing DTW moving from left to right along Axis 1. Axis 2 was mainly correlated with a combination of DTW and location indicating that plots higher on Axis 2 corresponded to those in the south east with greater depth to water and plots lower on Axis 2 tended to be those in the northwest with shallower depth to water

Contour plots revealed complex interactions between DTW and microtopography for most species. The probability of occurrence of *A. tridentata* increased with DTW. Higher microtopography was associated with increased occurrence of *A. tridentata* at low to moderate DTW but had little effect on occurrence probability at high DTW (Fig. 3). *A. torreyi* abundance was highest in plots with low DTW and high microtopography. Probability of occurrence of *J. arcticus* increased with lower DTW and lower microtopography.

Some species showed specialization toward either high or low microtopographical positions within each vegetation group particularly within groups 1 and 3 corresponding to communities at the extremes of the water table gradient, i.e., plots with shallow and deep DTW, respectively. For shallow DTW vegetation group, *A. tridentata*, *S. vermiculatus*, and *Atriplex confertifolia* showed strong affinities toward higher microtopographical positions, whereas most other species occurred primarily in low to moderate microtopographical positions (Fig. 4). Separation of species occurrences based on microtopography was much less clear for group 2 (intermediate DTW) with most species overlapping in microtopographical ranges (Fig. 4). Species including *A. confertifolia* and *S. vermiculatus* were absent in the lowest topographical plots for intermediate DTW (Fig. 4). Many species displayed specialization to microtopography in deep DTW (Fig. 4).

Species Richness as Affected by Groundwater and Microtopography

Species richness by vegetation group at the transect level (Table 4) and species accumulation curves at the plot level (Fig. 5) were highest in shallow followed by deep and finally intermediate DTW levels. Comparisons of species accumulation curve-based random expectation of the order that plots were added compared to plot addition based on order of microtopographical percentiles indicated that microtopography was related to variation in species richness in at least part of our study area (Fig. 5). This is particularly clear for group 3, corresponding to plots with the greatest DTW. The rate of species accumulation with sample area was much lower than expected when plots were added based on their microtopographical percentiles compared to random expectation, indicating that much more species richness was contained within the highest microtopography sites than would be expected by chance. While the species accumulation curve based on microtopographical percentiles for group 1 (shallow DTW) is mostly within the 95% confidence range of the expected curve, there is a dramatic increase in species richness between the 70th and 80th percentile of microtopography indicating some potential influence in the highest microtopographical positions adding to richness in shallow DTW. In addition, the plots ($n = 394$) in the highest 20th percentile (microtopography) of the dataset contribute to much of the variation in the dataset that result in such a wide 95% CI for group 2 (intermediate DTW) that further suggests that species richness is influenced by microtopography in shallow DTW. The species accumulation curve based on microtopography is similar to the expected curve for intermediate DTW indicating little influence of microtopography on species richness for this group.

Discussion

Plant Species and Groundwater

The depth to which plant species can root, height of capillary fringe, and DTW collectively determine if plants can rely on groundwater-derived water. In this study, the

Table 2 Abundance of the ten most dominant (based on average cover) species from each of the three vegetation groups

Species	Freq	Mean cover (%)	SD (%)
Group 1			
Distichlis spicata	100	26.2	18.0
Leymus triticoides	68	11.2	12.8
Juncus arcticus	92	8.2	8.1
Sporobolus airoides	60	2.3	2.7
Atriplex torreyi	5	2.4	6.8
Ericameria nauseosa	40	2.1	4.9
Anemone canadensis	8	1.5	6.0
Bassia hyssopifolia	48	1.1	2.5
Glycyrrhiza lepidota	16	0.6	2.1
Pyrrocoma racemosa	44	0.5	1.3
Group 2			
Sporobolus airoides	96	18.1	11.5
Distichlis spicata	96	17.6	18.4
Ericameria nauseosa	65	8.9	10.9
Leymus triticoides	35	3.8	8.2
Atriplex torreyi	61	2.8	4.6
Sarcobatus vermiculatas	22	1.0	2.4
Juncus arcticus	57	0.9	1.8
Glycyrrhiza lepidota	48	0.8	1.6
Helianthus annuus	9	0.7	2.4
Anemone canadensis	13	0.7	2.4
Group 3			
Atriplex torreyi	79	9.9	9.8
Sarcobatus vermiculatas	63	5.5	6.8
Artemisia tridentata	53	5.2	6.6
Distichlis spicata	74	2.3	3.7
Sporobolus airoides	68	1.9	2.2
Ericameria nauseosa	58	1.3	3.6
Cordylanthus ramosus	37	0.9	1.5
Suaeda moquini	21	0.7	2.0
Glycyrrhiza lepidota	42	0.6	1.0
Atriplex confertifolia	32	0.4	0.7

three wetland graminoids (*J. arcticus*, *D. spicata*, and *L. triticoides*) had strong affinities to areas where DTW levels were less than 1.5 m, which are similar to the findings reported for these species with the exception of *L. triticoides* in the same region (Mata-González et al. 2012a). The higher abundances of these graminoids in shallow groundwater areas indicate their reliance on groundwater sources in the Owens Valley. The rooting depths of *J. arcticus* tend to be found at 0.4 m depth (Manning et al. 1989), but likely reach greater depths of 1.3 m (Sala and Nowak 1997). *J. arcticus* contains greater leaf nitrogen concentration in treatments with subsurface moisture (0.25–0.5 m depth) compared to no subsurface moisture at the same depth (Abdallah et al. 2017), thereby the root system of this species is efficient at absorbing water from groundwater deposits. *D. spicata* is an indigenous species of arid and semi-arid environments (Pessarakli and Marcum 2013), and whose maximum reported root depth is 0.7 m (Dahlgren et al. 1997). Nevertheless, *D. spicata* may utilize groundwater at a depth of 2.5 m in the Owens Valley (McLendon et al. 2008). *L. triticoides* is a grass that is likely distributed in low-lying areas (Mata-González et al. 2012a), and its root system can reach a depth of 1.5 m (Smoliak et al. 1990).

These three graminoids most associated with shallow DTW share common characteristics such as a creeping rhizomatous root system, adaptation to wetlands or shallow-groundwater areas, affinities for depressions, high transpiration rates, and high root-shoot ratio (Mata-González et al. 2012a, 2014; Evans et al. 2013). In addition, these graminoids have been found to exhibit significant correlations between increased summer precipitation and increased uptake of certain nutrients (phosphorus and potassium) (Mata-González et al. 2021). However, these species are ecologically and physiologically well adapted to different local conditions (Abdallah et al. 2017, 2018). *L. triticoides* relies heavily on the upper soil layers (0–0.25 m depth) for nitrogen uptake, while *J. arcticus* and *D. spicata* are more dependent on subsurface moisture (0.25–0.5 m depth) (Abdallah et al. 2017). Unlike *J. arcticus* and *L. triticoides* that had similar water uptake from the topsoil layer (0–0.25 m depth) and the subsurface soil layer (0.25–0.5 m depth), *D. spicata* depleted approximately three times more water in top roots compared to bottom roots (Abdallah et al. 2018). That is consistent with Goedhart et al. (2010) and Kray et al. (2012) who reported that *D. spicata* primarily absorbed more water from the surface than the deeper groundwater sources. In addition, *D. spicata* tends to display higher photosynthesis rates than the other two species *J. arcticus* and *L. triticoides* (Abdallah et al. 2018).

One salt-adapted species, *S. airoides*, and one shrub, *E. nauseosa*, dominated intermediate DTW. *S. airoides* is halophytic plant species known to survive under highly saline and arid conditions (Pessarakli et al. 2017). Arbuscular mycorrhizal fungi have been shown to afford *S. airoides* with greater resistance to alleviate effects of drought stress on nutrient acquisition (Hernández et al. 2020). Likewise, as aforementioned in graminoids, *S. airoides* species have shallow and fibrous rooting systems with high root-shoot ratio (Evans et al. 2013). *E. nauseosa* is a perennial shrub that has excellent drought tolerance and a high adaptability to a wide range of soil conditions (Ma 2019). The species that we identified with strong affinities to intermediate DTW exhibit different water relations. The grass species *S. airoides* is more dependent on the upper soil layers, whereas the shrub *E. nauseosa* is more dependent on deeper layers (McLendon et al. 2008; Kray et al.

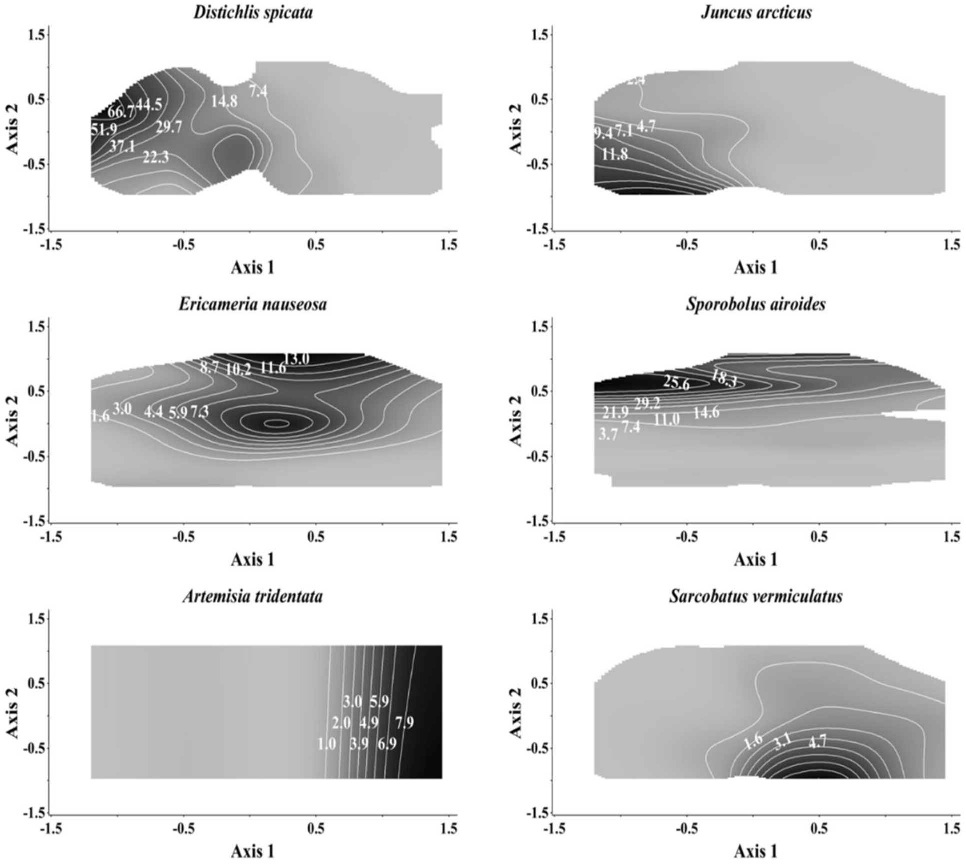


Fig. 2 Target species NPMR response surfaces (percent cover) to NMS ordination axes 1 and 2. Axis 1 was mainly correlated with depth to groundwater (DTW) with increasing DTW moving from left to right along Axis 1. Axis 2 was mainly correlated with a combination of DTW and location indicating that plots higher on Axis 2 corresponded to those in the south east with greater depth to water and plots lower on Axis 2 tended to be those in the northwest with shallower depth to water

2012). Thus, the shrub *E. nauseosa* might be less affected by a water table decline in comparison with the grass *S. airoides*.

Three shrubs (*A. torreyi*, *S. vermiculatus*, and *A. tridentata*) dominated deep DTW. These findings are partially in line with Mata-González et al. (2012a). Being capable of utilizing nitrogen within the saline surface soil (Goedhart et al. 2010) could enable *A. torreyi*, a C_4, winter deciduous, halophytic shrub to cope with water-stressed and non-water-stressed conditions (Naumburg et al. 2005). *S. vermiculatus*, a deep-rooted shrub, mainly uses deeper soil water (Kray et al. 2012; Wagner 2016) or partially relies on groundwater to satisfy plant water requirements (Devitt and Bird 2016). Both shrubs *A. torreyi* and *S. vermiculatus* were reported to occur in areas with deeper, but sill accessible, groundwater (Sorenson et al. 1991). The evergreen shrub mountain big sagebrush, *A. tridentata*, possesses root traits associated with faster proliferation and resource acquisition (Chesus and Ocheltree 2018), which allows it to access water from deeper soil layers (Ryel et al. 2008).

The graminoid *D. spicata*, while distributed throughout the study area and a relatively dominant species in every group, showed quite a bit of variation in cover along the DTW gradient. Although it was a strong indicator for group 1 (shallow DTW), *D. spicata* was also a dominant in the other two groups as well, likely reflecting its plasticity that is widespread in arid regions of western North America. More specifically, this finding may indicate *D. spicata*'s wider range of adaptation to soil moisture and competitive advantage in more drought conditions especially over the other graminoids (e.g., *J. arcticus*, etc.) that were associated with shallow DTW. The saltgrass *D. spicata* possesses special morphological and anatomical features (Ram et al. 2004; Hauser 2006), enabling it to tolerate diverse soil types and moisture levels. *D. spicata*, which is a dominant species in the Owens Valley, is resistant to drought and can grow in saline environments (Sargeant et al. 2008; Pessarakli and Marcum 2013; Abdallah et al. 2017).

Species Distribution as Affected by Groundwater and Microtopography

In this study, the three wetland graminoids (*J. arcticus*, *L. triticoides*, and *D. spicata*) and the shrub *A. tridentata* were the species most associated with DTW and microtopography, with species probability of occurrence decreased in the order *J. arcticus* > *D. spicata* > *L. triticoides* > *A. tridentata*. Depth to water was mostly correlated with the distribution of *J. arcticus*, whereas microtopography was a better predictor for the distribution of *D.*

Table 3 NPMR results for species probability of occurrence as a function of depth to water (DTW) and microtopography for common species (occurring in >5% of transects)

Species	logB	DTW		Microtopography	
		Tolerance	Sensitivity	Tolerance	Sensitivity
Anemone canadensis	28.18	0.18	0.18	0.17	0.20
Artemisia tridentata	92.9	0.55	0.15	0.17	0.33
Atriplex confertifolia	27.95	0.91	0.02	0.17	0.05
Atriplex serenana	11.25	0.36	0.01	0.34	0.03
Atriplex torreyi	83.42	0.18	0.70	0.34	0.40
Atriplex truncata	39.27	0.18	0.33	0.17	0.26
Bassia hyssopifolia	36.37	0.18	0.44	0.17	0.46
Carex spp.	19.83	0.18	0.11	1.00	0.00
Cleomella plocasperma	5.63	0.18	0.10	0.17	0.08
Cordylanthus maritimus	18.90	0.18	0.17	0.17	0.18
Cordylanthus ramosus	56.01	0.18	0.21	0.50	0.07
Distichlis spicata	147.1	0.18	1.44	0.17	1.59
Ericameria nauseosa	36.13	0.18	0.85	0.17	0.78
Glycyrrhiza lepidota	17.82	0.18	0.39	0.17	0.30
Helianthus annuus	61.15	0.18	0.55	0.34	0.12
Iva axillaris	25.87	0.18	0.32	0.17	0.20
Juncus arcticus	168.9	0.18	1.16	0.34	0.42
Leymus triticoides	93.91	0.18	1.05	0.17	1.23
Malvella leprosa	5.11	0.18	0.05	0.17	0.06
Nicolletia occidentalis	15.78	0.18	0.10	0.50	0.02
Polypogon monspeliensis	23.56	0.18	0.18	0.17	0.10
Poa secunda	8.72	0.18	0.06	0.17	0.09
Pyrrocoma racemosa	75.34	0.18	0.74	0.17	0.53
Salix exigua	4.65	0.18	0.01	0.17	0.03
Sarcobatus vermiculatus	69.64	0.18	0.52	0.17	0.52
Sporobolus airoides	78.39	0.18	1.22	0.17	1.19
Suaeda moquinii	31.46	0.18	0.19	0.17	0.21

Tolerance, bandwidth of the multiplicative kernel smoother in units of the predictor; Sensitivity, unitless measure of predictor importance (0 = no response, 1 = 1:1 change in predictor and response proportionally)

spicata, *L. triticoides*, and *A. tridentata* with respect to DTW. The correlation between groundwater and vegetation has been investigated in several studies (Gou et al. 2015; Koirala et al. 2017; Albano et al. 2020). Groundwater plays a major role in determining and shaping vegetation distribution in arid environments (Silvertown et al. 2015; Zhang et al. 2018), and it has been contemplated that groundwater may also influence ecological patterns universally (Fan 2015). Furthermore, microtopography strongly affects vegetation patterns and distribution (Mata-González et al. 2012a; Ward et al. 2016; Bhattarai et al. 2020). Our findings demonstrate that *J. arcticus* distribution, a shallow-rooted species compared to the other graminoids and the shrub *A. tridentata*, is likely to be significantly impacted by DTW.

Groundwater is directly correlated with and affected by topography (Condon and Maxwell 2015; Mulyadi et al. 2020). Identifying the interactions among groundwater, topography, and vegetation therefore enhances understanding of mechanisms that control vegetation dynamics. Specifically, since water table range is a significant factor in the formation of microtopography (Wilson 2012), vegetation distributions that are controlled by water table are also controlled by microtopography. Plant species were contained within narrow elevation ranges of 0 to a maximum 1.2 m. This study indicated that small differences in elevation, of the magnitude of 0.4 m, appeared to have effect on the occurrence of plants. The interactions among DTW and microtopography for the graminoids; *D. spicata*, *L. triticoides*, and *S. airoides* were complex with higher distributions of these species occurring at different relative microtopographies at different depth to water. Two deep-rooted shrubs (*A. tridentata* and *A. torreyi*) had highest occurrence in areas of low and/or moderate DTW and high

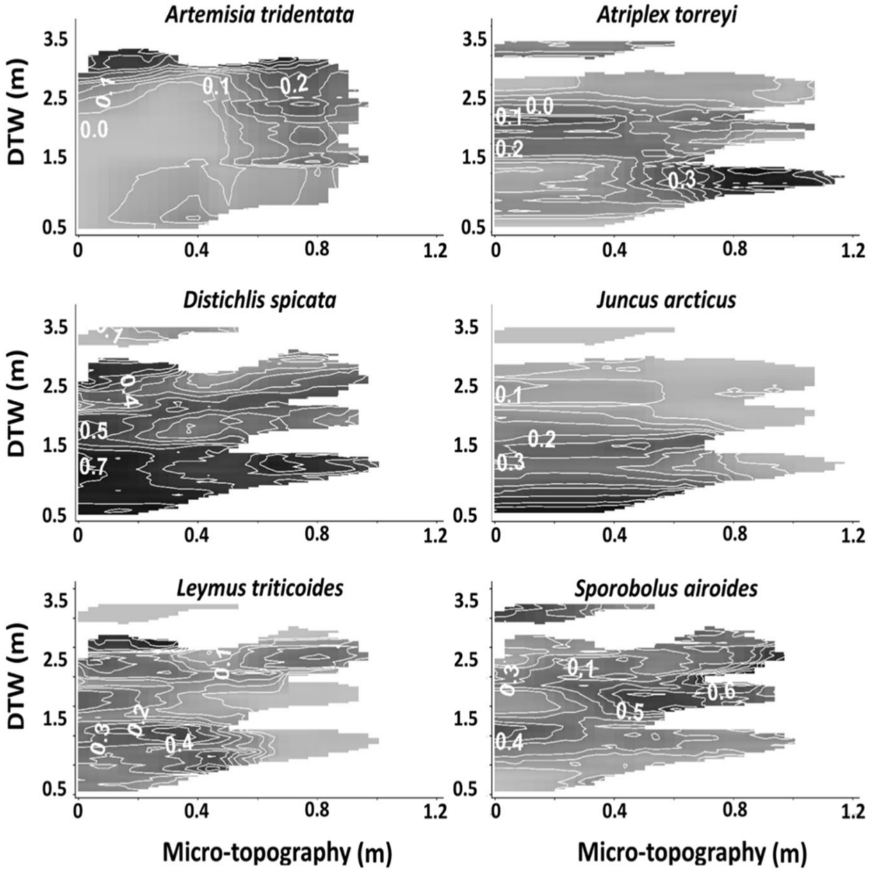
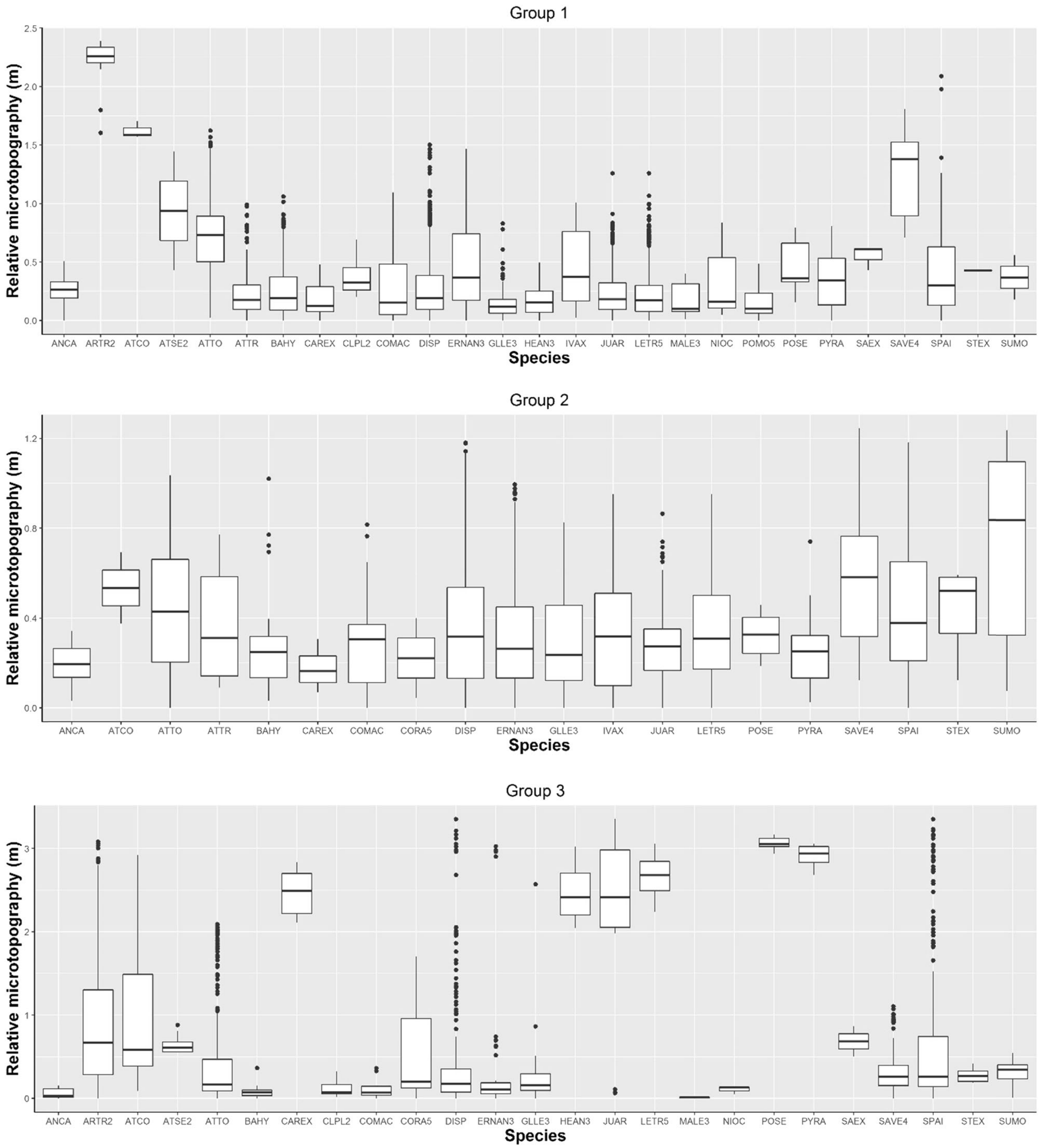


Fig. 3 NMPR species response surfaces (probability of occurrence) to depth to water (DTW) and microtopography for species with the strongest relationships to these predictors

microtopography, but the short-rooted graminoid (*J. arcticus*) occurred in areas of low DTW and low microtopography, showing that these deep- and shallow-rooting species occupy distinctly different habitats. *J. arcticus* species seem to be more dependent on shallow aquifer areas than similar species of the Great Basin. Our findings of the shrubs *A. tridentata* and *A. torreyi*, and the grass *J. arcticus* distributions at different microtopographic positions are consistent with Mata-González et al. (2012a). Changes in microtopography that is likely related to changes DTW may influence the competitive balance between shrubs and graminoids with their contrasting rooting patterns.

In addition, microtopographical specialization within each vegetation group was analyzed to determine the microtopographical range for each vegetation group and to suggest the species with narrowest microtopographical ranges. Species at the extremes of the water table depth gradient, shallow, and deep DTW showed different degrees of microtopographical specialization. Species in these groups tended to occur either at high or low microtopographical positions. For shallow DTW vegetation group, more drought-tolerant species (e.g., *A. tridentata* and *A. torreyi*) with the narrowest microtopographical range occurred on the highest sites presumably due to reduced competition (Bannister et al. 2013; Hannam and Wyllie-Echeverria 2015), improved drainage (Fivash et al. 2020), and enhanced soil stability linked to an extensive root system (Caners et al. 2019; Tauc et al. 2020). Therefore, higher sites (mounds) facilitated the colonization by these shrub species that are not well adapted to waterlogged soils.

In contrast, less drought-tolerant species (e.g., *J. arcticus*, *L. triticoides*) had the narrowest microtopographical ranges for deep DTW vegetation group and were also only found on the highest sites. This pattern may be explained by the accumulation of soil organic matter and increased nutrient availability that tend to occur in arid land mounds because of their higher biological activity (Mora and Lázaro 2013). In addition, these mounds tend to have decreased salinity (Blank et al. 1998), deeper soil with more water holding capacity (Durre et al. 2019), and lower bulk density (Mora and Lázaro 2014) associated with increased infiltration due to higher porosity (Valtera and Schaetzl 2017). Thus, more facultative wet species were found on high spots (mounds) in the driest areas. However, species in intermediate DTW had a relatively narrower and overlapping microtopographical range, suggesting that species of this group might be affected more by DTW compared to microtopography.


Group 1

Group 2

Group 3

Fig. 4 Boxplots showing relative microtopographical ranges for common species (occurring in >5% of transects) in our study area for each of the three vegetation groups

Species Richness as Affected by Groundwater and Microtopography

Measuring and estimating the patterns of species richness and community structure along environmental gradients are essential for studies on ecosystem functions and services (Li et al. 2009). Species richness in arid and semi-arid regions has most often been investigated along DTW gradients (Xu et al. 2015; Lou et al. 2016; Zhang et al. 2018; Tsheboeng 2018; Diamond et al. 2020) and microtopographical gradient (Ruifrok et al. 2014; Sleeper and Ficklin 2016; Hong et al. 2020). Our findings showed that species richness was

Table 4 Species richness for each vegetation group at the transect level

Group	Sample size (*n*)	Total richness	Average richness	Minimum	Maximum	Standard deviation (SD)
1	25	60	9.4	3	35	6.12
2	23	32	7.52	3	14	2.56
3	19	45	7.53	3	12	1.98

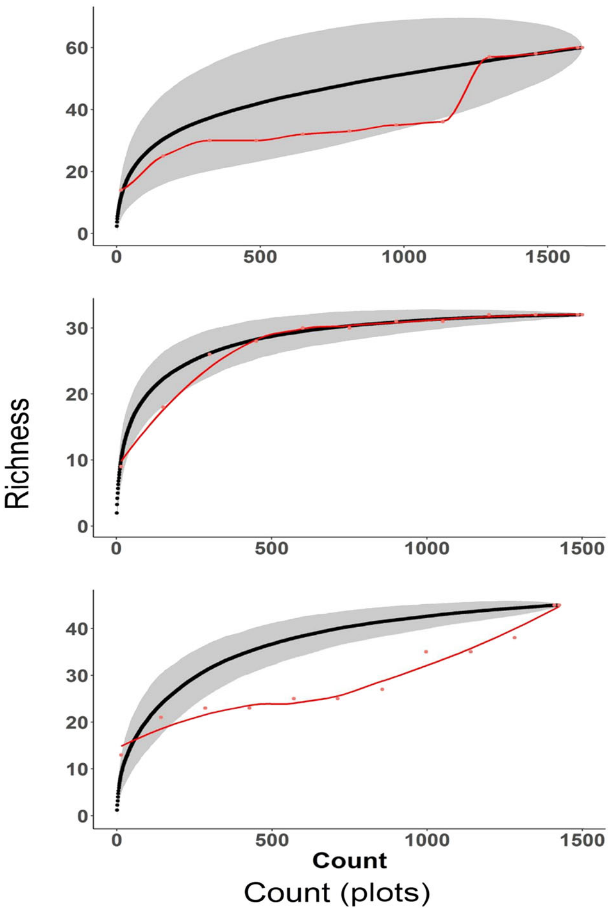


Fig. 5 Species accumulation curves for each vegetation group based on: (1) a random number of plots sampled (1000 permutations; black points shown with 95% confidence interval displayed in gray); and (2) microtopography percentiles (red points corresponding to: 10th, 20th, 30th, 40th, 50th, 60th, 70th, 80th, 90th, and 99th percentiles with a smooth fitted line)

greatest in shallow, followed by deep, and finally intermediate DTW levels. Shallow DTW levels dominated mainly by the short-rooted graminoids (*J. arcticus, D. spicata*, and *L. triticoides*) had the highest species richness, which can be explained by the growth of these species in sites with greater resource availability (Mata-González et al. 2012a). Increasing water availability improves plant growth and yield, and results in greater plant species richness (Pennington et al. 2017; Jordan et al. 2020). Thus, our findings imply that the presence of a groundwater table close to the soil surface is associated with increased species richness in the Owens Valley region, consistent with Audet et al. (2015).

The decrease in species richness estimated at intermediate DTW may be due to absence of hydrological extremes between high and low microtopographical positions that may have reduced the variation in niches and resource partitioning by increasing niche overlap (Silvertown and Charlesworth 2001). Niche separation along hydrological gradients related to tolerance to waterlogging and drought is common in semi-arid and arid habitats (Silvertown and Charlesworth 2001). Variations in hydrological conditions with microtopography likely resulted in higher variation in hydrological conditions in the most stressful (shallow and deep DTW) vegetation groups that may have decreased niche overlap and increased resource partitioning and thus resulted in increased coexistence of species with different tolerances to hydrological conditions (Silvertown and Charlesworth 2001) in both the shallow and deep DTW groups compared to the intermediate DTW vegetation group. The variations in species richness along DTW levels indicate different species establishments along groundwater depth gradients, confirming the observation of species occurrences at different DTW levels.

Variation in microtopography corresponds to variation in nutrients, moisture, DTW, and other resources (Di Virgilio et al. 2018; Liu et al. 2020), contributing to species richness (Cramer and Verboom 2017). In this study, we found that variations in microtopography increased overall species richness at the extremes of the DTW gradient that we observed; shallow and deep DTW levels dominated mostly by graminoids and shrubs, respectively. Species richness was influenced by microtopography in both DTW levels where high microtopographical areas provided refugia for species that were otherwise not adapted to conditions at the site. This may indicate that microtopography at the hydrological extremes of the DTW gradient act to increase niche separation, resource partitioning, and coexistence of species with varying tolerances to drought and waterlogging in this system (Silvertown and Charlesworth 2001). As discussed above, high microtopographical areas (mounds) likely provided microsites that offered better drainage to species not tolerant of shallow water tables (anoxic soils) in wet sites, but they also provided something (presumably better water availability) to species that are not as drought tolerant in the driest sites. Based on these results, the differences in species richness in these DTW levels were probably determined by microtopographical variations. However, the influence of microtopography on species richness was less evident in intermediate DTW, confirming the earlier observation that species of this group might be affected more by DTW levels instead of microtopography.

Conclusions and Implications

While vegetation relations with DTW and with microtopography have been researched previously, to our knowledge, this study is the first to assess vegetation relations with microtopography and DTW together, using an approach based on a combination of multivariate and nonparametric multiplicative analyses. NMS was used: (1) to identify the dominant community compositional gradients; and (2) combined with NPMR to relate community variation and species abundances to DTW and microtopography. Cluster analysis and ISA were used to group plots according to compositional similarity and identify species affinities to identified groups. This study showed that different plant species establish at different groundwater levels, with shallow and deep DTW levels favoring mostly graminoids and shrubs, respectively.

Moreover, we found strong associations between species and DTW and microtopography at the extremes of groundwater levels (shallow and deep DTW). At these depths, high microtopographical positions create small-scale refugia for species that were otherwise not adapted to conditions at the site, influencing species abundances and richness. Species richness (the number of different species) is highest in habitats with shallow DTW where graminoids are dominant, indicating that continuing groundwater declines in this region may cause graminoid dominant vegetation to be gradually replaced by desert shrubs.

Our results suggest that variation in species composition, individual species abundances, and species richness in the Owen Valley are influenced by DTW and microtopography. In addition, microtopography plays an important role at the hydrologic extremes (both shallow and deep DTW) to increase small-scale diversity in this system. Therefore, alteration of the microtopography might affect the ecological integrity of the Owens Valley, shifting plant species assemblages. The findings of this research have implications for land managers in terms of nature conservation, ecological restoration, and monitoring since variations in DTW and microtopography can lead to significant changes in species distribution, composition, and richness.

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Compliance with Ethical Standards

Conflict of Interest The authors declare no competing interests.

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