

ARTICLE

Ecology of Critical Zones

Consistent microbial and nutrient resource island patterns during monsoon rain in a Chihuahuan Desert bajada shrubland

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Abstract

In dryland soils, spatiotemporal variation in surface soils (0–10 cm) plays an important role in the function of the “critical zone” that extends from canopy to groundwater. Understanding connections between soil microbes and biogeochemical cycling in surface soils requires repeated multivariate measurements of nutrients, microbial abundance, and microbial function. We examined these processes in resource islands and interspaces over a two-month period at a Chihuahuan Desert bajada shrubland site. We collected soil in *Prosopis glandulosa* (honey mesquite), *Larrea tridentata* (creosote bush), and unvegetated (interspace) areas to measure soil nutrient concentrations, microbial biomass, and potential soil enzyme activity. We monitored the dynamics of these belowground processes as soil conditions dried and then rewetted due to rainfall. Most measured variables, including inorganic nutrients, microbial biomass, and soil enzyme activities, were greater under shrubs during both wet and dry periods, with the highest magnitudes under mesquite followed by creosote bush and then interspace. One exception was nitrate, which was highly variable and did not show resource island patterns. Temporally, rainfall pulses were associated with substantial changes in soil nutrient concentrations, though resource island patterns remained consistent during all phases of the soil moisture pulse. Microbial biomass was more consistent than nutrients, decreasing only when soils were driest. Potential enzyme activities were even more consistent and did not decline in dry periods, potentially helping to stimulate observed pulses in CO₂ efflux following rain events observed at a co-located eddy flux tower. These results indicate a critical zone with organic matter cycling patterns consistently elevated in shrub resource islands (which varied by shrub species), high decomposition potential that limits soil organic matter accumulation

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across the landscape, and nitrate fluxes that are decoupled from the organic matter pathways.

KEYWORDS

biogeochemistry, Critical Zone Collaborative Network, dryland critical zone, Jornada Experimental Range, rangeland, semiarid

INTRODUCTION

Elucidating belowground function in the “critical zone”—the functionally integrated zone of Earth’s surface extending from canopy to groundwater—is a frontier in understanding coupled biosphere–geosphere Earth systems (Brantley et al., 2007; Richter & Billings, 2015). This frontier is underexplored in drylands, that is, areas with an aridity index <0.65 (Právilie, 2016; Tchakerian & Pease, 2015). As in any critical zone, surface soils in drylands are an important exchange interface between soils and the atmosphere for water (Scott & Biederman, 2019), carbon (C) (Barnes et al., 2021; Darrouzet-Nardi et al., 2015), nutrients (Belnap, 2011; Sinsabaugh et al., 2015), and energy (Rasmussen et al., 2011). Surface soils in drylands experience especially large moisture (Duniway et al., 2018) and temperature (Nobel & Geller, 1987) fluctuations, substantial exchange of eolian materials (Okin et al., 2006), and exhibit disproportionate biological activity in these otherwise hostile environments (Garcia-Pichel et al., 2003). For these reasons, examining water, microbial, and nutrient dynamics in surface soils is a useful anchor for investigations of dryland critical zone function.

In this study, we define surface soils as the top 10 cm, a typical depth for investigations of soil microbial and nutrient processes. Surface soils in drylands, particularly in shrublands, are often characterized by spatial heterogeneity in “resource islands” (a.k.a. islands of fertility) and exhibit temporal dynamics controlled by rainfall pulses (Huxman et al., 2004; Reynolds et al., 2000; Schlesinger et al., 1996). Spatially, patches under shrub canopies function as resource islands that exhibit a higher concentration of limiting nutrients and more consistent soil temperature and moisture regimes relative to interspaces (Cross & Schlesinger, 1999; Garner & Steinberger, 1989; Herman et al., 1995; Kidron, 2009; Reynolds et al., 1999). Resource island patterns have also been documented for microbial abundance, soil enzyme activity, and CO_2 efflux (Bachar et al., 2012; Cao et al., 2011; Ladwig et al., 2015; Potts et al., 2008; Thompson et al., 2006; Wang et al., 2013). Temporally, plant growth and microbial activity are stimulated in wet periods following rainfall, especially multiyear wet periods due to the importance of legacy precipitation effects on production (Sala et al., 2012). Plants build

biomass during these wet periods that then persists during dry periods (pulse-reserve concept), while microbial and nutrient cycling processes are thought to more closely track rainfall pulses, being active during wet periods and dormant during dry periods (Bell et al., 2008; Collins et al., 2014). Crucially, during wet periods, C substrate, soil enzymes, and other nutrients needed for microbial function can be dissolved and/or transported within the soil matrix (Schimel, 2018). Thus, the extent to which these resource island and rainfall pulse patterns are present in dryland critical zones have consequences for water movement, carbon and nutrient cycling, vegetation dynamics, and soil development.

Conversely, if the expected spatiotemporal patterns are not present, this can help to reveal critical zone function. For example, despite changing nutrients and microbial biomass in response to rainfall, soil hydrolytic and oxidative potential enzyme activities are often more stable during changing weather conditions and in response to experimental manipulations (Holguin et al., 2022; Ladwig et al., 2015), suggesting a high inherent capacity for decomposition when water is present in these ecosystems (Stursova & Sinsabaugh, 2008). As another example, microbial biomass does not always decrease with drying and increase with wetting (e.g., Clark et al., 2009), indicating that dryland microbes may have adaptations to survive dry–wet cycles or that more complex microbial community or trophic phenomena are at play (Schimel, 2018). A recent study has further shown a lack of response in extractable nutrients to rainfall pulses (Brown et al., 2022). To better characterize these phenomena that either match or do not match expectations based on existing theories of resource islands and pulse dynamics (Collins et al., 2014), combined examinations of these surface soil functions are needed across dryland areas.

When examining patterns of ecosystem function in surface soils, multivariate measurements of microbial and nutrient dynamics with co-located weather and soil moisture data can be an effective strategy (Brown et al., 2022; Darrouzet-Nardi et al., 2019; Holguin et al., 2022). Here we take such an approach by investigating resource island and rainfall response patterns simultaneously in a Chihuahuan Desert shrubland site slated for intensive critical zone study. We address three questions concerning

soil nutrient and microbial properties at this site: (1) What are the overall magnitudes of soil nutrients, microbes, and soil enzyme activities in the surface soil? (2) To what extent do the expected resource island patterns occur for soil nutrients, microbes, and soil enzyme activities? and (3) How do soil microbes and nutrients inside and outside of shrub canopies respond to a summer monsoonal precipitation event? In the well-developed soils at our site, we predicted strong adherence to typical resource island and pulse-response patterns with the hypothesis that nutrient island effects are maintained over the course of a rainfall pulse. Finally, we will make preliminary observations about linkages between these soil and microbial variables and integrated measures of ecosystem function from a co-located eddy covariance tower and sensor network to build toward a holistic understanding of critical zone function.

METHODS

To address the objectives above, we collected surface soil samples (0–10 cm) weekly from three cover types: beneath creosote bush (*Larrea tridentata*), beneath honey mesquite (*Prosopis glandulosa*), and from unvegetated interspace soil. In the soils collected, we measured soil moisture, soil nutrient concentrations, microbial biomass, and potential soil enzyme activity rates during a two-month period in the summer that encompassed soil drying followed by soil wetting in response to rainfall.

Site description

The study site is a Chihuahuan Desert shrubland on a relatively flat (3°) piedmont slope (a.k.a. “bajada”) located within the Jornada Experimental Range near Las Cruces, NM (32.582868, –106.634631). Mean annual temperature and precipitation (1991–2020) are 15.2°C and 244 mm respectively (Hernandez Rosales & Maurer, 2022; Menne & Williams, 2012). Soils at the site are part of the “Jornada I” landform, which is characterized by depositional parent materials from eolian and ancestral Rio Grande sources dated to 500–700 ka that have developed thick (stage IV) petrocalcic horizons known as caliche (Gile, 1981; Monger et al., 2006). Caliche accumulation dates to ~100 ka and begins at ~60 cm in depth at the site (Nyachoti et al., 2017). The site is dominated by *L. tridentata* (creosote bush; 11% aerial cover as measured by line point intercept transects as part of this study) and *P. glandulosa* (honey mesquite; 1% aerial cover). Most of the remaining surface is unvegetated (interspace). Some biocrusts are present, but cover is minimal at the site:

there are sparse lichens (e.g., *Clavascidium lacinulatum*, *Peltula* sp., and *Collema* sp.) that typically occur under shrub canopies and some patchy but low-biomass cyanobacterial and incipient crusts in the interspace (N. Pietrasiak, personal communication). Soils are typical calcargids and organic C has been previously reported as 0.42% by mass in the 0–10 cm layer of the soil (Nyachoti et al., 2017). Soil pH, measured as part of our enzyme assays, was 8.1. The surface soil texture is loamy, approximately 40% silt, 40% sand, 20% clay (M. Engle, personal communication), and also has a substantial coarse rock fragment fraction.

Soil collection

Eight representative individuals of creosote bush, honey mesquite, and unvegetated soil were selected as our sampling locations (24 total sampling locations). Weekly from June 4 through July 15, 2015, we collected soil cores from each location with a 5-cm diameter metal soil corer to a depth of 10 cm. Immediately after collection, live plant material was removed, and the top 10 cm of soil material was sieved in a 1-mm sieve. Once sieved, subsamples were separated for (1) C and nitrogen (N) content analysis, (2) extractable nutrients, (3) microbial biomass, (4) soil enzyme assays, and (5) gravimetric water content (oven dried for 24 h at 60°C).

Bulk soil C and N

Bulk soil organic C (SOC) and total N were measured in a dry combustion elemental analyzer with a thermal conductivity detector (TCD; Elementar PyroCube). A subsample of soil was dried, ground to a homogenous consistency, packed in a silver capsule (target mass 50 mg soil), and moistened and acid fumigated before analysis to remove inorganic C (Harris et al., 2001).

Extractable nutrients

Fresh soil from each sample (5 ± 0.01 g) was extracted with 25 mL of 0.5 M K_2SO_4 . Samples were shaken for 2 h and then vacuum filtered and stored in a freezer until analysis. Ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4^{3-}) were analyzed using colorimetric assays run on microplates. NH_4^+ was determined using a modified Berlethot reaction (Rhine et al., 1998). NO_3^- was analyzed using a modified Griess reaction (Doane & Horwath, 2003), which involves the reduction of nitrate to nitrite, followed by colorimetric determination of

nitrite. Inorganic phosphorus (P) was analyzed with the malachite green method (D'Angelo et al., 2001).

Microbial biomass C and N

To quantify microbial biomass C and N (MBC and MBN), we used a modified version of the chloroform fumigation–extraction technique (Brookes et al., 1985; Scott-Denton et al., 2003). Fresh soil (5 g) was combined with 2 mL of ethanol-free chloroform and incubated at room temperature for 24 h in a stoppered 250-mL Erlenmeyer flask. At the end of the incubation period, flasks were extracted using the same procedure described in the *Extractable nutrients* section using 25 mL of 0.5 M K₂SO₄. Fumigated extracts were analyzed for dissolved organic carbon (DOC) and total dissolved N (TDN) concentrations on a Shimadzu analyzer (TOC-VCPN; Shimadzu Scientific Instruments, Columbia, MD, USA). The difference between DOC and TDN concentrations from fumigated and nonfumigated samples was used to calculate MBC and MBN, respectively. No correction factor was applied for incomplete CHCl₃ release because these values are not known for K₂SO₄ extractions for this ecosystem.

Soil enzyme activity

Activity assays for hydrolytic soil enzymes were performed on fresh soils. We assayed the activity of a suite of hydrolytic enzymes that release carbon, nitrogen, and phosphorus at the terminal stages of organic matter decomposition: cellulose-degrading β -glucosidase and cellobiohydrolase, hemicellulose-degrading β -xylosidase, carbohydrate-degrading α -glucosidase, chitin-degrading *N*-acetyl-glucosaminidase, and phosphate-releasing acid phosphatase. Enzyme assay methodology follows the principles described in German et al. (2011). One gram of soil was blended with pH-balanced Tris base and HCl buffer to reflect natural soil conditions (pH = 8.1). Aliquots of the slurries were pipetted onto 96-well plates, with eight replicates per soil. Fluorescing, 4-methylumbelliferone (MUB) tagged substrate (β -D-glucoside, β -D-cellobioside, β -D-xyloside, β -D-glucoside, *N*-acetyl- α -D-glucosaminidase and phosphate) was added to each assay. Assays were incubated at 20°C for 2.5 h, with half-hourly measurements ensuring activity was measured in the linear range of the reaction. Sample fluorescence was read with a BioTek Synergy HT microplate reader (BioTek Instruments, Winooski, VT, USA) at 360 nm excitation and 460 nm emission. For each substrate, we measured the background fluorescence of soils and substrate and the quenching of

MUB by soils and used standard curves of MUB to calculate the rate of substrate hydrolyzed. Soil oxidative activity was assayed using L-3,4-dihydroxyphenylalanine (L-DOPA), a substrate for phenol oxidase and peroxidase. These enzymes aid in degradation of compounds such as lignin by oxidizing irregular molecular structures (German et al., 2011). We also note that oxidation of L-DOPA can be abiotic in some cases, hence we refer to soil oxidation activity (Hall & Silver, 2013; Jones et al., 2020). Color absorbance was measured at 460 nm using a BioTek Synergy HT microplate reader (BioTek Instruments).

Soil respiration

Soil respiration was measured using a static closed-path infrared gas analyzer (IRGA)-based chamber system (PP Systems EGM-4) on two different sample collection days (July 8 and 15, 2015). Measurements were taken on these measurement dates between 8:00 and 10:00 a.m. at each of the 24 sampling locations (eight each mesquite, creosote bush, and interspace). CO₂ efflux was recorded every 4.8 s for 120 s and a quadratic equation was used to estimate the respiration rate over that time period. Data from the instrument were reported in units of micromoles of CO₂ per square meter per second. To compare with net ecosystem exchange (NEE) measurements, we also converted units to grams of carbon per square meter per day.

Carbon fluxes and meteorological data

NEE of C was measured using a three-dimensional sonic anemometer (CSAT3-SONIC CSI) and an open-path IRGA (LI-7500 LICOR). The overall footprint size of the tower was estimated using 1D footprint models (Kljun et al., 2004) in EddyPro 7.0.4 (LICOR), and for this tower, 90% of the fluxes come from within 125 m from a prevailing southeast to southwest direction. The high-frequency 10 Hz data were processed using community-accepted standards to establish NEE fluxes every 30 min (EddyPro 7.0.4, LICOR: default basic settings). The 30 min NEE data underwent quality assurance (QA) to eliminate erroneous data points. Data filtering removed fluxes flagged in the steady state and developed turbulence tests (using flag columns in EddyPro), during low turbulence (u^* filter after [Papale et al., 2006] using Reddypoc [Wutzler et al., 2018]), fluxes measured during rainfall events, and flux values that fall outside 3 standard deviations of a 3-day running mean. The NEE flux reporting follows the convention of negative values showing net C uptake and positive values showing net C release.

Rainfall (TE525; Campbell Scientific) and air temperature (HMP155; Campbell Scientific) were also measured at the site on a 30-min basis. Volumetric soil moisture content was measured using capacitance probes (ECH₂O EC-5, Decagon Devices). Moisture probes were installed horizontally at depths of 5 cm ($n = 5$), 15 cm ($n = 6$), 30 cm ($n = 8$) distributed in interspace and vegetated areas. We report average soil moisture from 5 to 30 cm and across both cover types because there was little difference between vegetated and interspace areas. The tower was in operation throughout the measurement period except for a period of eight days (June 18–25), which was a period of instrument downtime.

Statistical analysis

Differences in the magnitudes of each response variable were calculated (1) among the three cover types (creosote bush and mesquite resource islands, and interspaces); and (2) between wet and dry periods. For the differences among cover types, we averaged data across the season to evaluate the overall trend during the sampling period, although in a few cases we examined specific dates of interest. The wet versus dry periods were averages of the two wettest dates (July 8 and 15) versus the two driest (June 24 and July 1). The differences in magnitude are reported as ratios such as $\bar{X}_M/\bar{X}_C$, where $\bar{X}_M$ is the mean of mesquite samples and $\bar{X}_C$ is the mean of creosote bush samples (Hedges et al., 1999). Our data were non-negative, showed some degree of log-normality, and contained zeroes (Fletcher et al., 2005). Thus, to statistically constrain our estimates of the ratios, we calculated 95% confidence intervals for differences among cover types and between wet and dry periods using a maximum likelihood method described in Zhou and Tu (2000), which is specifically designed for lognormal data containing zeroes.

RESULTS

Weather and rainfall pulse dynamics during the observation period

Rainfall measurements showed substantial precipitation at the site prior to our soil collections (38 mm total in May 2015), the last event being 11 mm on May 21 (Figure 1a). Soils were still moist on our first measurement date of June 4 (Figure 1b). June was dry, with only 8 mm total precipitation and soils dried to <1% gravimetric water content. A 7-mm rainfall event occurred on June 25, just after our third sampling date (June 24). There was then a larger series of sustained precipitation events from July 3 to 11,

occurring before and during the July 8 sampling date, preceding the final July 15 sampling date, during which soils were still relatively wet. Air temperatures were in the range of 20–30°C, with cooler temperatures during storm events. Interspace soil consistently showed the highest gravimetric soil moisture throughout the six sampling dates (seasonal averages: interspace, $2.06 \pm 0.08\%$; creosote, $1.33 \pm 0.09\%$; and mesquite, $1.34 \pm 0.05\%$), except on June 24 when all soils were at their driest (Figure 1b).

SOC and total nitrogen

Evaluation of SOC numbers suggested that the fumigation procedure we used was insufficient to remove all of the inorganic carbonates. We have included these data in the Appendix with some further explanation (Appendix S1: Figure S1). Soil total nitrogen was elevated under creosote and even more so under mesquite (Figure 2: interspace, $N = 0.048 \pm 0.002\%$; creosote, $N = 0.053 \pm 0.002\%$; and mesquite, $N = 0.065 \pm 0.003\%$).

Extractable nutrients

Extractable nutrients from soil core samples showed consistent differences among cover types and several temporal trends (Figures 1c–e and 3). Throughout the measurement period, ammonium ($\text{NH}_4^+\text{-N}$; Figure 1c) values differed consistently, with mesquite soils showing the highest levels (seasonal average = $2.24 \pm 0.14 \mu\text{g g soil}^{-1}$; mean $\pm$ SE), creosote bush showing intermediate levels ($1.62 \pm 0.09 \mu\text{g g soil}^{-1}$), and interspace soils showing the lowest ($1.17 \pm 0.08 \mu\text{g g soil}^{-1}$). Temporal patterns were similar in all soil types, with a peak in NH_4^+ availability around June 17 and June 24 and lower levels during July, coinciding with the most substantial rain event of the sampling period. Contrasts of the two wettest measurement dates with the two driest indicated that NH_4^+ pools were around half as large in wet soils as dry soils (e.g., for mesquite wet/dry = 0.51 [0.43, 0.61]; Figure 4). Temporal patterns in nitrate ($\text{NO}_3^-\text{-N}$) showed the opposite pattern, with the lowest levels around June 17 and 24, followed by rising availability (Figure 1d). Thus, NO_3^- levels were higher during the wet portion of our sampling period (Figure 4). NO_3^- pools were generally more variable than NH_4^+ pools (12% of NO_3^- samples accounted for 55% of total NO_3^- observed during the study), which left substantial uncertainty in the sizes of differences among cover types and less evidence of a resource island pattern (Figure 3). Some of this was due to the influence of the largest measurement of $26 \mu\text{g g}^{-1}$, but even without that value, the

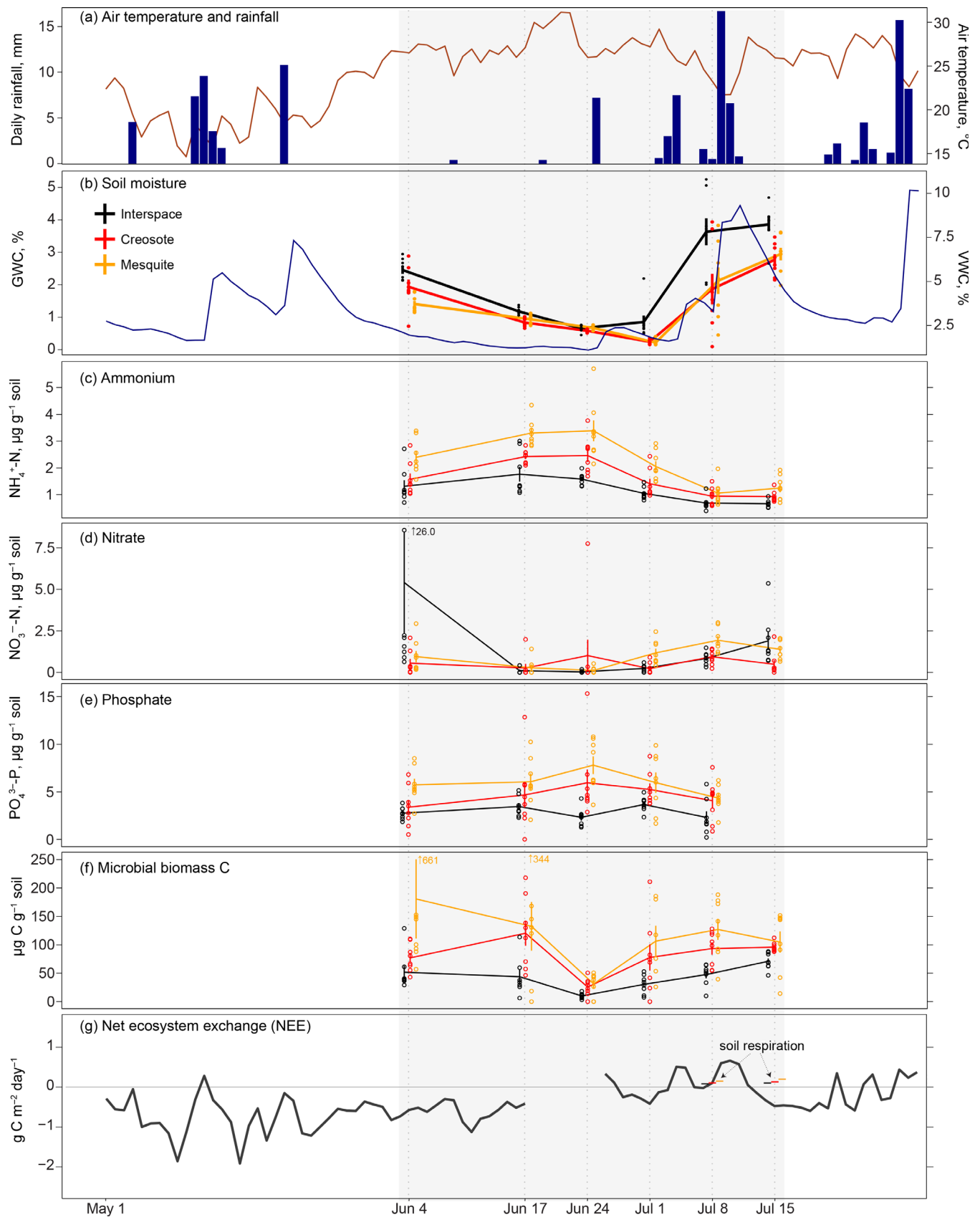


FIGURE 1 Legend on next page.

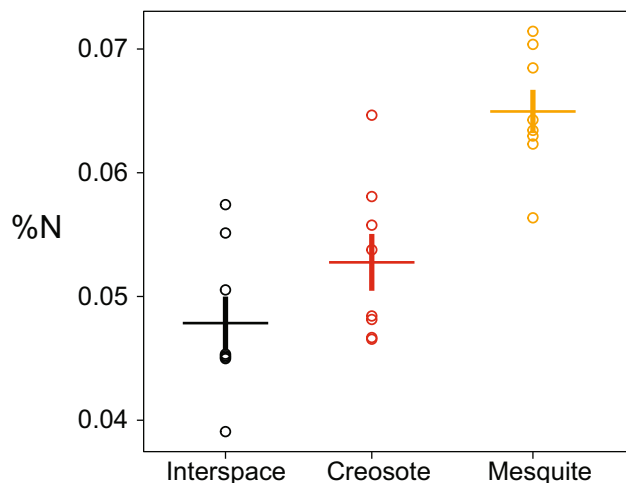


FIGURE 2 Bulk soil %N (mean $\pm$ SE). Each value is the average of all time points at each of the eight sampling locations.

overall distribution was still right-skewed, containing other high values of 8.6 and 7.6 $\mu\text{g g}^{-1}$. Finally, phosphate (PO_4^{3-}) concentrations also reflected cover type but exhibited less of a temporal trend throughout the measurement period, with seasonal means of mesquite, $\text{PO}_4^{3-} = 5.98 \pm 0.59 \mu\text{g g soil}^{-1}$; creosote, $\text{PO}_4^{3-} = 4.66 \pm 0.74 \mu\text{g g soil}^{-1}$; and interspace, $\text{PO}_4^{3-} = 2.90 \pm 0.17 \mu\text{g g soil}^{-1}$ (Figure 1e).

Microbial biomass C and N

Within our 140 total samples measured, MBC ranged from undetectable to 661 $\mu\text{g g dry soil}^{-1}$, with a median value of 63 $\mu\text{g g}^{-1}$ (Figure 1f). Without the highest value of 661 $\mu\text{g g}^{-1}$, the mean for the mesquite cover type on the first measurement date would be $112 \pm 14 \mu\text{g g}^{-1}$ instead of $181 \pm 70 \mu\text{g g}^{-1}$. MBN, which showed very similar spatial and temporal trends to MBC, ranged from undetectable to 71 $\mu\text{g g}^{-1}$, with a median value of 4 $\mu\text{g g}^{-1}$ (Appendix S1: Figure S2). Averaged throughout the summer, MBC and MBN were similar in mesquite and creosote bush (mesquite/creosote MBC = 1.37 [0.96, 1.96]; Figures 1f and 3; Appendix S1: Figure S1). Resource islands had around

double the microbial biomass (creosote/interspace = 1.94 [1.55, 2.42] and mesquite/interspace = 2.66 [1.97, 3.59]; Figure 3). Microbial biomass was relatively consistent throughout the sampling period with the exception of sampling dates when soils were driest, during which it was around half as large as during the other dates (e.g., wet/dry MBC for mesquite = 1.89 [1.24, 2.88]; Figure 4). Overall, microbial biomass was higher under shrubs and lower during the driest date.

Soil enzyme activity

The hydrolytic soil enzyme activities showed pronounced resource island patterns among the three canopy cover types (Figure 5a–f; e.g., for β -glucosidase, Figure 5b), seasonal average for mesquite, β -glucosidase = $284 \pm 23 \text{ nmol g soil}^{-1} \text{ h}^{-1}$, creosote, β -glucosidase = $177 \pm 14 \text{ nmol g soil}^{-1} \text{ h}^{-1}$; and interspace, β -glucosidase = $71 \pm 5 \text{ nmol g soil}^{-1} \text{ h}^{-1}$). For soil oxidative activity, the peroxidase assay (Figure 5h) was elevated under creosote bush and mesquite relative to interspace soil, while the phenol oxidase assay (Figure 5g) showed less difference among cover types (Figure 3). The potential enzyme activities did not show consistent seasonal variations, even among wet and dry periods, unlike NH_4^+ and NO_3^- availability (Figure 4). Though we were missing some data, seasonal trends in soil oxidative activity were more erratic, with higher values on the first measurement date, a treatment difference between creosote bush and interspace in July (creosote/interspace = 3.1 [1.5, 6.2], and then a return to similarity among cover types on the last measurement date (Figure 5g,h). Across all samples, hydrolytic soil enzyme activities were correlated with one another (e.g., r^2 [95% CI] = 0.74 [0.63–0.81] for β -D-glucosidase vs. phosphatase; Appendix S1: Figure S3).

C fluxes

The eddy covariance tower measurements indicated that this ecosystem was primarily a sink for C during the

FIGURE 1 (a) Precipitation as daily sum (blue bars; axis is on left) and air temperature (brown line; axis is on right); (b) soil moisture measured gravimetrically in 0–10 cm soil cores by cover type (gravimetric soil water content, left axis) and by time domain reflectometry probes (volumetric soil water content, right axis; daily averages of 5–30 cm depths); (c–e) NH_4^+ , NO_3^- , and PO_4^{3-} concentrations from soil core extractions; (f) soil microbial biomass C by chloroform fumigation. Soil microbial biomass N trends were similar and are shown in Appendix S1: Figure S1. (g) Net ecosystem exchange and mean soil respiration for each cover type on the two measurement dates (see Appendix S1: Figure S4 for more detail); the sampling period is indicated by the gray background, with specific sampling dates connected by dotted lines. Samples from the three cover types were collected simultaneously but are offset slightly to prevent overplotting. For soil samples, points indicate values for each core and mean $\pm$ SE is shown on each date, connected by lines. Outlier values of 26 $\mu\text{g g}^{-1}$ for NO_3^- in an interspace sample, 661 $\mu\text{g g}^{-1}$ for a microbial biomass C sample, and 344 $\mu\text{g g}^{-1}$ are outside the scale shown on the graph (to allow better resolution of other data) but were used for calculations of mean and SE.

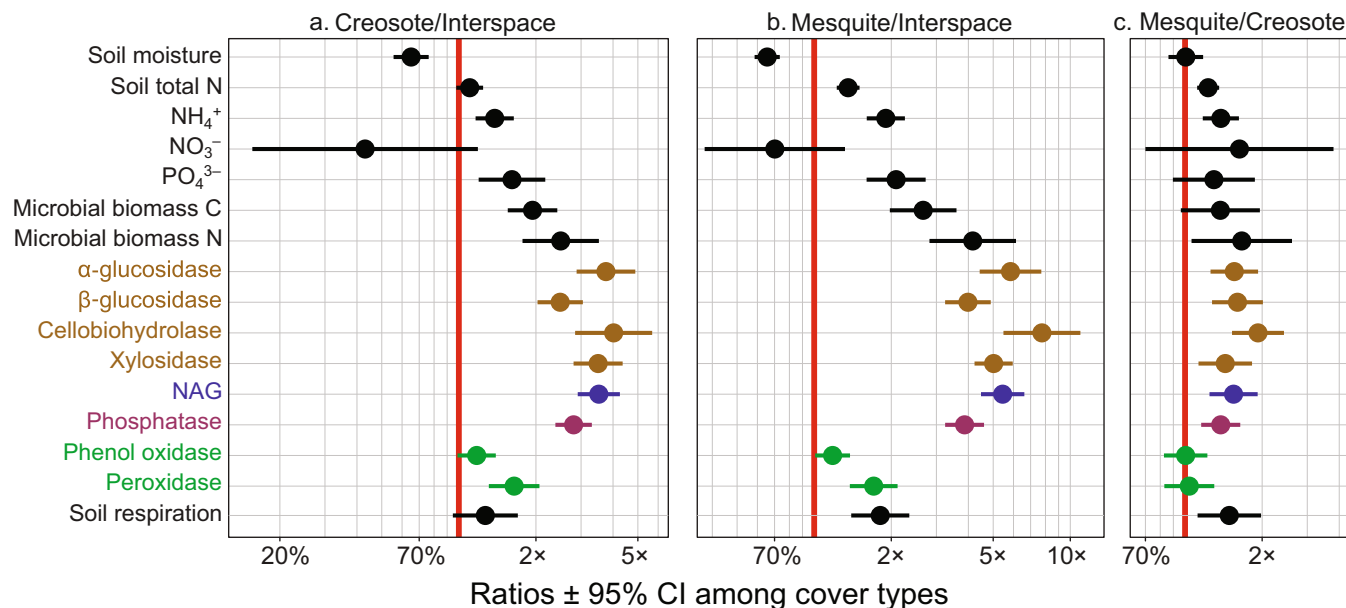


FIGURE 3 Ratios among cover types with 95% CI (log scale) averaged over all dates in the sampling period. $n = 8$ for all samples. As an example, gravimetric soil moisture was 65% [55, 76] as high in creosote as in interspace during the study period. The red vertical lines indicate a 1:1 ratio. Enzyme function is encoded by color (C-acquiring, brown; N-acquiring, blue; P-acquiring, violet; and oxidative, green). NAG, *N*-acetyl-glucosaminidase.

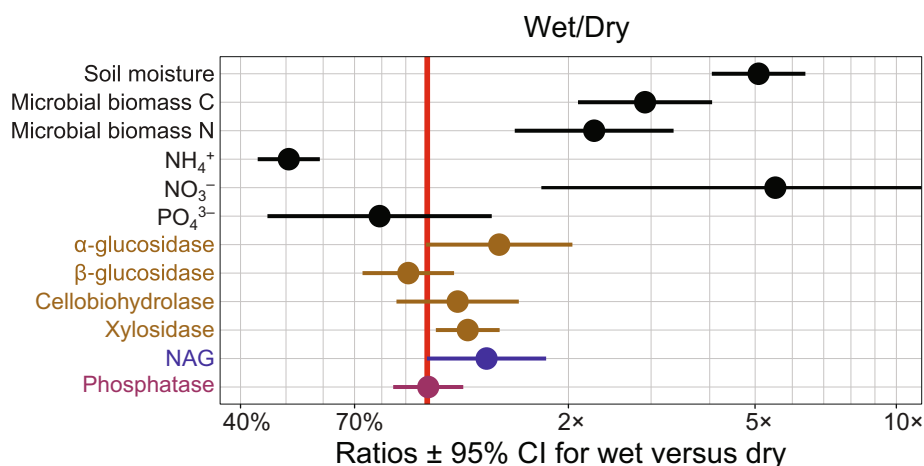


FIGURE 4 Ratios of wet/dry with 95% CI for wet versus dry periods on a log scale to describe response to rainfall. Data were spatially averaged across the three cover types. Higher percentages are denoted as fold change (i.e., 500% = 5 $\times$). NO_3^- ratios for interspace and creosote are poorly constrained due to some near-zero values and thus extend outside of the plotting area. $n = 8$ for all samples. Enzyme function is encoded by color (C-acquiring, brown; N-acquiring, blue; P-acquiring, violet). NAG, *N*-acetyl-glucosaminidase.

measurement period (Figure 1g). However, following rain events, we observed net C loss from the ecosystem to the atmosphere. Measurements of soil respiration using soil chambers on two dates showed elevated rates under creosote bush (July 8, creosote/interspace = 1.29 [0.8, 2.08]; July 15, 1.27 [1.04, 1.58]; Appendix S1: Figure S4) and even higher rates under mesquite (July 8, mesquite/interspace = 1.88 [1.25, 2.96]; July 15, 1.89 [1.35, 2.56]; Appendix S1: Figure S4).

DISCUSSION

Spatial patterns for nutrient and elemental concentrations, microbial biomass, and potential enzyme activities largely followed the patterns expected for a dryland site with shrub islands and interspaces. These findings are consistent with previous studies in which limiting nutrients such as N and P are concentrated under shrub canopies relative to the surrounding interspace soil (Bachar

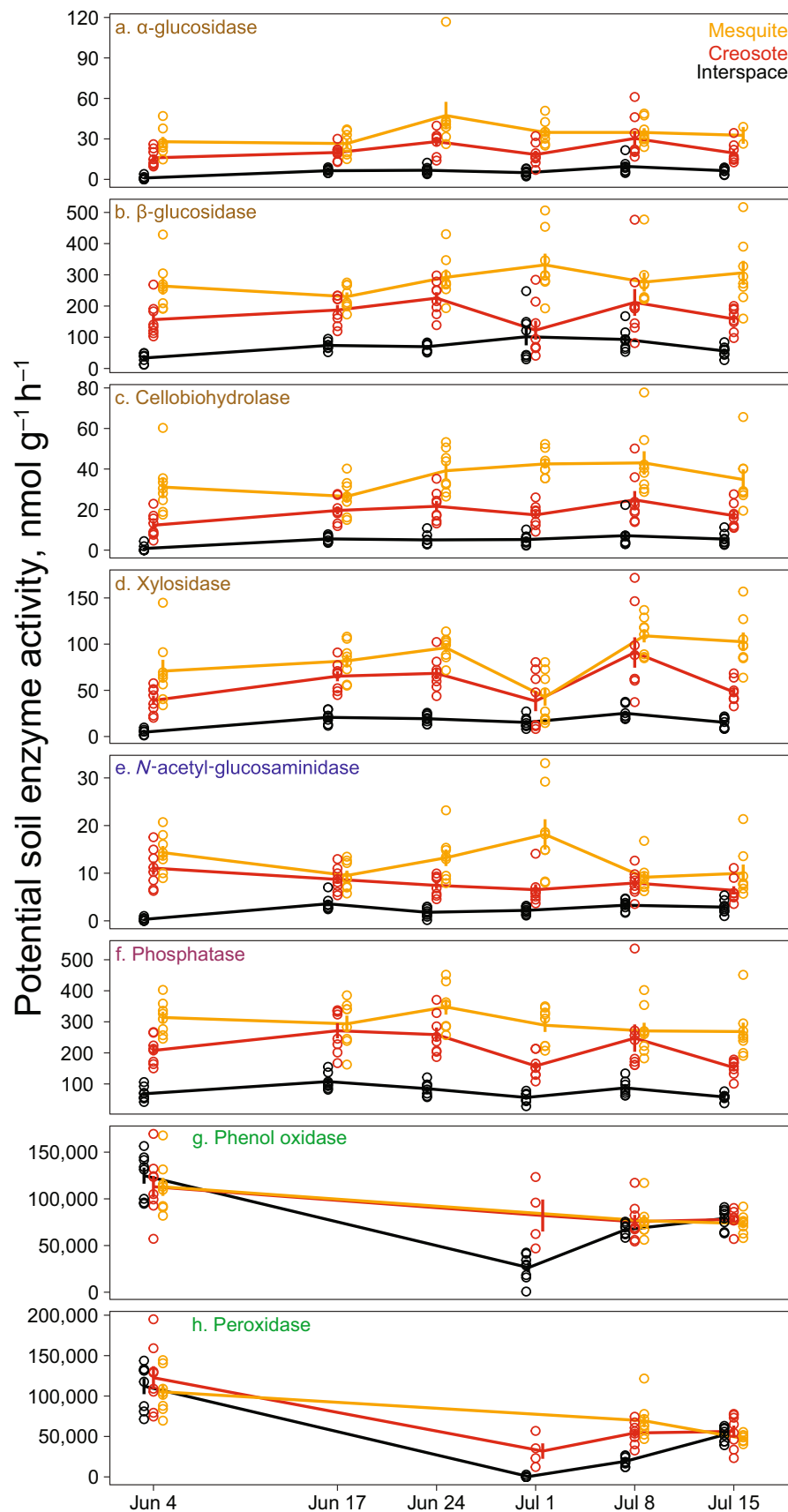


FIGURE 5 Soil potential enzyme activities (mean $\pm$ SE on each date). Points indicate values for each soil core and mean $\pm$ SE is shown on each date, connected by lines. Enzyme function is encoded by color (C-acquiring [a–d], brown; N-acquiring [e], blue; P-acquiring [f], violet; and oxidative [g, h], green). We note that the oxidative activities shown in panels (g) and (h) may additionally be affected by abiotic processes.

et al., 2012; Cross & Schlesinger, 1999; Herman et al., 1995; Schlesinger et al., 1996; Thompson et al., 2006). The mesquite resource islands were consistently larger than those for creosote bush, likely because mesquite has more litter as a deciduous shrub and greater nutrient content as a N-fixing legume. This consistent difference indicates that the strength of resource island effects can vary by shrub species. The magnitudes of nutrient concentrations, microbial abundances, and enzyme activities indicated low biotic activity in surface soils compared with those in nearby landscape components and in similar climates more generally (Bell et al., 2008; Cross & Schlesinger, 1999; Ladwig et al., 2015; Wagner & Jones, 2004; Whitford et al., 2008). Low microbial biomass is consistent with the rocky soils, low vegetation cover, and minimal biocrust cover observed at the site. Over the course of the rainfall pulse that occurred during our study, even though nutrient concentrations changed in response to increased water availability, resource island patterns in most of our measured variables remained consistent, with mesquite > creosote > interspace. Thus, our hypothesis that resource island patterns would be maintained over the course of a rainfall pulse for dynamic processes such as microbial turnover and enzyme activity was supported. Together, these findings suggest that the critical zone at this site has a smaller biotic influence compared with other more productive dryland sites, but that spatial heterogeneity linked to resource islands is a substantial influence on critical zone development and function. Below we focus on several variables that deviated from the expected resource island or rainfall pulse-response patterns and discuss our findings in the context of landscape-scale C balance at the site.

Nitrate

Our NO_3^- data were a notable exception to expected spatiotemporal patterns in surface soils at this site. NO_3^- concentrations generally did not follow the resource island pattern as did NH_4^+ and PO_4^{3-} , suggesting that NO_3^- fluxes are not as tied to the cycling of organic matter between plant production and decomposition. These fluxes may be more microbially controlled via processes such as nitrification and the accompanying gaseous N losses from the system (Homyak et al., 2016; Soper et al., 2016). Downward NO_3^- transport is also a possibility, although during monsoon rains, water rarely infiltrates deeper than ~30 cm in this area (Duniway et al., 2018). Temporal trends in NO_3^- ran counter to those of NH_4^+ , increasing as the ecosystem transitioned from dry to wet, a trend documented in several studies (Bell et al., 2008; Clark et al., 2009; Jensen et al., 2003), but not universally

observed (e.g., Brown et al., 2022). A possible explanation is that nitrification may increase as microbial activity increases after rain (Bell et al., 2008; Clark et al., 2009). NO_3^- concentrations were highly variable, suggesting a substantial role for hot spots or hot moments in NO_3^- fluxes (Darrouzet-Nardi & Bowman, 2011). While some of the values measured were quite high relative to the mean, we have no reason to suspect the measurements are incorrect as they are in line with previous values we have measured in a range of ecosystems, as well as studies demonstrating high variation and right skew in distributions of inorganic N values (Darrouzet-Nardi & Bowman, 2011; Jackson & Caldwell, 1993; Mellert et al., 2008). Furthermore, there is evidence that NO_3^- can build up in surface soils in arid systems, for example, Stursova et al. (2006) report mean values of 5.57 and 3.42 $\mu\text{g g}^{-1}$ under grasses and biocrusted interspace, respectively. Finally, our NO_3^- values were lower than NH_4^+ , a difference with some other Chihuahuan Desert sites (Brown et al., 2022; Holguin et al., 2022; Stursova et al., 2006). This low NO_3^- could indicate greater biotic immobilization or NO_3^- loss from soils at this site (Peterjohn & Schlesinger, 1990). NO_3^- production and loss processes in the surface soils are worthy of further investigation as potentially important features of N cycling and long-term balance in dryland critical zones.

Microbial biomass and potential soil enzyme activity during rainfall pulses

In contrast to the dynamic nutrient pools, microbial biomass was more stable throughout the summer except for a decrease in microbial biomass observed on one measurement date (June 24) that coincided with the driest soil conditions measured. Rain in the period preceding our sampling period may have led to a more active microbial community, which then declined in mid-June as soils dried out, before a rainfall event on June 25 reactivated the microbes. Further rainfall events of similar intensity did not appear to further increase microbial biomass, suggesting that the microbial community is relatively stable once activated by an increase in soil moisture, at least during the length of our study period. This trend would be consistent with the idea that there is not always a positive association between water availability and microbial biomass (Holguin et al., 2022; Schimel, 2018). Other studies have shown a more dynamic microbial community over longer time periods (i.e., beyond a single monsoon season) in which microbial biomass fluctuates with precipitation pulses (Bachar et al., 2012; Bell et al., 2008; Liu et al., 2000; Steinberger et al., 1999).

Several drought studies have also shown that bursts of microbial activity are more pronounced after rainfall events following longer periods of drought than following high-frequency soil wetting and drying events (Clark et al., 2009; Reynolds et al., 1999).

For soil potential hydrolytic enzyme and oxidative activities, our results show a lack of response to different moisture conditions during the monsoon season (Bell & Henry, 2011; Holguin et al., 2022; Ladwig et al., 2015). Because these are potential activities, the enzymes are not likely active during dry periods (Steinweg et al., 2012); however, the consistent potentials may indicate that enzymes in these surface soils are adapted to withstand drought and respond quickly to moisture (Schimel, 2018). Over a longer sampling period than in our study, decreases in potential enzyme activities have been observed at the onset of the monsoon season (Bell et al., 2008; Ladwig et al., 2015). For the hydrolytic enzymes, the activities varied substantially between resource islands and interspaces, likely because the hydrolytic enzyme activity is linked to plant litter substrate (Liu et al., 2000; Martinez et al., 2021). Elevated hydrolytic enzymes under shrub canopies have been documented in many studies (Cao et al., 2011; Ladwig et al., 2015; Thompson et al., 2006). In contrast, soil oxidative activity showed relatively even distributions across cover types with the exception of one measurement date, July 1; at least one other study has hinted at this trend (Cao et al., 2011). Soil oxidative activity also showed the characteristic high rates for arid alkaline soils (Stursova et al., 2006). The consistency in potential activities indicates that the redox chemistry associated with the biota (Falkowski et al., 2008) in the surface soil of dryland critical zones can re-engage rapidly upon wetting alongside abiotic geochemical reactions.

Connections to eddy-covariance-measured NEE of carbon

The eddy covariance tower data indicated that just before and during the study period, the ecosystem was a sink for C except for brief periods during and immediately after rain events, when C balance shifted toward an atmospheric source (positive NEE). A similar summer rainfall respiration pulse was observed in a semiarid shrubland in Idaho (Flerchinger et al., 2019). The maintenance of hydrolytic and oxidative potential in the soil during drought may contribute to the rapid but temporary transition from C sink to C source during and immediately following rainfall events, possibly due to rapid breakdown of accumulated litter or fresh root exudates (Sponseller, 2007). We note, however, that physical factors such as displacement of CO₂-rich air from the soil

could also play a role in the NEE trends we observed (Huxman et al., 2004; Sponseller, 2007) and such processes are worthy of further measurement. Similarly, a water addition experiment in a semiarid shrubland in Idaho showed that SOC did not build up in the soil even with additional water and plant growth if the water was supplied outside of the main growing season, which they attributed to high decomposition rates (Campos et al., 2017; Huber et al., 2019). An assessment of long-term SOC dynamics in the Chihuahuan Desert came to similar conclusions (Hou et al., 2021). Over the long term, the stability of the oxidative enzymes in dryland soils is a possible factor contributing to rapid C oxidation when water becomes available, and has been suggested to lead over the long term to a lack of C buildup in semiarid systems because they promote decomposition and limit C accumulation (Stursova & Sinsabaugh, 2008; Zak et al., 1995). Abiotic oxidation mechanisms could also contribute to this phenomenon (Hall & Silver, 2013; Jones et al., 2020).

The spatial patterns we documented indicate that at the landscape level, belowground C cycling activity occurs disproportionately under shrubs, as expected. However, because the interspace is much greater in extent (~88% of surface), belowground processes in the interspace cannot be neglected in assessments of landscape-level processes such as eddy covariance measurements of NEE. It is likely that soil processes such as plant root growth, nutrient acquisition, and decomposition are occurring in the interspace and that these areas contribute substantially to landscape totals for these processes. This is in contrast with aboveground C uptake, which of course is concentrated in plant leaves. Biocrust cover can sometimes contribute to C uptake in the interspace (Darrouzet-Nardi et al., 2015; Elbert et al., 2012), but at this site, biocrusts are low in abundance, particularly in the interspace. Taken together, our comparisons between shrub and interspace dynamics suggest that belowground biotic processes in the surface soil interspaces are reduced, but still important for critical zone function given the high proportion of interspace. In the future, longer monitoring of these soil processes (at least one year, ideally longer) at similar resolution (~weekly) would be useful to develop a better understanding of the connections between NEE and surface soil processes.

CONCLUSIONS

The patterns and processes we observed in the surface soil interface within this dryland critical zone showed high spatial structuring that is maintained over varying

moisture conditions, with relevance of species identity (mesquite vs. creosote bush). Microbial decomposition potential was high and responded quickly to water, which may influence the timing of landscape-level C exchange. These results suggest that over longer time scales, biotic activity in surface soils serves to dynamically process materials over the course of rainfall pulses and returns carbon and nutrients to the atmosphere rather than building fertility by storing them in the bulk soil.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Darrouzet-Nardi, 2022), variable descriptions, and analysis scripts are available from HydroShare: <https://doi.org/10.4211/hs.c6f91fd7407e4e038a27b487e2f8627f>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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