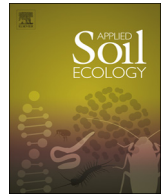




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## Soil microbial activity is resistant to recreational camping disturbance in a *Prosopis* dominated semiarid savanna

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### ABSTRACT

Recreational camping has been shown to suppress plant cover and expand bare ground area. These shifts have important implications for soil health. We used campsites in a semiarid savanna at the Santa Rita Experimental Range (SRER) in Arizona to test the hypotheses that 1) recreational camping is a disturbance that limits plant cover and soil microbial activity, and 2) the presence of *Prosopis*, which is known to encourage a fertility island effect, increases soil microbial activity within campsites. Camping disturbance did not influence any sampled measures of edaphic properties, plant cover, or soil microbial biomass and exoenzyme activities. However, the presence of *Prosopis* resulted in elevated litter, total dissolved nitrogen (TDN), and dissolved organic carbon (DOC). Multiple linear regression models suggest that observed resistance of soil microbial activities to camping disturbance may be due to both increased availability of organic C and N substrates beneath *Prosopis* and heightened seasonal water availability.

### 1. Introduction

United States residents spend approximately \$646 billion each year on recreation (White et al., 2016). Therefore, considering the ecological impacts of recreation is important for both establishing sustainable ecosystem management and for maintaining revenue. Camping, one of the most common recreation activities, disturbs ecosystems in several ways, including trampling, off road vehicle use, campfires, and trash (Marzano and Dandy, 2012). As recreation became increasingly popular over the past twenty years, researchers have explored the ecological impacts of camping. Demonstrated impacts include reductions in plant cover, changes in plant community composition, and increases in soil erosion (Alessa and Earnhart, 2000; Cole, 1995). However, some key aspects of recreation impacts remain poorly understood. In particular, the effects of camping on soil health have been understudied. Healthy soils host microbial communities that facilitate crucial biogeochemical cycles and promote ecosystem function (Hall et al., 2016). Understanding soil microbial responses to disturbance in campsites can therefore help inform their effective management (Zabinski and Gannon, 1997).

Recreation impacts in water limited systems, such as those in the Southwestern United States, are particularly poorly understood. This gap in knowledge is especially important to address considering the fact

that recreation in this region provides a significant stream of revenue. For example, recreational birding opportunities in the State of Arizona drew  $\approx 1.3$  million visitors and generated \$838 million in trip related spending in 2006 alone (U.S. Fish & Wildlife Service 2006). In mesic systems, recreation has been shown to increase soil erosion, and decrease herbaceous plant cover and soil microbial metabolic activity (Cole, 1995; Zabinski and Gannon, 1997). Water limitation exerts a strong influence on patterns in plant and soil mediated nutrient cycling (Cui et al., 2019); it is therefore likely that responses to recreational disturbance in semiarid systems differ substantially from those in mesic systems.

This study seeks to address these knowledge gaps using the following guiding question: what impact does recreational camping have on plant cover, soil microbial activity, and their interactions in a semiarid savanna? We hypothesized that: 1) recreational camping is a disturbance that limits herbaceous plant cover, soil microbial biomass, and extracellular enzyme (exoenzyme) activity and 2) that the presence of *Prosopis* increases soil microbial activity in campsites at the Santa Rita Experimental Range (SRER) in Southern Arizona.

Losses in plant cover are some of the most visually striking and commonly documented examples of ecological responses to camping (Cole, 1995; Cole and Monz, 2003; Crisfield et al., 2012; Leung and Marion, 1999). Soil microbes are especially abundant and active within

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the root zones of plants (Barea et al., 2005). Therefore, we expected that limited plant cover in campsites would correspond with diminished soil microbial activity. Exoenzymes, which microbes excrete to facilitate degradation of large organic molecules, are useful for estimating soil microbial activities (Wallenstein and Burns, 2011). Exoenzyme activities' responses to recreation have been shown to vary by temporal extent (Kissling et al., 2009); that is, some exoenzyme activities are inhibited predominantly by short term disturbance and others by long term disturbance. Camping disturbance was expected to have a negative effect on soil microbial biomass and exoenzyme activity at the SRER due to substrate removal and changes to herbaceous plant cover (Alessa and Earnhart, 2000).

Conducting this study at the SRER allowed us to examine ecological impacts of seasonal high intensity camping in a system under the long term influence of woody plant expansion (Throop and Archer, 2008). Woody expansion has affected grasslands and savannas all over the world (Archer and Pierper, 1994). Woody plants obtain and distribute water and nutrients differently than herbaceous plants; this has been demonstrated to initiate distinct plant-soil feedbacks which encourage fundamental ecological changes (Hibbard et al., 2001). Due to the interdependence of plants and soils, these unique conditions may influence the responses of corresponding soil microbial communities to camping disturbance at SRER. In particular, 'fertility islands,' which have been observed beneath the dominant *Prosopis* (mesquite) in semiarid ecosystems of the southwestern United States, exhibit high nitrogen (N) concentrations relative to surrounding soils (McClaran et al., 2008; Ridolfi et al., 2008). Therefore, *Prosopis* cover was expected to positively correlate with soil microbial biomass and exoenzyme activities in campsites.

Many biological, chemical, and physical properties of soil microbial communities exert strong influences on plant communities (Ehrenfeld et al., 2005; Hall et al., 2016; Zak et al., 2003). Therefore, an understanding of plant-soil interactions can elucidate the impacts of camping on soil microbial activities. Here, we combine measures of activity of exoenzymes that degrade carbon (C), N, and phosphorus (P) substrates found in soil organic matter (see Table 1) with soil biogeochemistry, microbial biomass, plant cover, and litter depth to provide insight on how human recreation influences semiarid ecosystems.

## 2. Materials and methods

### 2.1. Field site and sampling design

The SRER is a 21,512 ha field station located at the northwest edge of the Santa Rita Mountains in Southeastern Arizona, USA. It is dominated by alluvial derived soils and semiarid savanna vegetation ranging in elevation from about 884 m in the northwest to 1585 m in the southeast. Average annual precipitation ranges from 250 to 500 mm, increasing with elevation at the SRER (McClaran et al., 2002). Recent vegetation dynamics in the area have been characterized by increases in woody cover, dominated by velvet mesquite (*Prosopis velutina*), and the spread of Lehmann's lovegrass (*Eragrostis lehmanniana*), an introduced perennial grass (McClaran et al., 2010). Other common understory vegetation at the SRER includes succulents, annual forbs, and perennial

grasses. In addition to serving as a research facility, the SRER is a popular site for recreational activities such as hunting, birdwatching, and camping.

There are over 100 informally established campsites at the SRER. Four campsites at similar elevations (1169–1241 m) were included in this study. Combate-Diaspar is the dominant soil type, characterized by a gravelly loamy coarse sand texture and 1–8% slopes (McClaran et al., 2002). Containment fences were installed at campsites between 2013 and 2015 to limit the spread of camping disturbance. This developed a spatial gradient of short-term camping recovery at each site. Patterns of use at these sites occur predominantly on a seasonal basis, especially during deer hunting periods between September and December. We refer to this camping regime as low frequency and high intensity because campsites are only used during particular times of year, during which there are many visitors and heavy campsite use.

Field sampling was conducted in August 2017 at the peak of the monsoon growing season. At this time, the monsoon rains had been ongoing for a few weeks. Plant responses to this increased water availability, such as annuals sprouting and perennials blooming, were already apparent. We chose to sample at this time in order to be able to detect a difference, if present, between plant cover in campsites and natural areas. We expected that this difference might not be apparent in dry conditions because plant cover is already sparse under natural conditions in semiarid savannas. Prior to sampling, *Prosopis* trees were selected in areas distinguished by categories of disturbance at each site: active campsite area (Ca), fenced recovering area (Re), and undisturbed control area (Co). To account for known differences in soil nutrient availability based on tree size, sampled trees were limited to 25–60 cm diameter at breast height (McClaran et al., 2008). Samples beneath *Prosopis* canopies were collected 1 m from the trunk of each tree. Four locations within a 1 m radius of each tree were randomly selected to serve as duplicates which we used to capture heterogeneity. These were later consolidated by means to avoid pseudo replication. Samples in bare canopy were collected 1 m from the edge of the leaf canopy drip line (see Fig. 1).

We collected stratified measures of herbaceous plant cover, litter depth, and topsoil samples (10 cm deep) for microbial and biogeochemical assays. Samples were stratified based on a gradient of recreational use and the presence or absence of *Prosopis*. At each site, areas with different camping disturbance regimes were adjacent to one another. The Daubenmire class method was employed to calibrate visual estimates of plant cover within 40 × 40 cm quadrats (Daubenmire, 1959). At the center of each quadrat, 10 cm of surface soil was collected using a bulb corer. Measures of soil temperature and litter depth were taken at the site of collection using a temperature probe and calipers. Previous measures of topsoil bulk density at the Santa Rita Experimental Range were not significantly different in areas beneath *Prosopis* and in bare canopy (McClaran et al., 2008). We therefore opted to exclude measures of bulk density from this study.

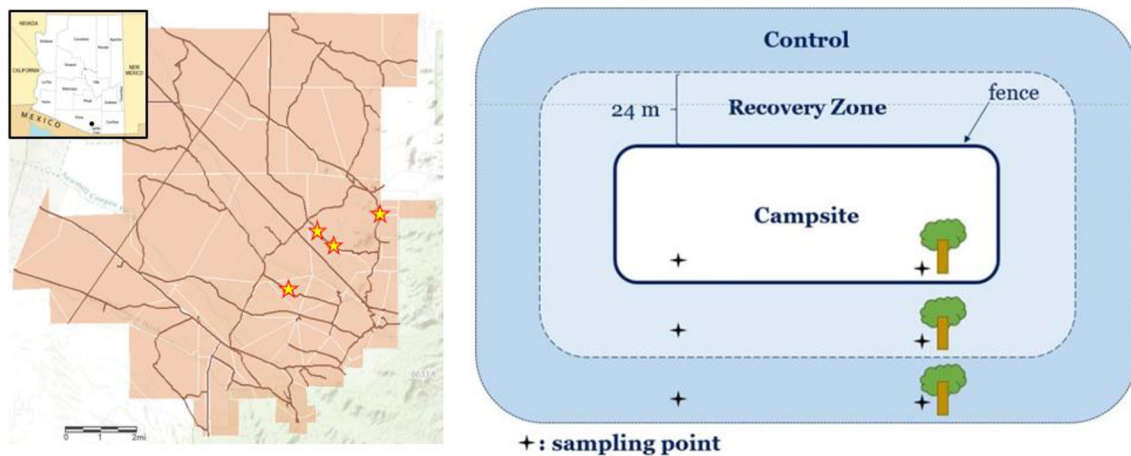
### 2.2. Soil processing and microbial assays

Soil samples were sieved (2 mm) and stored in a refrigerator at 4 °C. Gravimetric water content (GWC), total organic carbon (TOC), and pH

**Table 1**

Exoenzyme activities and their primary function. Exoenzymes assayed in this study catalyze a variety of reactions in soils.

Exoenzyme	Primary function	Predominant biogeochemical cycle
β-D-cellobiosidase (CB)	Cellulose degradation: releases disaccharides from cellulose	C
α-Glucosidase (AG)	Sugar degradation: releases glucose from soluble saccharides	C
β-Glucosidase (BG)	Sugar degradation: releases glucose from cellulose	C
β-xylosidase (XYL)	Hemicellulose degradation	C
Leucine aminopepsidase (LAP)	Protein degradation	N
N-acetyl-β-Glucosaminidase (NAG)	Chitin degradation	N
Phosphatase (PHOS)	Phosphorus mineralization	P



**Fig. 1.** Field site and experimental design. Data was collected from four campsites at the Santa Rita Experimental Range in Green Valley, Arizona. Campsites (yellow stars) are located in comparable natural areas adjacent to dirt roads (brown lines). Sampling was stratified by categories of canopy cover (*Prosopis* or bare) and camping disturbance (campsite, recovery, or control). At each sampling point, four randomly located (within a 1 m radius) 40 × 40 cm quadrats were used to sample herbaceous vegetation and soil. At each campsite,  $n = 24$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

protocols followed Gebhardt et al. (2017). Fluorimetric extracellular enzyme assays were conducted in deep-well microplates following Gebhardt et al. (2017), modified from Wallenstein et al. (2012). TOC and GWC were measured by incubating samples in a Barnstead Thermolyne muffle furnace at 450 °C for 4 h; a symphony Model SB20 meter was used to measure soil pH. The potential activities of the following hydrolytic enzymes were measured:  $\beta$ -D-cellobiosidase (CB),  $\alpha$ -Glucosidase (AG),  $\beta$ -Glucosidase (BG), leucine aminopepsidase (LAP), *N*-acetyl- $\beta$ -Glucosaminidase (NAG), Phosphatase (PHOS), and  $\beta$ -xylosidase (XYL) (see Table 1). Samples were incubated at 25 °C and 35 °C to mimic the lower and upper ranges of observed *in situ* soil temperatures (Steinweg et al., 2012). Soil slurries were prepared with 2.75 g of soil and 91 mL of 50 mM Tris buffer, which was titrated to a pH of 7 using glacial acetic acid. Each soil slurry was incubated with 100  $\mu$ L of 200  $\mu$ M fluorimetric substrate. Final measurements were made with a Synergy™ 4 Multi-Mode microplate reader with an excitation wavelength of 365 nm and an emission wavelength of 450 nm. Raw data were corrected against a standard curve developed from a serial dilution of reference fluorescent indicators, 4-methylumbelliferone and 7-amino-4-methylcoumarin (Gebhardt et al., 2017).

Measures of dissolved organic carbon (DOC), total dissolved nitrogen (TDN), and microbial biomass C and N were quantified using a fumigation-extraction method (Voroney et al., 1993). Ten grams of each soil sample were separated and weighed, and 5 g were prepared for extraction immediately. Twenty-five mL of Ultra-pure water was added to the soil; this mixture was then mixed at 200 rpm for 1 h to mix contents. Vacuum filtration was used to extract microbial biomass, which was stored in a freezer at -20 °C. The remaining 5 g of each soil sample were treated with 2 mL of chloroform (CHCl<sub>3</sub>) and fumigated for 24 h. Microbial biomass was extracted from fumigated samples in the same way. Microbial biomass extract was diluted (3:1) and quantified using a Shimadzu TOC analyzer (Shimadzu Scientific Instruments, Inc., Columbia, MD, USA). Finally, as in Gebhardt et al. (2017), we used efficiency factors for microbial biomass C (kEC = 0.45) (Beck et al., 1997) and microbial biomass N (kEN = 0.54) (Brookes et al., 1985) to calculate the respective biomass as the difference between fumigated and non-fumigated samples.

### 2.3. Data analysis

All statistical analyses were conducted in R (R Development Core Team 3.4.4, [r-project.org](http://r-project.org)). Two-factor ANOVAs were conducted ( $n = 24$ ) to determine the concurrent influence of a gradient of camping

disturbance and the presence or absence of *Prosopis* canopy on the following variables: microbial biomass C, microbial biomass N, C exoenzyme activity (EEA), N EEA, P EEA, litter depth, plant cover, pH, gravimetric water content, soil temperature, DOC, TDN, specific activity of C enzymes and specific activity of N enzymes (see Fig. 1). Before running ANOVAs, we consolidated the four duplicates of each sample by means. Analyses of exoenzyme activities were pooled based on which biogeochemical cycle (C, N, or P) they are each predominantly involved in (Table 1). Finally, multiple linear regressions ( $n = 96$ ) were conducted to characterize the relationships between microbial and soil environmental measures. Predictors in regression models were selected *a priori* and adjusted using AIC. These predictors included litter depth, mesquite canopy, herbaceous plant cover, GWC, and C:N ratios. Where more than one of these predictors contributed significantly to the observed variance, we tested models with the interaction(s) of these predictors. We reported multiple linear regression models with the lowest AIC values. For all analyses, an  $\alpha$  of 0.05 was used to determine statistical significance. Data published in this study can be referenced on the Gallery Lab GitHub server at the following link: <https://github.com/SudanKariuki/Soil-Microbe-Campsite-SRER-Data>.

## 3. Results

### 3.1. Soil environment

Percent plant cover was not significantly different in campsites across categories of camping disturbance ( $F_{2,18} = 2.09$ ,  $p = 0.153$ ; Fig. 2d); it was also not different based on the presence or absence of *Prosopis* ( $F_{1,18} = 0.19$ ,  $p = 0.668$ ). Similar results were found for GWC (camping disturbance:  $F_{2,18} = 0.19$ ,  $p = 0.826$ ; *Prosopis* canopy:  $F_{1,18} = 0.83$ ,  $p = 0.375$ ; Fig. 2c). Litter depth did not differ across categories of camping disturbance ( $F_{2,18} = 3.34$ ,  $p = 0.0582$ ; Fig. 2e), but it did differ based on the presence of *Prosopis* canopy ( $F_{1,18} = 26.20$ ,  $p < 0.001$ ), where it was 73% greater. DOC and TDN were also elevated beneath *Prosopis* (DOC:  $F_{1,18} = 15.16$ ,  $p < 0.001$ ; TDN:  $F_{1,18} = 11.10$ ,  $p < 0.001$ ; Fig. 2b and f) but unaffected by camping disturbance (DOC:  $F_{2,18} = 0.08$ ,  $p = 0.922$ ; TDN:  $F_{2,18} = 0.09$ ,  $p = 0.917$ ). The interaction of camping disturbance and *Prosopis* canopy did not demonstrate any effect on plant cover, GWC, soil pH, litter, DOC or TDN.

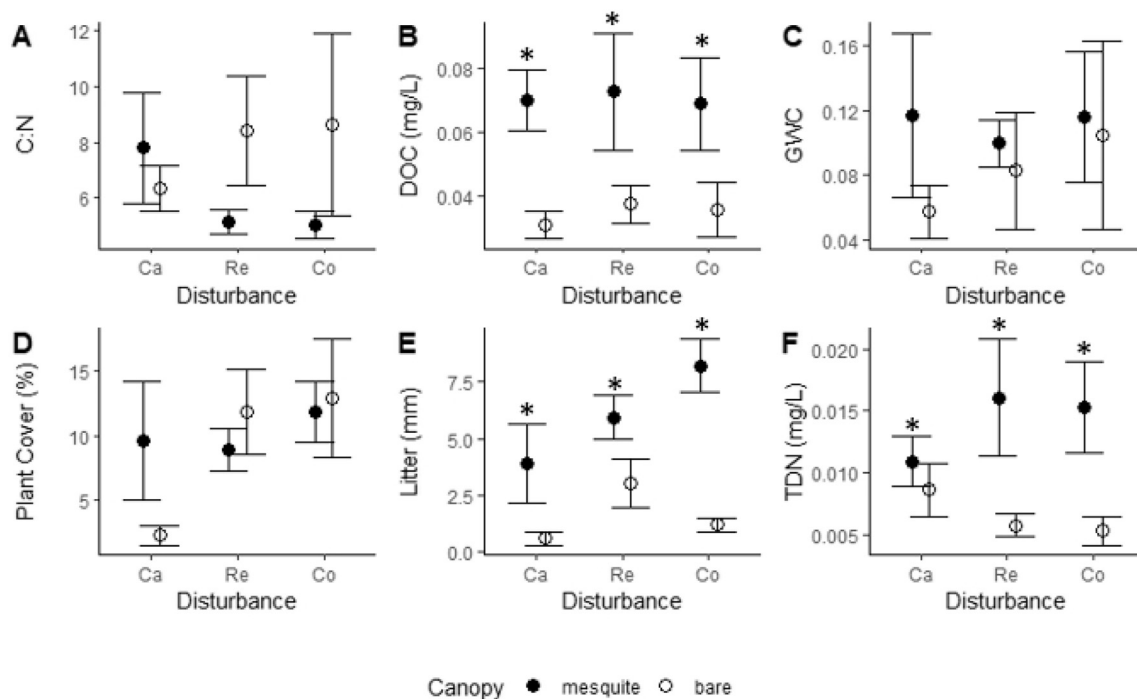


Fig. 2. Ecological responses to camping disturbance and *Prosopis*. Points represent sample means and lines represent standard errors of the following variables: C:N ratio [A], Dissolved Organic Carbon (mg/L) [B], Gravimetric Water Content [C], herbaceous plant cover (%) [D], litter depth (mm) [E], and Total Dissolved Nitrogen (mg/L) [F]. Two factor ANOVAs ( $n = 24$ ) demonstrated that all variables were the same across different levels of camping disturbance (Ca = campsite, Re = recovery, Co = control). Litter, TDN, and DOC were significantly greater (where  $p < 0.05$ ) in the presence of *Prosopis* canopy (closed points = *Prosopis* canopy, open points = bare canopy) than in its absence, as indicated by asterisks.

### 3.2. Exoenzyme activities

Neither camping nor the presence of *Prosopis* significantly changed exoenzyme activities determined at 25 or 35 °C (Fig. 3). In a multiple linear regression, C exoenzyme activity at 25 °C was explained best by GWC and plant cover ( $R^2 = 0.2698$ ,  $p < 0.001$ ; Table 2). N exoenzyme activity at 25 °C was explained best by litter, GWC, and the interaction of these variables ( $R^2 = 0.3845$ ,  $p < 0.001$ ). P exoenzyme activity at 25 °C was explained best by litter, GWC, plant cover, and the interaction of litter and GWC ( $R^2 = 0.245$ ,  $p < 0.001$ ). Exoenzyme activity at 35 °C was best explained by various combinations of these same variables. However, N exoenzyme activity at 35 °C was also affected by pH ( $R^2 = 0.2806$ ,  $p < 0.001$ ). The interaction of camping disturbance and *Prosopis* canopy did not demonstrate any effect on exoenzyme activities. Multiple linear regressions demonstrated that variability in C exoenzyme activities was determined best by GWC (25 °C incubation:  $R^2 = 0.2703$ ,  $p < 0.001$ ; 35 °C incubation:  $R^2 = 0.3585$ ,  $p < 0.001$ ; Table 2). Variability in N exoenzyme activities were explained best by the interaction of litter depth and GWC at 25 °C ( $R^2 = 0.382$ ,  $p < 0.001$ ) and by the interaction of *Prosopis* canopy presence and GWC at 35 °C ( $R^2 = 0.2815$ ,  $p < 0.001$ ). Variability in P exoenzyme activity was determined best by GWC and litter at 25 °C ( $R^2 = 0.2241$ ,  $p < 0.001$ ) and by GWC at 35 °C ( $R^2 = 0.1401$ ,  $p < 0.001$ ).

### 3.3. Microbial biomass

Microbial biomass C was significantly influenced by the presence of *Prosopis* ( $F_{1,18} = 4.852$ ,  $p = 0.0409$ ; Fig. 3c), where it was 55% greater. However, it was not affected by recreational camping ( $F_{2,18} = 0.238$ ,  $p = 0.7909$ ) or the interaction of these factors ( $F_{2,18} = 0.021$ ,  $p = 0.9796$ ). Microbial biomass N demonstrated the same pattern (*Prosopis*:  $F_{1,18} = 4.519$ ,  $p = 0.0476$ ; camping disturbance:  $F_{2,18} = 0.433$ ,  $p = 0.6549$ ; *Prosopis*\*camping:  $F_{2,18} = 0.643$ ,  $p = 0.5376$ ; Fig. 3d). The interaction of camping disturbance and

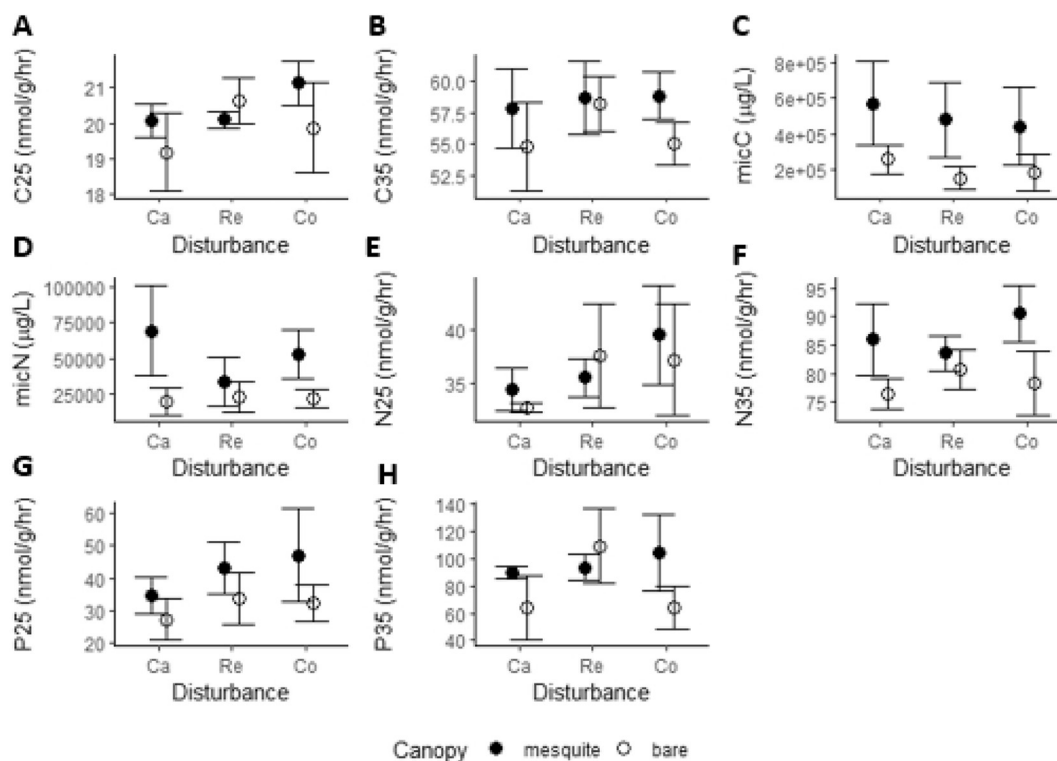
*Prosopis* canopy did not demonstrate any effect on microbial biomass. Multiple linear regressions demonstrated that variability in microbial biomass C was determined best by GWC and the presence of *Prosopis* ( $R^2 = 0.4195$ ,  $p < 0.001$ ; Table 2). Variability in microbial biomass N was determined best by GWC, litter depth, plant cover, and C:N ratio ( $R^2 = 0.2433$ ,  $p < 0.001$ ).

## 4. Discussion

Recreation ecologists, working in mesic temperate systems such as the Great Smoky Mountains of North Carolina, the subalpine zone of the Wind River Mountains in Wyoming, and the boreal forest region of northwestern Ontario, have long established that camping decreases plant cover (Cole, 1995; Cole and Monz, 2003; Leung and Marion, 1999; Monti and Mackintosh, 1979). However, measures of herbaceous plant cover in the semiarid savanna of the SRER were not significantly different under low frequency, high intensity recreational camping regimes versus under undisturbed conditions (Fig. 2d). Litter depth and soil properties such as GWC, DOC, and TDN were also not influenced by camping disturbance (Fig. 2). This suggests that these variables may be resistant to degradation under this type of disturbance.

There are many potential explanations for this resistance: In a semiarid savanna with highly variable water availability, biotic communities are accustomed to quickly adapting to changing conditions (Tielbörger and Salguero-Gómez, 2014). This adaptive capacity may protect plant communities from the potentially damaging effects of trampling in campsites. In addition, differences in plant cover may not be detectable considering the sparse distribution of vegetation inherent in semiarid systems (Butterfield et al., 2010). Finally, high intensity camping at low frequencies could provide adequate timing between disturbance events for plant communities to recover and maintain their roles in soil nutrient cycling.

Contrary to our original hypothesis, neither exoenzyme activities nor soil microbial biomass C or N were affected by camping disturbance



**Fig. 3.** Microbial activities' responses to camping disturbance and *Prosopis*. Points indicate sample means and lines indicate standard errors for the following variables: C exoenzyme activities at 25 °C (nmol/g/h) [A], C exoenzyme activities at 35 °C (nmol/g/h) [B], microbial biomass C (μg/L) [C], microbial biomass N (μg/L) [D], N exoenzyme activities at 25 °C (nmol/g/h) [E], N exoenzyme activities at 35 °C (nmol/g/h) [F], P exoenzyme activities at 25 °C (nmol/g/h) [G] and P exoenzyme activities at 35 °C (nmol/g/h) [H]. Exoenzyme activities were determined on a dry weight basis. C exoenzymes included summed activities of BG, AG, CB, and XYL. N exoenzymes included LAP and NAG. Two factor ANOVAs ( $n = 24$ ) demonstrated that no soil microbial activities were influenced by camping disturbance (Ca = campsite, Re = recovery, Co = control) nor by the presence of *Prosopis*.

**Table 2**

Environmental influences on soil microbial activities. Multiple linear regression models ( $n = 96$ ) on microbial biomass C (micC), microbial biomass N (micN), and C, N, and P exoenzyme activities measured at 25 °C and 35 °C (C25, N25, P25, etc.), indicated that GWC and litter are particularly important predictors of observed soil microbial activities. All  $p$ -values < 0.05.

y	x <sub>1</sub>	x <sub>2</sub>	x <sub>3</sub>	x <sub>4</sub>	R <sup>2</sup>
micC	GWC	Canopy	Plant cover		0.42
micN	GWC	Litter	Plant cover	C:N	0.24
C25	GWC				0.27
N25	litter*GWC				0.38
P25	GWC	Litter			0.22
C35	GWC				0.36
N35	canopy*GWC				0.28
P35	GWC				0.14

(Fig. 3c–d). These results are in contrast to previously published findings that soil microbial communities in campsites use fewer C substrates than in undisturbed soils in temperate forests (Zabinski and Gannon, 1997). We hypothesize that seasonal camping disturbance may not be sufficient to alter the composition of microbial communities and thereby microbial C and N metabolic rates. Soil microbial communities in semiarid ecosystems may also be more sensitive and responsive to pulse-driven dynamics of water availability than to camping disturbance unlike microbial communities in mesic, temperate systems. It is therefore possible that our choice to sample during the monsoon season, while increasing our ability to detect a difference in plant cover, may have decreased our ability to detect a difference in camping-driven differences in soil microbial activity. Biological activity in semiarid systems is often driven primarily by water availability; recent rains may have dampened the signal of camping disturbance within soil microbial

communities.

Fertility islands beneath *Prosopis* were expected to increase soil microbial activities and organic substrate availability (McClaran et al., 2008; Ridolfi et al., 2008). When variables were assessed separately, only litter depth, DOC, and TDN supported this expectation (Fig. 2). However, when examined in multiple linear regression models, microbial biomass C and N exoenzyme activities demonstrated relationships with *Prosopis*. Additionally, all soil microbial activities demonstrated relationships with GWC, and most with litter depth (Table 2). These results together suggest that water is the most limiting resource for soil microbial activities in this semiarid savanna (Porporato et al., 2002). With sufficient water availability, soil microbial activities can reflect *Prosopis*'s fertility island effect. These patterns may also be due, in part, to *Prosopis*-mediated water distribution, which can increase local soil moisture through soil aggregation, throughfall, and hydraulic lift (Hibbard et al., 2001; Zou et al., 2005).

Traditional models of succession suggest that biological activities would be limited immediately following disturbance, and increase over time once the disturbance is no longer inflicted (Christensen, 2014; Harris, 2003). However, in this case study of campsite impacts, disturbance does not appear to initially limit biological activity. The effect of camping on soil microbial activities is weaker than the strength of local biological water dependence and the *Prosopis*-driven fertility island effect in a semiarid system (D'Odorico et al., 2007; Ridolfi et al., 2008). Campsites in this study were approximately 20–40 years old, but experience sporadic disturbance. In contrast, *Prosopis* is a woody native plant in a savanna that has continually influenced local soil properties and communities for up to 150 years (McClaran et al., 2010; Wilson and Thompson, 2005).

This study demonstrates that soil microbial communities are resistant to camping disturbance and that *Prosopis* supports these

communities by augmenting local water, C, and N availability. However, more information is needed to determine the degree to which *Prosopis* contributes to soil microbial resistance to camping impacts. Understanding this relationship requires the study of camping disturbance across a wide range of intensities, frequencies, and spatio-temporal scales. Additionally, partitioning ecohydrological processes mediated by *Prosopis*, such as nitrogen fixation and litter accumulation, can help determine exactly how the fertility island effect interacts with campsite disturbance (Hibbard et al., 2001). Our foundational examination of these relationships will support studies conducted in similar dry environments to advance understanding and improve sustainable management of soils in recreation areas.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2019.103424>.

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