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Consumers stabilize grassland ecosystem functions by destabilizing belowground communities under abiotic stress

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Abstract

Consumers play a critical role in mediating plant and ecosystem responses to abiotic stress, yet their influence on belowground processes under changing environmental conditions remains underexplored. Insect consumers are vital components of grassland ecosystems that can shape ecosystem function and stability by mitigating how plant and microbial communities respond to abiotic stress, like drought. This study investigates how small-bodied consumers influence the magnitude and stability of grassland belowground functions across gradients of abiotic stress. We conducted a fully factorial field experiment manipulating consumer presence and induced drought over a growing season. Our results reveal that the presence of consumers stabilizes bacterial biomass and microbial activity across variable soil moisture conditions. Interestingly, this consumer-induced increase in ecosystem stability was driven by a destabilization of microbial communities, as indicated by increased variability in bacterial community composition and abundance. Consumer presence also shifted soil bacterial community composition and richness, while fungal communities were less affected. Combined, our results highlight another important dimension of ecosystem stability: community responsiveness and rapid adaptability. Additionally, our findings underscore the critical role of consumers in maintaining belowground ecosystem stability and highlight the need to consider trophic interactions when predicting the impacts of global change on grassland ecosystems.

KEYWORDS
above-belowground interactions, carbon use efficiency, drought, grassland, herbivores, insects, microbial diversity, nutrient cycling, plant–microbial interactions

INTRODUCTION

High biodiversity can mitigate the impacts of abiotic stress, including those driven by climate change, on ecosystem function (Tilman & Downing, 1994). Yet most biodiversity research focuses on plant communities despite biodiversity loss being especially acute at higher trophic levels (Estes et al., 2011; Schmitz et al., 2000). Many consumers, for example, are under threat from global change (Dirzo et al., 2014) and yet are also critical to mediating plant responses to abiotic stress (Bakker et al., 2006; Gruner et al., 2008). It is therefore possible that reduced consumer abundances or diversity due to overharvesting or land-use change can impact the stability and resilience of ecosystem function to climate change. Unfortunately, experiments that simulate both abiotic stress and consumer presence are relatively rare. Given the drastic reductions in consumer abundances occurring worldwide (Biggs et al., 2008; Dirzo et al., 2014), it is imperative that we understand how the loss of consumers from an ecosystem might affect the resilience of ecosystem function to disturbances (Hautier et al., 2009).

Consumers influence ecosystem processes through both direct and indirect pathways. While large animals contribute nutrient-rich waste and carcasses that enhance soil C and N (Liu et al., 2018; Reed et al., 2025), small consumers like insects also play critical roles (Lemoine & Smith, 2019; van de Zande et al., 2024). Their inputs (e.g., frass, cadavers) provide frequent, spatially distributed additions of bioavailable nutrients (Lovett et al., 2002; Schowalter, 2022). Indirectly, small-bodied consumers alter soil chemistry by increasing detrital fall, stimulating root growth, and affecting the quantity and composition of root exudates (Bardgett et al., 1998; Belovsky & Slade, 2000; Nat Holland, 1995; Potthast et al., 2021). These shifts can shape the diversity and stability of microbial community structure and function. For example, grasshoppers shifted plant communities in a coastal prairie soil, which ultimately increased microbial biomass and oligotrophic (slow-growing, nutrient-poor adapted) fungal diversity (Lucas, Jonas, et al., 2021a). Increased microbial biomass and oligotrophic diversity often lead to higher carbon use efficiency and lower metabolic quotients (CUE, Domeignoz-Horta et al., 2020, $q\mathrm{CO}_2$, Ashraf et al., 2022), characteristics associated with increased drought resistance of belowground function (Liu et al., 2024; Malik et al., 2020; Tao et al., 2023). These mechanisms suggest that small consumers influence both the magnitude and stability of belowground communities and C-cycling, especially under abiotic stress—yet their role in shaping these dynamics under global change remains underexplored.

Grasslands are particularly vulnerable to global change, with increasingly frequent droughts threatening to shift grasslands from carbon sinks to sources (Diffenbaugh et al., 2015; Parolari et al., 2012). Simultaneously, grassland animals are experiencing significant global declines. Grassland insects, such as grasshoppers, crickets, and katydids, and every orthopteran species with an IUCN-documented population trend has declined in abundance by 70%–75% (Dirzo et al., 2014; Welti et al., 2020). The loss of insect consumers can impact soil microbial community composition and their functions (Lucas, Jonas, et al., 2021a). Yet the ultimate impacts of defaunation on belowground functional capacity and stability, such as microbial respiration (i.e., carbon flux) and microbial biomass are poorly understood. Small consumers can promote ecosystem stability by enhancing diversity, modulating plant–microbe interactions, buffering productivity under variable climate conditions, and maintaining carbon cycling feedbacks (Post, 2013; Thébault & Loreau, 2005). Their loss may reduce resistance and resilience to disturbance, amplifying the destabilizing effects of drought. Investigating the combined effects of drought and the loss of consumers in grasslands, which cover 31%–43% of terrestrial land area and store 650–810 Gt of carbon in soils, is critical for determining how small-bodied consumers shape grassland stability in current and future climates (Ebel et al., 2022; Gibson & Newman, 2019; O'Mara, 2012).

In this study, we address two central ecological questions: (1) Do consumers contribute to the magnitude and stability of grassland belowground functions under normal conditions? (2) Does defaunation alter grassland belowground responses to drought? Using a fully factorial field experiment, we manipulated the presence of small-bodied consumers (primarily invertebrates) and drought conditions over a growing season. We hypothesized that consumers stabilize grassland ecosystem function by mitigating the adverse effects of drought. Specifically:

> **H1.** Consumer loss destabilizes belowground function, amplifying the negative effects of drought on microbial biomass, respiration, and soil carbon pools.
>
> **H2.** Consumers stabilize microbial community composition and function via consistent nutrient inputs and plant-mediated effects, mitigating drought impacts (H2a). Alternatively, herbivores could increase temporal turnover of microbial communities, enhancing adaptive capacity under abiotic stress (H2b).

By examining these questions, we aim to advance understanding of how consumers shape belowground ecosystem function and how defaunation might impact how belowground communities respond to abiotic stress, contributing to the broader ecological framework of trophic-level interactions and ecosystem resilience under global change.

METHODS

Site description

We examined how drought and consumer removal affect soil function at the University of Wisconsin-Milwaukee at Waukesha (UWM-W) field station in Oconomowoc, Wisconsin. A detailed description of the field site can be found in Lemoine et al. (2023). Briefly this 40-ha field station has a mixed composition including oak savannas, jack pine, maple forests and oak forests, and tallgrass prairie. The soils are roughly 56% sand, 26% silt, and 18% clay and contain 5% organic matter, 0.22% nitrogen, and 4.75-ppm phosphorus. From April to September, the average daily temperature is about 20°C, and the region receives an average of 520 mm of precipitation during this period (Figure 1). Natural droughts commonly occur between May and September (Appendix S1: Figure S1). With respect to consumers, white-tailed deer (*Odocoileus virginianus*) are the only large consumer present at the site and do not forage within the prairie (Lemoine camera trap observations). Small rodents, such as mice and voles, are present but only in small numbers (Lemoine personal observations). Thus, consumers within the UWM-W prairie are almost exclusively small-bodied animals, predominantly insects but also including occasional small vertebrates.

Rainfall reduction and consumer removal treatments

We simulated drought using the Drought-Net rainout shelter design (Yahdjian & Sala, 2002) and detailed descriptions of our drought design can be found in our Supplementary Methods. Briefly, we created 20 2 × 2 m experimental plots assigned as either 'Ambient' or 'Drought' treatments ($n = 10$ per treatment). Ambient plots received normal growing season precipitation, while Drought plots experienced a 66% reduction in rainfall through passive rainout shelters. We excluded consumers using cages constructed of a 0.5 × 0.5 × 1 m wooden frame (Lemoine & Smith, 2019). In each 2 × 2 experimental plot, we placed two cages ($n = 10$ per drought × consumer treatment), ensuring minimal variation in plant species composition between cages and avoiding bare ground. One cage in each pair was randomly assigned to the 'No Consumers' treatment and kept fully enclosed. The other, designated as the 'Consumers' treatment, had the bottom half of its screen removed to allow small animal access while maintaining similar light reduction to that of the fully enclosed 'No Consumers' cages (following Lemoine & Smith, 2019). Additionally, we removed any animals, primarily Hymenoptera, found inside the "No Consumers" cages over the course of the experiment.

Soil sampling

We took soil cores on 16 June, 14 July, and 11 August (Figure 1). Specifically, we collected the top 10 cm of soil using a 1-cm-diameter soil corer. Soil cores were kept on ice and transported to the lab where they were sieved to remove roots, rocks, and other plant debris. Sieves were cleaned using 70% ethanol between samples. The sieved soils were divided into two batches: one was immediately processed to measure soil respiration, gravimetric water content (GWC), and soil organic content (details below), while the second batch was stored at −70°C for DNA extraction. DNA was extracted from approximately 0.25 g of soil from the second batch using DNeasy PowerSoil Pro kits (Qiagen). The extracted DNA was split into two aliquots: one for qPCR analysis and the other for 16S rRNA amplicon sequencing. Both aliquots were stored at −70°C until further analysis (details below).

Microbial respiration, metabolic quotient, soil organic matter, carbon and nitrogen content

We characterized microbial activity throughout the growing season in all treatments by measuring microbial CO_2 respiration using the same incubation method as Lemoine et al. (2023). Subsequently, the soils were dried at 60°C for 24–48 h, or until a stable mass was reached, to determine dry mass. After drying, we calculated the GWC of each soil sample as $\mathrm{GWC} = (\mathrm{Soil}_{\mathrm{Wet}} - \mathrm{Soil}_{\mathrm{Dry}})/\mathrm{Soil}_{\mathrm{Dry}}$. We calculated the partial metabolic quotient as the ratio: $q\mathrm{CO}_2 = \text{respiration/bacterial cell copy number}$, where cell copy number was derived using qPCR (*see below*). The metabolic quotient is a measurement of how effectively microbes convert carbon into mass versus how much is lost via respiration (Geyer et al., 2019; Lucas, Sone, et al., 2021b; Xu et al., 2017). We used 16S copy number to determine total bacterial biomass as it is often used as an absolute abundance of bacteria estimate (Bender et al., 2018) and has been shown to be one tightly correlated with microbial biomass in soil (Dandie et al., 2007). However, we recognize the limitation in this approach as it is not able to account for fungal biomass. Therefore, our measurement is a partial metabolic quotient.

We calculated soil organic matter content via loss-on-ignition. After respiration trials, soils were dried and weighed to obtain dry masses, and then combusted at 550°C for 4 h and reweighed (Hoogsteen et al., 2015). We then calculated organic content as the percent of mass loss during combustion. To determine total C and N content, soil samples were dried, ground and sieved (2 mm mesh)

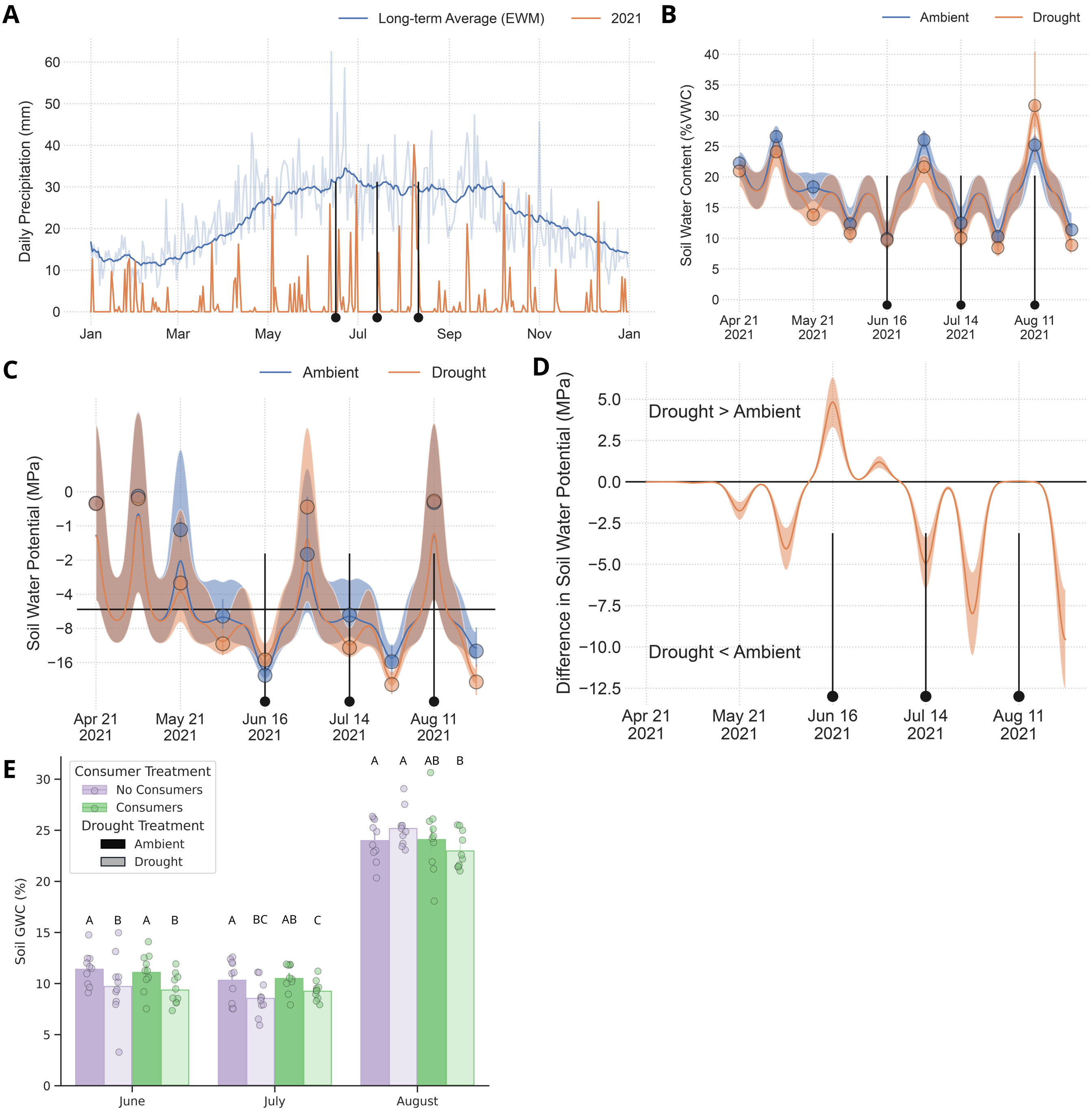

FIGURE 1 Weather, climate, and soil moisture profiles during our experiment. (A) Average daily total precipitation and observed daily precipitation for our study site at Oconomowoc, WI during the experimental year of 2021. Precipitation data come from a long-term weather station in Waukesha, WI (USC00478937), and temperature data were obtained from a nearby weather station in Brookfield, WI (USC00471062). Black points and vertical lines represent the three sampling events. (B) Soil moisture profiles during the course of our experiment as estimated by field measurements of VWC. Points and bars show means ±1 SE, and trend lines were fitted via a Gaussian Process Model. Black points and vertical lines represent the three sampling events. (C) Soil water potential profiles during the course of our experiment, as estimated from a soil water release curve using field-based VWC measurements (see Appendix S1: Figure S2). Points and bars show means ±1 SE, and trend lines were fitted via a Gaussian Process Model. Black points and vertical lines represent the three sampling events. (D) The difference in soil water potential between drought and ambient temperatures as estimated by Gaussian Process Model. Black points and vertical lines represent the three sampling events. (E) Soil gravimetric water content as measured directly on collected soil samples. Letters denote statistically significant differences [Pr(Difference) > 0.95].

for subsequent analysis. Soil organic C and total N contents were determined by a dry combustion method using a C/N Analyzer (Vario Macro, Elementar, Germany).

Bacterial abundance via qPCR, microbial sequencing and data processing and analyses

We estimated bacterial abundance using quantitative PCR and examined bacterial and fungal communities through 16S rRNA and ITS gene amplicon sequencing. Our qPCR protocol was based on Fierer et al. (2005) and Rousk et al. (2010) and involved amplification of the 16S rRNA gene using the forward primer Eub338 and reverse primer Eub518. After qPCR, cycle numbers were converted to "*16S rRNA gene copy numbers per gram of dry soil*", using the dry mass of the soil from which DNA was extracted for each sample. For amplicon sequencing we analyzed bacterial communities by amplifying the V4 region of the 16S rRNA gene using the 515F (GTG YCAGCMGCCGCGGTAA) – 806R (GGACTACNVGGGT WTCTAAT) primer set. For fungal communities, we amplified the internal transcriber spacer (ITS) region using the ITS1F (CTTGGTCATTTAGAGGAAGTAA) and ITS2 (GCTGCGTTCTTCATCGATGC) primer set. Detailed descriptions of the qPCR and amplicon sequencing protocols are provided in Appendix S2.

To understand whether our treatments shifted soils along the fast-growing, copiotrophic to slow-growing, oligotrophic spectrum, we calculated the mean ribosomal copy number for each sample. Bacterial taxa with higher 16S copy numbers are considered to be faster reproducing and therefore more copiotrophic (Roller et al., 2016), whereas lower copy number represents higher oligotrophy. We used the RDP database (Stoddard et al., 2015) to assign the average 16S operon count to each bacterial amplicon sequence variant (ASV), and then averaged these values to create a community mean copy number per sample (Kearns & Shade, 2018). We report this metric as our "degree of copiotrophy", with higher values representing more copiotrophic organisms and lower values representing more oligotrophy.

Decomposition

We estimated decomposition rates of both labile and refractory material using green and red tea bags following the method of Keuskamp et al. (2013). On July 16, 2021, one green tea bag and one red tea bag were buried at the center of each plot ($n = 10$ per treatment) 10 cm below the soil surface. On September 11, 2021, the tea bags were retrieved. We removed large soil particles from the outside of the bags and small roots that had grown on or through the bags. The tea was then extracted, dried, and weighed, and we calculated decomposition rates as the percentage of mass loss for each tea type.

Statistical analyses

Rainout shelter effects

Time series for soil moisture, soil water potential, and treatment effects on soil water potential were analyzed using Gaussian process models (GPMs). These models are well suited for time series analyses because they inherently account for temporal autocorrelation and can capture nonlinear trends (Roberts et al., 2013). A key advantage of GPMs is their Bayesian framework, which smooths out outliers, reducing the risk of overfitting and misinterpreting noise as a signal (Lemoine, 2019). Prior to analysis, both the response variables and the predictor variable (week of the experiment) were standardized to N (0,1). Soil GWC was analyzed using a Bayesian three-way ANOVA (details below).

Partial metabolic quotient and ecosystem-level responses

Partial $q\mathrm{CO}_2$, respiration, soil %C, soil %N, 16S copy number, and degree of copiotrophy-oligotrophy were initially analyzed using Bayesian three-way ANOVAs. These ANOVAs incorporated month, drought treatment, and consumer treatment as fully interacting categorical predictors. Analyses were conducted within a hierarchical Bayesian framework, applying weakly informative priors on hyperparameters to constrain effect sizes in cases of small sample sizes (Lemoine, 2019). This approach effectively biases against detecting spurious effects from small sample sizes, acting as a conservative measure akin to a post hoc correction for multiple comparisons (Gelman et al., 2012). Significance was evaluated by calculating the probability of a contrast being positive or negative, where $\Pr > 0.90$ indicated a moderately significant effect, and $\Pr > 0.95$ indicated statistical significance (Lemoine et al., 2023; Lemoine & Budny, 2022; Rode et al., 2017). Contrasts were conducted only within months; no across-month comparisons were made. To explore further relationships between partial $q\mathrm{CO}_2$, respiration, and 16S copy number, these variables were analyzed using an analysis of covariance (ANCOVA) design. The ANCOVA included soil GWC, consumer treatment, and their interaction as predictor variables.

Stability was calculated as 1/CV for each plot across the growing season. Specifically, we calculated temporal stability for each plot as μ/σ, where μ is the mean of a plot over the growing season and σ is the standard deviation of the plot ($n = 20$ plots total). A two-way Bayesian ANOVA using the above framework was then applied to analyze stability, with drought and herbivory treatments as interacting factors. We also analyzed decomposition rates using a Bayesian two-way ANOVA as described.

Microbial community analyses

We compared microbial community composition and taxonomic changes using Primer (Ver. 7.0.13) and R (package vegan). We square-root-transformed the microbial community data before calculating Bray–Curtis dissimilarity. We used community distance matrices to generate ordinations (non-metric multidimensional scaling or NMDS) for bacteria and fungi and used GGPLOT to visualize differences. We used permutational multivariate analysis of variance (PERMANOVA) to compare community composition and used PERMDISP tests to compare beta diversity (Anderson & Walsh, 2013) across consumer treatments, moisture conditions and months, and their interactions, with plot as a random factor (Anderson & Santana-Garcon, 2015). To quantify microbiome stability over time, we calculated Bray–Curtis and Jaccard dissimilarity matrices for each site using ASV-level data. For each plot, we extracted the pairwise dissimilarity values for the three possible time point comparisons: June–July, June–August, and July–August. We then calculated temporal similarity as (1 − distance) for each pairwise comparison, such that values closer to 1 indicate higher community similarity between time points, and thus greater temporal stability. We averaged the three similarity values within each plot to yield a single plot-level stability score. This approach is based on methods from Byrd et al. (2021) and Revel-Muroz et al. (2023) and allows for a standardized comparison of microbiome stability across treatments. We calculated Shannon's H, Chao1 and the number of Observed ASVs using the command *estimate_richess* in the package *Phyloseq* (Mcmurdie & Holmes, 2013). These community stability and diversity metrics and their variance were analyzed in the same manner as microbial respiration and biomass, and degree of copiotrophy. We then analyzed the relationship between the stability of $q\mathrm{CO}_2$ and the stability of microbial communities (16S Bray–Curtis stability, 16S Jaccard stability, Copiotrophy stability) using gamma regression.

RESULTS

Rainout shelters reduced soil water potential

The growing season of our experiment was abnormally dry. Whereas average years maintain a volumetric water content (VWC) of 15%–20% (Lemoine et al., 2023), VWC in ambient soils was generally near 10% throughout much of summer (Figure 1A,B). Yet, for most of the growing season, soil water potential in "Drought" plots was significantly lower than in "Ambient" plots (Figure 1D). See supplementary results for more details regarding our rainout shelter effects.

Consumers stabilized partial metabolic quotient and ecosystem-level responses

Although microbial partial $q\mathrm{CO}_2$ varied throughout the season, the presence of consumers stabilized respiration and bacterial biomass in the face of seasonal changes in rainfall and temperature. In both June and July, drought decreased partial $q\mathrm{CO}_2$ by approximately 50% regardless of consumer presence [$\Pr(\text{Drt.} > \text{Amb.}) \geq 0.96$ for all comparisons, Figure 2A]. In August, the role of consumers switched to suppressing partial $q\mathrm{CO}_2$. The heavy rainfall event increased partial $q\mathrm{CO}_2$ in all plots, but partial $q\mathrm{CO}_2$ remained 33% lower in plots with consumers than in plots without [$\Pr(\text{Cons.} > \text{No Cons.}) > 0.99$ for both Amb. and Drt. Treatments, Figure 2A].

Interestingly, the switch in consumer effects was driven by a decoupling of the partial $q\mathrm{CO}_2$-GWC relationship. Without consumers, high soil water content increased partial $q\mathrm{CO}_2$ to 500% of its value in drier soils (Figure 2B). With consumers present, the partial $q\mathrm{CO}_2$-GWC relationship was significantly flatter [$\Pr(\text{H} \times \text{GWC}) = 1.00$, Figure 2B], which led to less seasonal variation in partial $q\mathrm{CO}_2$. Indeed, drought reduced the stability of partial $q\mathrm{CO}_2$ by nearly 50% without consumers [$\Pr(\text{Drt.} > \text{Amb.} | \text{No Cons.}) = 0.95$], but had no significant impact on $q\mathrm{CO}_2$ stability when consumers were present [$\Pr(\text{Drt.} > \text{Amb.} | \text{Cons.}) = 0.88$, Figure 2C]. Interestingly, consumers had a positive effect on $q\mathrm{CO}_2$ stability under both ambient and drought conditions [$\Pr(\text{Drt.} > \text{Amb.} | \text{Cons.}) > 0.95$, Figure 2C]. Thus, it is less likely that the role of consumers changed from inhibitory to stimulatory over the growing season and more likely that consumers act as a stabilizing force on partial $q\mathrm{CO}_2$ that mitigates the effects of seasonal variation in soil moisture.

The stabilizing effect of consumers on partial $q\mathrm{CO}_2$ derives in part from a stabilizing effect of consumers on

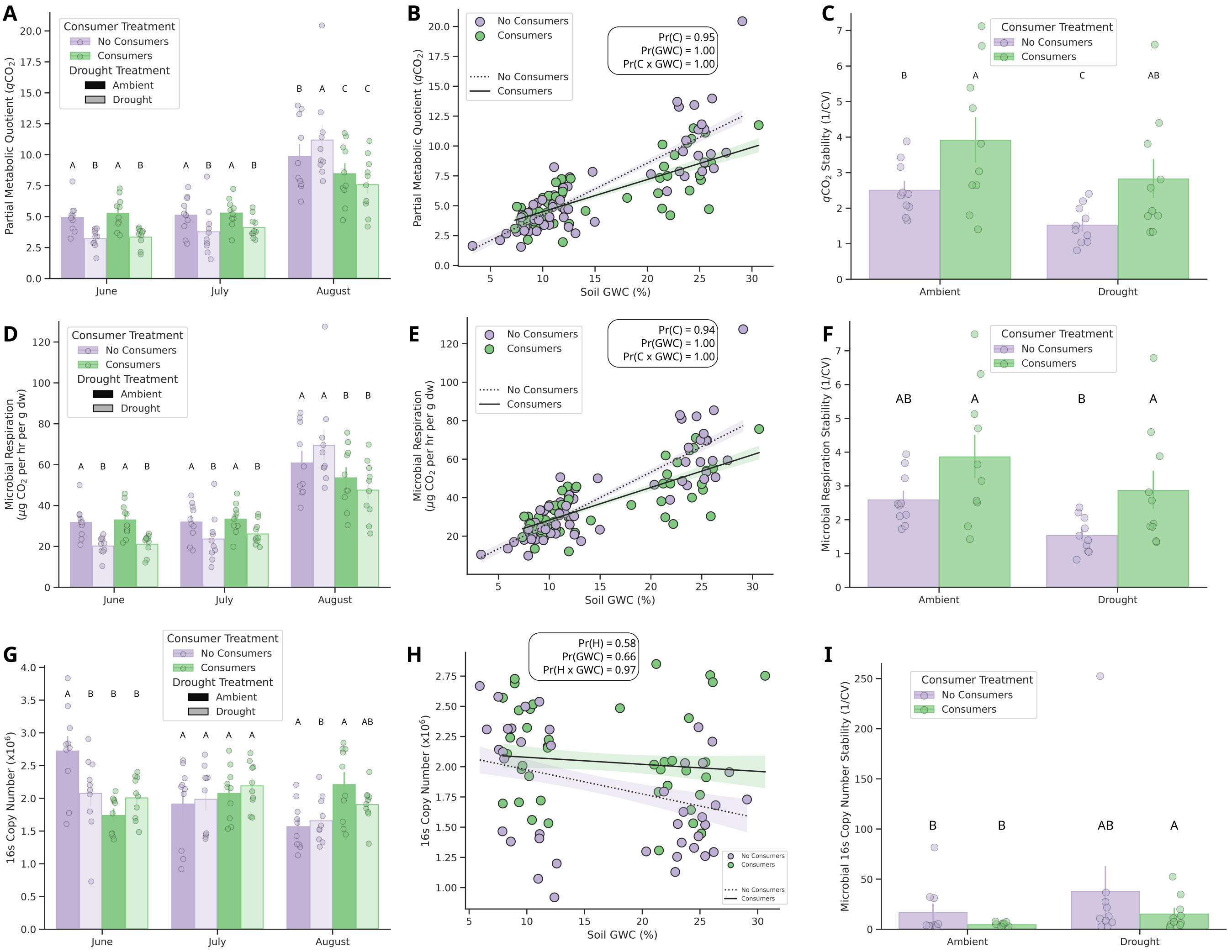

FIGURE 2 The effects of drought and herbivores on the magnitude and stability of belowground ecosystem function. (A, D, G) Barplots showing microbial $q\mathrm{CO}_2$, respiration, or 16S copy number in the factorial combination of drought and herbivore removals. Letters denote statistically significant differences [Pr(Difference) > 0.95]. (B, E, H) The relationship between $q\mathrm{CO}_2$, respiration, or 16S copy number and gravimetric water content in both herbivore present and removal plots. Lines show the mean trend ±1 S.E (shaded region) from a linear regression. (C, F, I) Barplots showing phenological stability of microbial $q\mathrm{CO}_2$, respiration, or 16S copy number in the factorial combination of drought and herbivore removals. Letters denote statistically significant differences [Pr(Difference) > 0.95].

microbial respiration throughout the growing season. In June and July, microbial respiration in Ambient plots was near the seasonal norm of 40 μg $\mathrm{CO}_2\ \mathrm{h}^{-1}\ \mathrm{g\ dw}^{-1}$ (Figure 2D). Also in both months, drought reduced microbial respiration by roughly 50% [Pr(Amb. > Drt.) > 0.94 for both Cons. and No Cons. treatments in June and July, Figure 2D]. In August, the heavy rainfall event stimulated microbial respiration in all plots, but did so more when consumers were absent given that consumers suppressed microbial respiration by 22% during August [Pr(No Cons. > Cons.|August) = 0.99 for both Amb. and Drt. treatments. Figure 2D]. As with partial $q\mathrm{CO}_2$, it is unlikely that the role of consumers changed throughout the growing season but rather that consumers again weakened the dependence of microbial activity on soil GWC [Pr(H × GWC) = 1.00, Figure 2E]. The weakening of this relationship again resulted in consumers minimizing within-season variability in microbial activity, especially under drought conditions (Figure 2F).

Small-bodied consumers destabilized microbial communities

The stabilizing effect of small consumers on microbial partial $q\mathrm{CO}_2$ and respiration was only weakly explained by the effect of consumers on bacterial abundance. In general, bacterial abundance was fairly stable across the growing season, although there was a slight decline from June to August (Figure 2G). The decline in bacterial abundance was largely driven by changes in the ambient "No Consumers" treatment. In June, No Consumers soils contained 16% more bacterial 16S copy numbers than Consumers treatments in Ambient plots [Pr(No Cons. > Cons.|Amb.) = 0.98, Figure 2G], while Drought plots contained $\sim 2.2 \times 10^6$ 16S copies regardless of consumer presence [Pr(No. Herb > Herb.|Drt.) = 0.80, Figure 2G]. By July, there were no differences in 16S copy number in any treatment, and in August, the impact of consumer loss on 16S copy number had switched from positive to slightly negative. Consumer removal did not significantly affect 16S copy number in ambient plots [Pr(Cons. > No. Cons.|Amb.) = 0.84], and marginally increased 16S copies by 15 ± 11 in drought plots [Pr(Cons. > No. Cons.|Drt.) = 0.94, Figure 2G]. Yet the general trend over the course of the growing season was a complete decoupling of 16S copy numbers from soil GWC when small consumers were present [Pr(C × GWC) = 0.97, Figure 2H], leading to a significant stabilizing effect (42% increase) of consumers in ambient conditions [Pr(Cons. < No. Cons.|Amb.) = 0.97], and a moderately significant increase in stability (23%) in drought conditions [Pr(Cons. < No. Cons.|Amb.) = 0.92, Figure 2I].

In contrast to ecosystem function, the presence of small consumers decreased the stability of bacterial communities across summer growing season (Figure 3). In both ambient [Pr(Cons. > No. Cons.|Amb.) = 0.95] and drought [Pr(Cons. > No. Cons.|Amb.) = 0.96] conditions, the consumers destabilized the relative abundances of bacterial communities, although the effect was only a 6% reduction in stability (Figure 3A). Likewise, presence–absence stability was also reduced by 3% when consumers were present in both ambient [Pr(Cons. > No. Cons.|Amb.) = 0.96] and drought [Pr(Cons. > No. Cons.|Amb.) = 0.97] treatments (Figure 3B). Consumers had no effect on the temporal stability of fungal communities (Pr <0.69 for all comparisons, Figure 3C). The community responses were accompanied by large reductions in functional group stability in ambient (53%) and drought (50%) treatments where consumers were present [Pr(Cons. > No Cons.|Amb.) = 0.99, Pr(Cons. > No Cons.|Drt.) = 1.00, Figure 3D]. In general, plots with consumers had a lower abundance of copiotrophic organisms (i.e., 4% lower CWM$_{16s}$) in June, but not in July or August (Figure 3E). In June, consumers significantly decreased CWM$_{16s}$ in ambient conditions [Pr(No Cons. > Cons.|

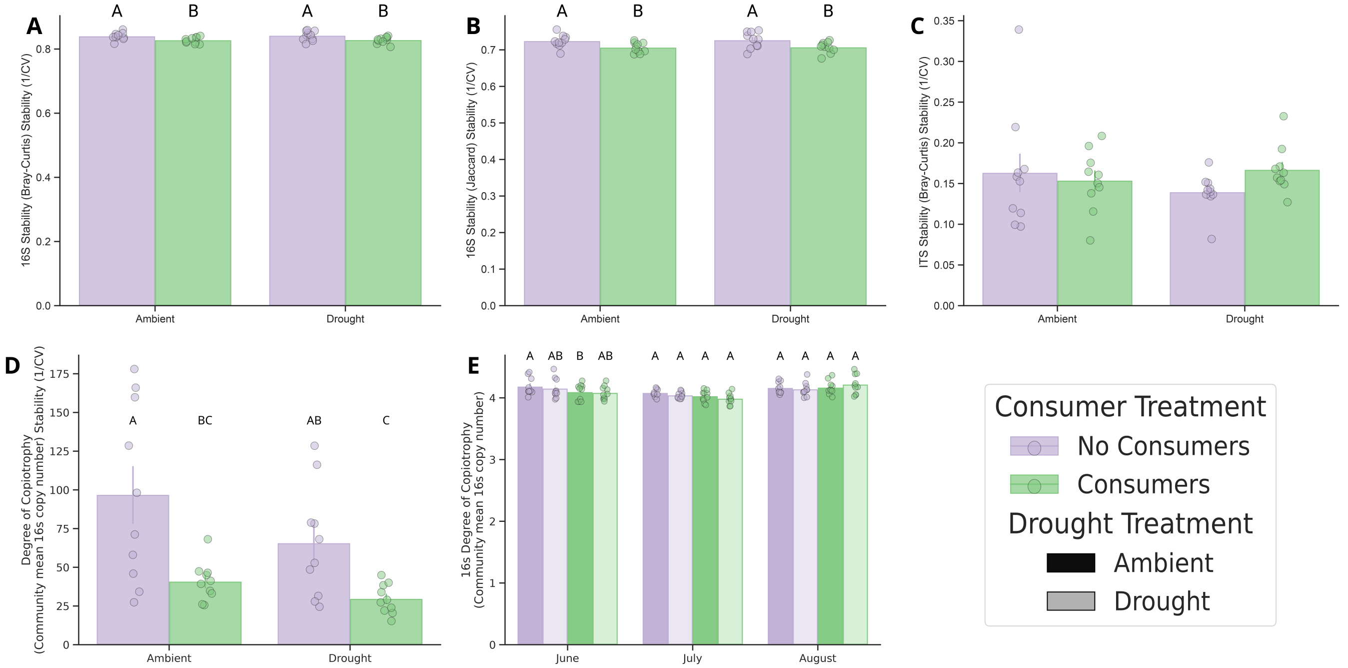

FIGURE 3 Herbivores destabilized belowground bacterial communities. Barplots showing phenological stability of (A) bacterial relative abundances, (B) bacterial presence/absences, (C) fungal relative abundances, and (D) degree of copiotrophy. Letters denote statistically significant differences [Pr(Difference) > 0.95]. (E) Barplots showing the degree of copiotrophy in the factorial combination of drought and herbivore removals. Letters denote statistically significant differences [Pr(Difference) > 0.95].

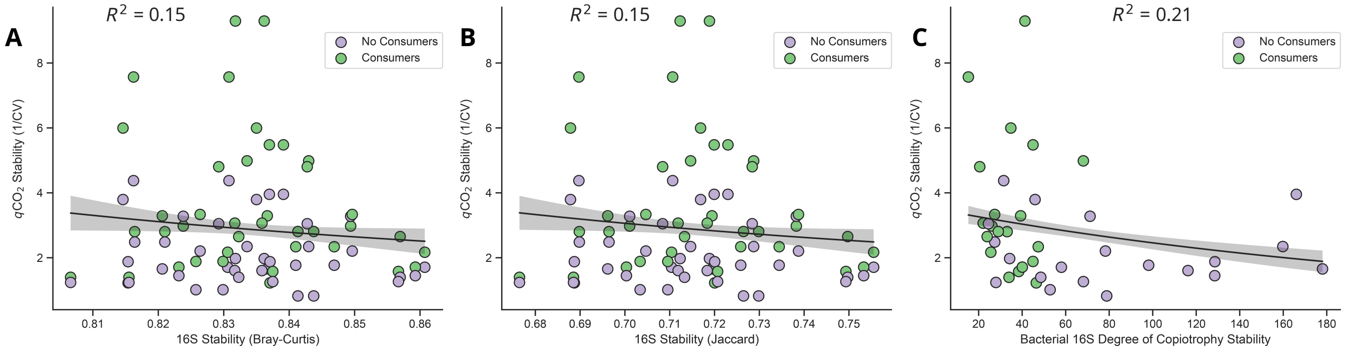

FIGURE 4 Unstable community composition led to more stable ecosystem function. Gamma regressions between the phenological stability of microbial qCO_2 and the phenological stability of (A) bacterial relative abundances, (B) bacterial presence/absences, and (C) degree of copiotrophy. Lines show the mean trend ±1 S.E (shaded region) from a gamma regression with log-link function.

Amb.) = 0.95] but had only weak effects on CWM_{16s} in drought plots [Pr(No Cons. > Cons.|Amb.) = 0.88]. Consumer removal did not affect CWM_{16s} in either ambient or drought plots in July or August (Pr(Cons. Effect) < 0.77 for all comparisons). Similarly, drought treatments did not influence the stability of bacterial communities, and there was no drought and consumer interaction (Pr <0.78 for all comparisons).

Importantly, the decreased stability of bacterial communities caused by consumer presence actually increased the stability of microbial partial qCO_2 (Figure 4). There was a moderately significant negative relationship between partial qCO_2 stability and 16S Bray–Curtis stability [Pr(Slope <0) = 0.89, Figure 4A] and 16S Jaccard stability [Pr(Slope <0) = 0.89, Figure 4B]. However, there was a much stronger negative relationship between partial qCO_2 stability and the stability of copiotrophy [Pr (Slope <0) = 0.93], suggesting that dynamic microbial communities help to stabilize overall ecosystem function (Figure 4C).

Consumer presence also led to shifts in the soil bacterial community composition across the duration of our experiment (PERMANOVA Consumer × Month: Pseudo-F = 1.71,p < 0.001, June: t = 1.49, df = 1,38, p = 0.003, July: t = 1.33, df = 1,38, p = 0.007, August: t = 1.30, df = 1,38, p = 0.011, Appendix S1: Figure S3). The presence of consumers reduced bacterial ASV richness, Shannon diversity, and Chao1 Richness, although the effect was weaker in August than in other months (Appendix S3: Table S2; Figure 5). There were negligible impacts of consumers on Simpson diversity and Simpson dominance, and neither consumers nor drought affected the variability of these metrics.

Consumer presence, drought and their interaction influenced fungal community composition (Consumer × Drought: Pseudo-F = 1.31, p = 0.001) and there was no interaction with month (Consumer × Month: Pseudo-F = 0.97, p =0.73; Drought × Month: Pseudo-F = 0.94; p =0.86, Appendix S1: Figure S3). However, we did not see any effect of consumers, drought, or their interaction on the stability of the fungal communities (Pr <0.64 for all comparisons). We also did not see an effect of consumers or drought on any measured alpha diversity metric (Pr <0.87 for all treatment comparisons across all months and metrics; Figure 5; Appendix S3: Table S3).

DISCUSSION

Small-bodied consumers, particularly herbivorous orthopterans, are the most diverse and abundant animal group in grasslands, yet we know little about how they impact important belowground ecosystem functions. Here, we hypothesized that consumer loss would destabilize soil carbon use efficiency and microbial activity by altering soil microbial community composition. We confirmed that defaunation reduced ecosystem functional stability, but surprisingly, did so by limiting variability within microbial communities. These results showcase that ecosystem stability can occur with, and may require, unstable and adaptable microbial communities. These findings provide new insights into the resilience of ecosystems, emphasizing the complex and sometimes paradoxical roles of biotic interactions in maintaining ecosystem function amidst environmental variability.

Consistent with our first hypothesis (H1), we found that the removal of small-bodied consumers significantly destabilized belowground ecosystem function. In particular, microbial respiration, microbial biomass, and partial qCO_2 were all more variable in plots where consumers were excluded. Given that lower qCO_2 generally enhances soil organic C stocks and stability (Tao et al., 2023; Wang et al., 2021), our results suggest that aboveground consumers may play important roles in maintaining soil

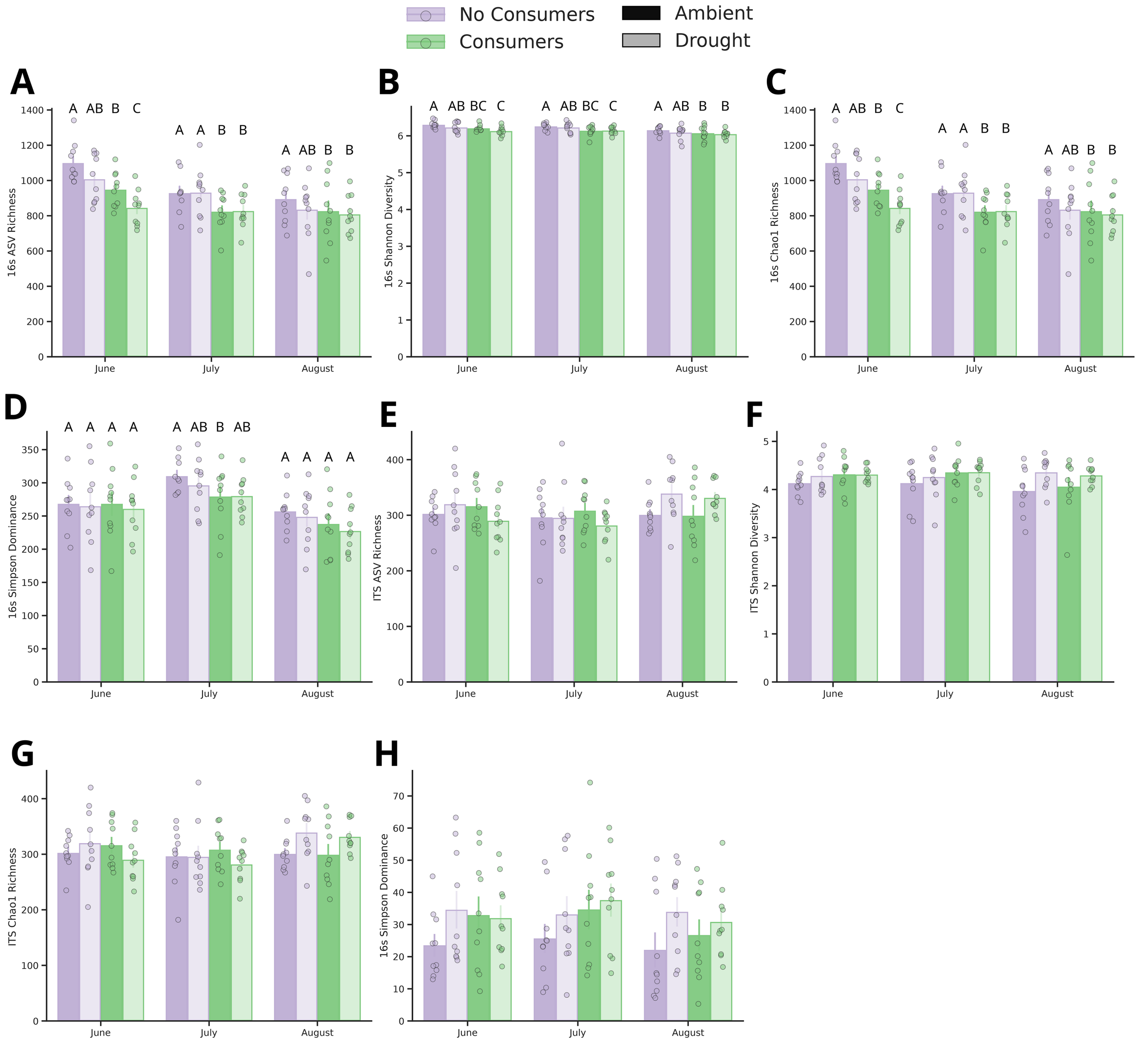

FIGURE 5 Herbivores altered bacterial community diversity. Barplots showing (A) bacterial ASV richness, (B) bacterial ASV Shannon diversity, (C) bacterial Chao1 richness, (D) bacterial ASV dominance, (E) fungal ASV richness, (F) fungal ASV Shannon diversity, (G) fungal Chao1 richness, and (H) fungal ASV dominance. Letters denote statistically significant differences [Pr(Difference) > 0.95]. Contrasts can be found in Appendix S3: Tables S1 (bacteria) and S2 (fungi).

organic C pools. Our findings also align with prior studies demonstrating that small-bodied consumers promote nutrient cycling and maintain microbial activity (Lemoine & Smith, 2019). In fact, the influence of small consumers on belowground function is comparable to that of large mammal herbivores, as both consumer guilds promote ecosystem functional stability (Chen et al., 2022). Aboveground small consumers are therefore critical components of our grassland ecosystems and global C stocks, potentially regulating soil CO_2 flux into the atmosphere.

Interestingly, our data suggest that the influence of small-bodied consumers on belowground processes is particularly strong under drought conditions. While drought alone increased microbial partial qCO_2 by reducing microbial activity, this effect was dampened by consumers, highlighting how aboveground consumers can buffer belowground processes against extreme abiotic stress. In contrast, drought magnified the impact of large mammalian herbivores on aboveground plant compositional turnover and biomass production (Riginos et al., 2018). We hypothesize that small consumer buffering capacity likely arises from the fact that small-bodied consumers generally disturb plants less (i.e., less trampling, only partial leaf consumption) than larger mammalian herbivores. Thus, while large mammalian herbivores might disrupt plant–soil feedbacks by removing plants and trampling soils, small consumers like insect herbivores, might promote plant–soil feedbacks by increasing root growth and exudate production even under water-limited conditions (Hallett et al., 2014; Irob et al., 2023). Consequently, microbial communities in consumer-present plots were better equipped to maintain activity and biomass, facilitating nutrient cycling and carbon sequestration during drought.

The ability of microbial communities to maintain function under drought seemed to rely, somewhat counterintuitively, on decreased stability of microbial community composition when consumers were present. Consumers increased microbial community turnover throughout summer growing season and created more variability in the relative amount of copiotrophic organisms. While mammalian herbivores often reduce plant community turnover throughout the growing season (Riginos et al., 2018), they tend to have a limited influence on grassland soil communities (Sveen et al., 2021). It is likely that small, mostly insect consumers in our study induced microhabitat heterogeneity via nutrient inputs or by stimulating patchy root exudation and detrital inputs (Badri & Vivanco, 2009), thereby enhancing microbial community heterogeneity. Nutrient inputs by frass and root exudates might also stimulate the proliferation of copiotrophic, high-nutrient specialist bacteria. Thus, while consumers effectively preserved key functional metrics of the ecosystem, they did so by seemingly destabilizing microbial communities.

Community stability might therefore not be a consistent predictor of ecosystem stability. Multiple studies have highlighted the diversity–stability relationship, emphasizing the value of diverse communities in buffering ecosystems against perturbations (Craven et al., 2018; Hooper et al., 2005; Tilman & Downing, 1994). Our study highlights another important dimension of ecosystem stability: community responsiveness and rapid adaptability. Microbial communities are capable of completing multiple generations over the course of a summer growing season (Panikov, 1999). This allows the community to rapidly shift to changing abiotic and biotic pressures. Here, we highlight that consumers can aid in this rapid adaptive response likely through direct and indirect pathways (e.g., frass inputs, plant community shifts, root exudates). Understanding these dynamics could redefine our approach to ecosystem management, highlighting the need for strategies that account for not just diversity but also the adaptive capacity of communities in an ever-changing environment.

Our study provides valuable insights into the roles of small consumers in grassland ecosystems under changing environmental conditions. Preserving consumer populations is crucial for maintaining the stability and resilience of grassland ecosystems, especially in the face of increasing drought frequency and severity due to climate change. Management practices that support consumer biodiversity, such as reducing pesticide use and maintaining habitat heterogeneity, could help sustain essential ecosystem functions (Dianzinga et al., 2020; Isenring, 2010; Tews et al., 2004; Tscharntke et al., 2021). Additionally, our results highlight the need for integrated approaches that consider both biotic and abiotic factors when assessing ecosystem health and function (Maestre et al., 2006; Wang et al., 2021). One limitation of our study was that we were unable to track the specific identity of all small mammals present in our consumer cages. Prior research has shown that consumer functional identity and behavior can have varying effects on above and belowground processes (Belovsky & Slade, 2000; Lucas, Jonas, et al., 2021a; Prather et al., 2017; Prather & Laws, 2018). Future research should continue to explore the complex interactions between consumer identity, plant communities, and soil microbial processes to develop more comprehensive strategies for ecosystem management.

In conclusion, our study highlights the vital role of consumers in stabilizing grassland belowground functions and mitigating the effects of drought. By mitigating the adverse effects of drought on microbial activity and carbon cycling, consumers help preserve the ecological integrity and carbon sequestration potential of grasslands. These findings emphasize the need to protect and manage consumer populations as part of broader efforts to sustain and restore these critical ecosystems in the face of global change.

AUTHOR CONTRIBUTIONS

Jane M. Lucas assisted in conceptualization, conducted data analyses, and wrote the manuscript. Michelle L. Budny collected data and assisted with data analysis. Nathan P. Lemoine designed the study, obtained funding, collected data, analyzed data, and assisted with manuscript preparation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Lemoine, 2024) are available in Figshare at https://doi.org/10.6084/m9.figshare.26969821.v1.

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REFERENCES

Anderson, M. J., and J. Santana-Garcon. 2015. "Measures of Precision for Dissimilarity-Based Multivariate Analysis of Ecological Communities." *Ecology Letters* 18(1): 66–73. https://doi.org/10.1111/ele.12385.

Anderson, M. J., and D. C. I. Walsh. 2013. "PERMANOVA, ANOSIM, and the Mantel Test in the Face of Heterogeneous Dispersions: What Null Hypothesis Are you Testing?" *Ecological Monographs* 83(4): 557–574. https://doi.org/10.1890/12-2010.1.

Ashraf, M. N., M. A. Waqas, and S. Rahman. 2022. "Microbial Metabolic Quotient Is a Dynamic Indicator of Soil Health: Trends, Implications and Perspectives." *Eurasian Soil Science* 55: 1794–1803.

Badri, D. V., and J. M. Vivanco. 2009. "Regulation and Function of Root Exudates." *Plant, Cell & Environment* 32(6): 666–681. https://doi.org/10.1111/j.1365-3040.2009.01926.x.

Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. "Herbivore Impact on Grassland Plant Diversity Depends on Habitat Productivity and Herbivore Size." *Ecology Letters* 9(7): 780–88.

Bardgett, R. D., D. A. Wardle, and G. W. Yeates. 1998. "Linking Above-Ground and below-Ground Interactions: How Plant Responses to Foliar Herbivory Influence Soil Organisms." *Soil Biology and Biochemistry* 30(14): 1867–78. https://doi.org/10.1016/S0038-0717(98)00069-8.

Belovsky, G. E., and J. B. Slade. 2000. "Insect Herbivory Accelerates Nutrient Cycling and Increases Plant Production." *Proceedings of the National Academy of Sciences* 97(26): 14412–17. https://doi.org/10.1073/pnas.250483797.

Bender, J. M., F. Li, H. Adisetiyo, D. Lee, S. Zabih, L. Hung, T. A. Wilkinson, et al. 2018. "Quantification of Variation and the Impact of Biomass in Targeted 16S rRNA Gene Sequencing Studies." *Microbiome* 6(1): 155. https://doi.org/10.1186/s40168-018-0543-z.

Biggs, R., H. Simons, M. Bakkenes, R. J. Scholes, B. Eickhout, D. Van Vuuren, and R. Alkemade. 2008. "Scenarios of Biodiversity Loss in Southern Africa in the 21st Century." *Global Environmental Change* 18(2): 296–309. https://doi.org/10.1016/j.gloenvcha.2008.02.001.

Byrd, A. L., M. Liu, K. E. Fujimura, S. Lyalina, D. R. Nagarkar, B. Charbit, J. Bergstedt, et al. 2021. "Gut Microbiome Stability and Dynamics in Healthy Donors and Patients with Non-Gastrointestinal Cancers." *Journal of Experimental Medicine* 218(1): e20200606. https://doi.org/10.1084/jem.20200606.

Chen, Q., S. Wang, E. W. Seabloom, A. S. MacDougall, E. T. Borer, J. D. Bakker, I. Donohue, et al. 2022. "Nutrients and Herbivores Impact Grassland Stability across Spatial Scales through Different Pathways." *Global Change Biology* 28(8): 2678–88. https://doi.org/10.1111/gcb.16086.

Craven, D., N. Eisenhauer, W. D. Pearse, Y. Hautier, F. Isbell, C. Roscher, M. Bahn, et al. 2018. "Multiple Facets of Biodiversity Drive the Diversity–Stability Relationship." *Nature Ecology & Evolution* 2(10): 1579–87. https://doi.org/10.1038/s41559-018-0647-7.

Dandie, C. E., M. N. Miller, D. L. Burton, B. J. Zebarth, J. T. Trevors, and C. Goyer. 2007. "Nitric Oxide Reductase-Targeted Real-Time PCR Quantification of Denitrifier Populations in Soil." *Applied and Environmental Microbiology* 73(13): 4250–58. https://doi.org/10.1128/AEM.00081-07.

Dianzinga, N. T., M.-L. Moutoussamy, J. Sadeyen, L. H. R. Ravaomanarivo, and E. Frago. 2020. "The Interacting Effect of Habitat Amount, Habitat Diversity and Fragmentation on Insect Diversity along Elevational Gradients." *Journal of Biogeography* 47(11): 2377–91. https://doi.org/10.1111/jbi.13959.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. "Anthropogenic Warming Has Increased Drought Risk in California." *Proceedings of the National Academy of Sciences* 112(13): 3931–36. https://doi.org/10.1073/pnas.1422385112.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. "Defaunation in the Anthropocene." *Science* 345(6195): 401–6. https://doi.org/10.1126/science.1251817.

Domeignoz-Horta, L. A., G. Pold, X.-J. A. Liu, S. D. Frey, J. M. Melillo, and K. M. DeAngelis. 2020. "Microbial Diversity Drives Carbon Use Efficiency in a Model Soil." *Nature Communications* 11(1): 3684. https://doi.org/10.1038/s41467-020-17502-z.

Ebel, C. R., M. F. Case, C. M. Werner, L. M. Porensky, K. E. Veblen, H. B. M. Wells, D. M. Kimuyu, R. E. Langendorf, T. P. Young, and L. M. Hallett. 2022. "Herbivory and Drought Reduce the Temporal Stability of Herbaceous Cover by Increasing Synchrony in a Semi-Arid Savanna." *Frontiers in Ecology and Evolution* 10: 867051. https://doi.org/10.3389/fevo.2022.867051.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333(6040): 301–6.

Fierer, N., J. A. Jackson, R. Vilgalys, and R. B. Jackson. 2005. "Assessment of Soil Microbial Community Structure by Use of Taxon-Specific Quantitative PCR Assays." *Applied and Environmental Microbiology* 71(7): 4117–20. https://doi.org/10.1007/3-540-47977-5_28.

Gelman, A., J. Hill, and M. Yajima. 2012. "Why We (Usually) Don't Have to Worry about Multiple Comparisons." *Journal of Research on Educational Effectiveness* 5(2): 189–211. https://doi.org/10.1080/19345747.2011.618213.

Geyer, K. M., P. Dijkstra, R. Sinsabaugh, and S. D. Frey. 2019. "Clarifying the Interpretation of Carbon Use Efficiency in Soil through Methods Comparison." *Soil Biology and Biochemistry* 128: 79–88. https://doi.org/10.1016/j.soilbio.2018.09.036.

Gibson, D. J., and J. A. Newman. 2019. *Grasslands and Climate Change*. Cambridge: Cambridge University Press.

Gruner, D. S., J. E. Smith, E. W. Seabloom, S. A. Sandin, J. T. Ngai, H. Hillebrand, W. S. Harpole, et al. 2008. "A Cross-System

Synthesis of Consumer and Nutrient Resource Control on Producer Biomass." *Ecology Letters* 11(7): 740–755.

Hallett, L. M., J. S. Hsu, E. E. Cleland, S. L. Collins, T. L. Dickson, E. C. Farrer, L. A. Gherardi, et al. 2014. "Biotic Mechanisms of Community Stability Shift along a Precipitation Gradient." *Ecology* 95(6): 1693–1700. https://doi.org/10.1890/13-0895.1.

Hautier, Y., P. A. Niklaus, and A. Hector. 2009. "Competition for Light Causes Plant Biodiversity Loss after Eutrophication." *Science* 324(5927): 636–38.

Hoogsteen, M. J. J., E. A. Lantinga, E. J. Bakker, J. C. J. Groot, and P. A. Tittonell. 2015. "Estimating Soil Organic Carbon through Loss on Ignition: Effects of Ignition Conditions and Structural Water Loss." *European Journal of Soil Science* 66(2): 320–28. https://doi.org/10.1111/ejss.12224.

Hooper, D. U., F. S. Chapin, III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, et al. 2005. "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge." *Ecological Monographs* 75(1): 3–35. https://doi.org/10.1890/04-0922.

Irob, K., N. Blaum, A. Weiss-Aparicio, M. Hauptfleisch, R. Hering, K. Uiseb, and B. Tietjen. 2023. "Savanna Resilience to Droughts Increases with the Proportion of Browsing Wild Herbivores and Plant Functional Diversity." *Journal of Applied Ecology* 60(2): 251–262. https://doi.org/10.1111/1365-2664.14351.

Isenring, R. 2010. *Pesticides and the Loss of Biodiversity*. London, UK: Pesticide Action Network Europe.

Kearns, P. J., and A. Shade. 2018. "Trait-Based Patterns of Microbial Dynamics in Dormancy Potential and Heterotrophic Strategy: Case Studies of Resource-Based and Post-Press Succession." *The ISME Journal* 12(11): 2575–81. https://doi.org/10.1038/s41396-018-0194-x.

Keuskamp, J. A., B. J. J. Dingemans, T. Lehtinen, J. M. Sarneel, and M. M. Hefting. 2013. "Tea Bag Index: A Novel Approach to Collect Uniform Decomposition Data across Ecosystems." *Methods in Ecology and Evolution* 4(11): 1070–75. https://doi.org/10.1111/2041-210X.12097.

Lemoine, N. 2024. "2021_herbivore_exclosure." Figshare. https://doi.org/10.6084/m9.figshare.26969821.v1.

Lemoine, N. P. 2019. "Moving beyond Noninformative Priors: Why and How to Choose Weakly Informative Priors in Bayesian Analyses." *Oikos* 128(7): 912–928. https://doi.org/10.1111/oik.05985.

Lemoine, N. P., and M. L. Budny. 2022. "Seasonal Soil Moisture Variability, Not Drought, Drives Differences in Photosynthetic Physiology of Two C4 Grass Species." *Plant Ecology* 223(6): 627–642. https://doi.org/10.1007/s11258-022-01236-7.

Lemoine, N. P., M. L. Budny, E. Rose, J. Lucas, and C. W. Marshall. 2023. "Seasonal Soil Moisture Thresholds Inhibit Bacterial Activity and Decomposition during Drought in a Tallgrass Prairie." *Oikos* 2024: e10201. https://doi.org/10.1111/oik.10201.

Lemoine, N. P., and M. D. Smith. 2019. "Drought and Small-Bodied Herbivores Modify Nutrient Cycling in the Semi-Arid Shortgrass Steppe." *Plant Ecology* 220(2): 227–239. https://doi.org/10.1007/s11258-019-00908-1.

Liu, J., Z. Peng, H. Tu, Y. Qiu, Y. Liu, X. Li, H. Gao, et al. 2024. "Oligotrophic Microbes Are Recruited to Resist Multiple Global Change Factors in Agricultural Subsoils." *Environment International* 183: 108429.

Liu, C., L. Wang, X. Song, Q. Chang, D. A. Frank, D. Wang, J. Li, H. Lin, and F. du. 2018. "Towards a Mechanistic Understanding of the Effect that Different Species of Large Grazers Have on Grassland Soil N Availability." *Journal of Ecology* 106(1): 357–366. https://doi.org/10.1111/1365-2745.12809.

Lovett, G. M., L. M. Christensen, P. M. Groffman, C. G. Jones, J. E. Hart, and M. J. Mitchell. 2002. "Insect Defoliation and Nitrogen Cycling in Forests: Laboratory, Plot, and Watershed Studies Indicate that Most of the Nitrogen Released from Forest Foliage as a Result of Defoliation by Insects is Redistributed within the Ecosystem, whereas only a Small Fraction of Nitrogen is Lost by Leaching." *Bioscience* 52(4): 335–341.

Lucas, J. M., J. Jonas, A. N. Laws, D. H. Branson, S. C. Pennings, C. M. Prather, and M. S. Strickland. 2021a. "Functional and Taxonomic Diversity of Grasshoppers Differentially Shape Above- and below-Ground Communities and their Function." *Functional Ecology* 35(1): 167–180. https://doi.org/10.1111/1365-2435.13682.

Lucas, J. M., B. M. Sone, D. Whitmore, and M. S. Strickland. 2021b. "Antibiotics and Temperature Interact to Disrupt Soil Communities and Nutrient Cycling." *Soil Biology and Biochemistry* 163: 108437. https://doi.org/10.1016/j.soilbio.2021.108437.

Maestre, F. T., F. Valladares, and J. F. Reynolds. 2006. "The Stress-Gradient Hypothesis Does Not Fit all Relationships between Plant–Plant Interactions and Abiotic Stress: Further Insights from Arid Environments." *Journal of Ecology* 94(1): 17–22. https://doi.org/10.1111/j.1365-2745.2005.01089.x.

Malik, A. A., J. B. H. Martiny, E. L. Brodie, A. C. Martiny, K. K. Treseder, and S. D. Allison. 2020. "Defining Trait-Based Microbial Strategies with Consequences for Soil Carbon Cycling under Climate Change." *The ISME Journal* 14(1): 1–9. https://doi.org/10.1038/s41396-019-0510-0.

Mcmurdie, P. J., and S. Holmes. 2013. "Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data." *PLoS One* 8: e61217. https://doi.org/10.1371/journal.pone.0061217.

Nat Holland, J. 1995. "Effects of Above-Ground Herbivory on Soil Microbial Biomass in Conventional and No-Tillage Agroecosystems." *Applied Soil Ecology* 2(4): 275–79. https://doi.org/10.1016/0929-1393(95)00055-2.

O'Mara, F. P. 2012. "The Role of Grasslands in Food Security and Climate Change." *Annals of Botany* 110(6): 1263–70. https://doi.org/10.1093/aob/mcs209.

Panikov, N. S. 1999. "Understanding and Prediction of Soil Microbial Community Dynamics under Global Change." *Applied Soil Ecology* 11(2): 161–176. https://doi.org/10.1016/S0929-1393(98)00143-7.

Parolari, A. J., M. L. Goulden, and R. L. Bras. 2012. "Fertilization Effects on the Ecohydrology of a Southern California Annual Grassland." *Geophysical Research Letters* 39(8): L08405. https://doi.org/10.1029/2012GL051411.

Post, E. 2013. "Erosion of Community Diversity and Stability by Herbivore Removal under Warming." *Proceedings of the Royal Society B: Biological Sciences* 280(1757): 20122722. https://doi.org/10.1098/rspb.2012.2722.

Potthast, K., S. Meyer, A. Tischer, G. Gleixner, A. Sieburg, T. Frosch, and B. Michalzik. 2021. "Grasshopper Herbivory Immediately Affects Element Cycling but Not Export Rates in an N-Limited Grassland System." *Ecosphere* 12(3): e03449. https://doi.org/10.1002/ecs2.3449.

Prather, C. M., and A. N. Laws. 2018. "Insects as a Piece of the Puzzle to Mitigate Global Problems: An Opportunity for Ecologists." *Basic and Applied Ecology* 26: 71–81. https://doi.org/10.1016/j.baae.2017.09.009.

Prather, C., M. S. Strickland, A. Laws, and D. Branson. 2017. "Herbivore Species Identity and Composition Affect Soil Enzymatic Activity through Altered Plant Composition in a Coastal Tallgrass Prairie." *Soil Biology and Biochemistry* 112: 277–280. https://doi.org/10.1016/j.soilbio.2017.05.013.

Reed, C. G., M. L. Budny, J. T. du Toit, R. Helcoski, J. P. Schimel, I. P. J. Smit, T. Strydom, et al. 2025. "Elephant Megacarcasses Increase Local Nutrient Pools in African Savanna Soils and Plants." *Biogeosciences* 22(6): 1583–96. https://doi.org/10.5194/bg-22-1583-2025.

Revel-Muroz, A., M. Akulinin, P. Shilova, A. Tyakht, and N. Klimenko. 2023. "Stability of Human Gut Microbiome: Comparison of Ecological Modelling and Observational Approaches." *Computational and Structural Biotechnology Journal* 21: 4456–68. https://doi.org/10.1016/j.csbj.2023.08.030.

Riginos, C., L. M. Porensky, K. E. Veblen, and T. P. Young. 2018. "Herbivory and Drought Generate Short-Term Stochasticity and Long-Term Stability in a Savanna Understory Community." *Ecological Applications* 28(2): 323–335. https://doi.org/10.1002/eap.1649.

Roberts, S., M. Osborne, M. Ebden, S. Reece, N. Gibson, and S. Aigrain. 2013. "Gaussian Processes for Time-Series Modelling." *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 371(1984): 20110550. https://doi.org/10.1098/rsta.2011.0550.

Rode, M., N. P. Lemoine, and M. D. Smith. 2017. "Prospective Evidence for Independent Nitrogen and Phosphorus Limitation of Grasshopper (Chorthippus Curtipennis) Growth in a Tallgrass Prairie." *PLoS One* 12(5): e0177754.

Roller, B. R. K., S. F. Stoddard, and T. M. Schmidt. 2016. "Exploiting rRNA Operon Copy Number to Investigate Bacterial Reproductive Strategies." *Nature Microbiology* 1(September): 16160. https://doi.org/10.1038/nmicrobiol.2016.160.

Rousk, J., E. Bååth, P. C. Brookes, C. L. Lauber, C. A. Lozupone, J. G. Caporaso, R. Knight, and N. Fierer. 2010. "Soil Bacterial and Fungal Communities across a pH Gradient in an Arable Soil." *The ISME Journal* 4(10): 1340–51. https://doi.org/10.1038/ismej.2010.58.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. "Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants." *American Naturalist* 155(2): 141–153.

Schowalter, T. D. 2022. *Insect Ecology: An Ecosystems Approach*. Cambridge, MA: Academic Press.

Stoddard, S. F., B. J. Smith, R. Hein, B. R. K. Roller, and T. M. Schmidt. 2015. "rrnDB: Improved Tools for Interpreting rRNA Gene Abundance in Bacteria and Archaea and a New Foundation for Future Development." *Nucleic Acids Research* 43: D593–D598. https://doi.org/10.1093/nar/gku1201.

Sveen, T. R., T. Netherway, J. Juhanson, J. Oja, P. Borgström, M. Viketoft, J. Strengbom, et al. 2021. "Plant-Microbe Interactions in Response to Grassland Herbivory and Nitrogen Eutrophication." *Soil Biology and Biochemistry* 156(May): 108208. https://doi.org/10.1016/j.soilbio.2021.108208.

Tao, F., Y. Huang, B. A. Hungate, S. Manzoni, S. D. Frey, M. W. I. Schmidt, M. Reichstein, et al. 2023. "Microbial Carbon Use Efficiency Promotes Global Soil Carbon Storage." *Nature* 618(7967): 981–85. https://doi.org/10.1038/s41586-023-06042-3.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. "Animal Species Diversity Driven by Habitat Heterogeneity/Diversity: The Importance of Keystone Structures." *Journal of Biogeography* 31(1): 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x.

Thébault, E., and M. Loreau. 2005. "Trophic Interactions and the Relationship between Species Diversity and Ecosystem Stability." *The American Naturalist* 166(4): E95–E114. https://doi.org/10.1086/444403.

Tilman, D., and J. A. Downing. 1994. "Biodiversity and Stability in Grasslands." *Nature* 367(6461): 363–65. https://doi.org/10.1038/367363a0.

Tscharntke, T., I. Grass, T. C. Wanger, C. Westphal, and P. Batáry. 2021. "Beyond Organic Farming – Harnessing Biodiversity-Friendly Landscapes." *Trends in Ecology & Evolution* 36(10): 919–930. https://doi.org/10.1016/j.tree.2021.06.010.

Wang, C., L. Qu, L. Yang, D. Liu, E. Morrissey, R. Miao, Z. Liu, Q. Wang, Y. Fang, and E. Bai. 2021. "Large-Scale Importance of Microbial Carbon Use Efficiency and Necromass to Soil Organic Carbon." *Global Change Biology* 27(10): 2039–48. https://doi.org/10.1111/gcb.15550.

Welti, E. A. R., K. A. Roeder, K. M. de Beurs, A. Joern, and M. Kaspari. 2020. "Nutrient Dilution and Climate Cycles Underlie Declines in a Dominant Insect Herbivore." *Proceedings of the National Academy of Sciences* 117(13): 7271–75. https://doi.org/10.1073/pnas.1920012117.

Xu, X., J. P. Schimel, I. A. Janssens, X. Song, C. Song, G. Yu, R. L. Sinsabaugh, D. Tang, X. Zhang, and P. E. Thornton. 2017. "Global Pattern and Controls of Soil Microbial Metabolic Quotient." *Ecological Monographs* 87(3): 429–441. https://doi.org/10.1002/ecm.1258.

Yahdjian, L., and O. E. Sala. 2002. "A Rainout Shelter Design for Intercepting Different Amounts of Rainfall." *Oecologia* 133(2): 95–101. https://doi.org/10.1007/s00442-002-1024-3.

van de Zande, E. M., M. Wantulla, J. J. A. van Loon, and M. Dicke. 2024. "Soil Amendment with Insect Frass and Exuviae Affects Rhizosphere Bacterial Community, Shoot Growth and Carbon/Nitrogen Ratio of a Brassicaceous Plant." *Plant and Soil* 495(1): 631–648. https://doi.org/10.1007/s11104-023-06351-6.

SUPPORTING INFORMATION

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

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