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Precipitation legacies amplify ecosystem nitrogen losses from nitric oxide emissions in a Pinyon–Juniper dryland

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Abstract

Climate change is increasing the variability of precipitation, altering the frequency of soil drying-wetting events and the distribution of seasonal precipitation. These changes in precipitation can alter nitrogen (N) cycling and stimulate nitric oxide (NO) emissions (an air pollutant at high concentrations), which may vary according to legacies of past precipitation and represent a pathway for ecosystem N loss. To identify whether precipitation legacies affect NO emissions, we excluded or added precipitation during the winter growing season in a Pinyon–Juniper dryland and measured in situ NO emissions following experimental wetting. We found that the legacy of both excluding and adding winter precipitation increased NO emissions early in the following summer; cumulative NO emissions from the winter precipitation exclusion plots (2750 ± 972 μg N-NO m^{-2}) and winter water addition plots (2449 ± 408 μg N-NO m^{-2}) were higher than control plots (1506 ± 397 μg N-NO m^{-2}). The increase in NO emissions with previous precipitation exclusion was associated with inorganic N accumulation, while the increase in NO emissions with previous water addition was associated with an upward trend in microbial biomass. Precipitation legacies can accelerate soil NO emissions and may amplify ecosystem N loss in response to more variable precipitation.

KEYWORDS
altered precipitation, climate change, drought, nitrification, nitrogen, soil, wetting

INTRODUCTION

Precipitation controls multiple ecological process that alter soil nitrogen (N) pools, transformations, and overall N cycling (Vitousek et al., 2022). Specifically, N cycling may be affected by past precipitation through legacy effects that alter the ecological processes that govern N availability (Ogle et al., 2015; Sala et al., 2012). For example, precipitation legacies from prior seasons can affect plant biomass (Reichmann et al., 2013; Sala et al., 2012), microbial communities (Veach & Zeglin, 2020; Wang & Allison, 2021), and N concentrations (Reichmann et al., 2013; Shen et al., 2016), which altogether control N availability. Yet, one key unknown is whether precipitation legacies affect the processes controlling N loss, with potential implications for ecosystem N limitation. In drylands, N losses via nitric oxide (NO) emissions may account for half of atmospheric N inputs

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over 48 h after wetting dry soils (Eberwein et al., 2020) and may increase as climate change alters the frequency of soil drying-rewetting cycles that favor NO emissions (Dai, 2013). In addition to reducing ecosystem N availability, NO emissions can also degrade regional air quality (Sha et al., 2021). Understanding whether the legacies of past precipitation affect NO emissions is important since most models predict NO as a function of soil moisture, N deposition, and temperature (Hudman et al., 2012; Sha et al., 2021), but do not consider whether precipitation legacies may improve their predictions.

It is well established that wetting dry soils stimulates large NO emission pulses (Davidson et al., 1991; Eberwein et al., 2020; Homyak et al., 2016). Within minutes of wetting, soil microorganisms and chemical reactions can convert soil N to NO before biological sinks for N (e.g., root N assimilation) recover from drought-induced stress (Homyak et al., 2016; Krichels et al., 2022). In contrast to dry soils, moist soils maintain active biological sinks for N, limiting N losses via NO (Homyak et al., 2016; McCulley et al., 2009). As such, rainfall-induced drying-rewetting cycles represent critical periods when a substantial fraction of ecosystem N inputs can be transferred to the atmosphere as NO (Eberwein et al., 2020; Krichels et al., 2022; Soper et al., 2016). However, it is not well established whether the magnitude of NO pulses vary as a function of the legacies of past precipitation.

Precipitation legacy effects influence both soil N availability and microbial growth (Shen et al., 2016; Veach & Zeglin, 2020), which, in turn, may affect the magnitude of NO pulses (Eberwein et al., 2020; Vourlitis et al., 2015). For example, pulsed NO emissions may be limited by N if past wet periods maintain active N sinks, reducing the carryover of available soil N to the next season (McCulley et al., 2009; Shen et al., 2016). In contrast, past dry periods may shut down N sinks (Dijkstra et al., 2015; Zhong et al., 2014), increasing soil available N and future NO emissions. Together, these dynamics may establish a negative relationship between past precipitation and NO emissions driven by carryovers of soil N (i.e., decreased precipitation increases N availability and future NO emissions; hereafter, the *N carryover hypothesis*; Figure 1a; Shen et al., 2016). Similarly, past precipitation may also affect ecosystem functions that are limited by plant or microbial biomass (Reichmann et al., 2013; Sala et al., 2012). Microbial biomass increases under optimal moisture but decreases if soils get too dry (Austin et al., 2004; Homyak et al., 2014; Homyak, Allison, et al., 2017; Wang & Allison, 2021). Thus, dry conditions during one season may reduce microbial biomass but wet conditions may increase it, controlling microbial capacity to produce NO the following season. This biomass carryover effect can establish a positive relationship between past precipitation and pulsed NO emissions (hereafter, the *biomass carryover hypothesis*; Figure 1b; Reichmann et al., 2013; Sala et al., 2012). In this sense, the direction of precipitation legacies may depend on whether they are driven by N or biomass carryovers (Figure 1c), leading us to ask: how does the legacy of past growing seasons' precipitation mediate pulsed NO emissions when dry soils are wetted?

To answer this question, we measured in situ soil NO pulses after experimental wetting in a Pinyon–Juniper dryland where we also manipulated seasonal precipitation for 2 years. We focused on the legacy of winter precipitation on summer NO pulses because dry summers amplify these emissions. To assess winter precipitation legacies, we also measured soil inorganic N and microbial biomass during the transition from winter to summer and tested two hypotheses. First, we tested predictions from the N carryover hypothesis (Figure 1a): (i) excluding winter precipitation would increase soil inorganic N and the magnitude of NO pulses in the subsequent summer, and (ii) adding more winter precipitation would instead lower inorganic N and NO pulses in the subsequent summer. We also tested predictions from the biomass carryover hypothesis (Figure 1b): (i) adding more winter precipitation would increase microbial biomass and NO pulses in the subsequent summer, and (ii) excluding winter precipitation would instead decrease microbial biomass and NO pulses in the subsequent summer.

METHODS

Study site and experimental design

This study took place at the Pinyon Flats precipitation manipulation experiment in Southern California (33°36′36.7″ N, 116°27′06.1″ W), part of the Philip L. Boyd Deep Canyon Desert Reserve. Between 1990 and 2020, the site received an average of 222 mm annual precipitation occurring in two distinct seasons, a cool winter between November and May (154 $\pm$ 85 mm; mean $\pm$ standard deviation [SD]) and a hot monsoonal summer from June through October (68 $\pm$ 46 mm). Daily maximum temperature is highest in July (34.7°C) and lowest in December (14.5°C). Soils are gravelly fine sandy loams in the Omstott series, and classified as loamy, mixed, superactive, nonacidic, mesic, shallow Typic Xerorthents. The soil pH is 7.6 and the mean soil total C content (upper 10 cm) is 0.48% $\pm$ 0.12% and 0.03% $\pm$ 0.01% for N.

To help understand changes in precipitation variability, summer and winter precipitation amount has been manipulated in 6 × 8.5 m plots since July 2018
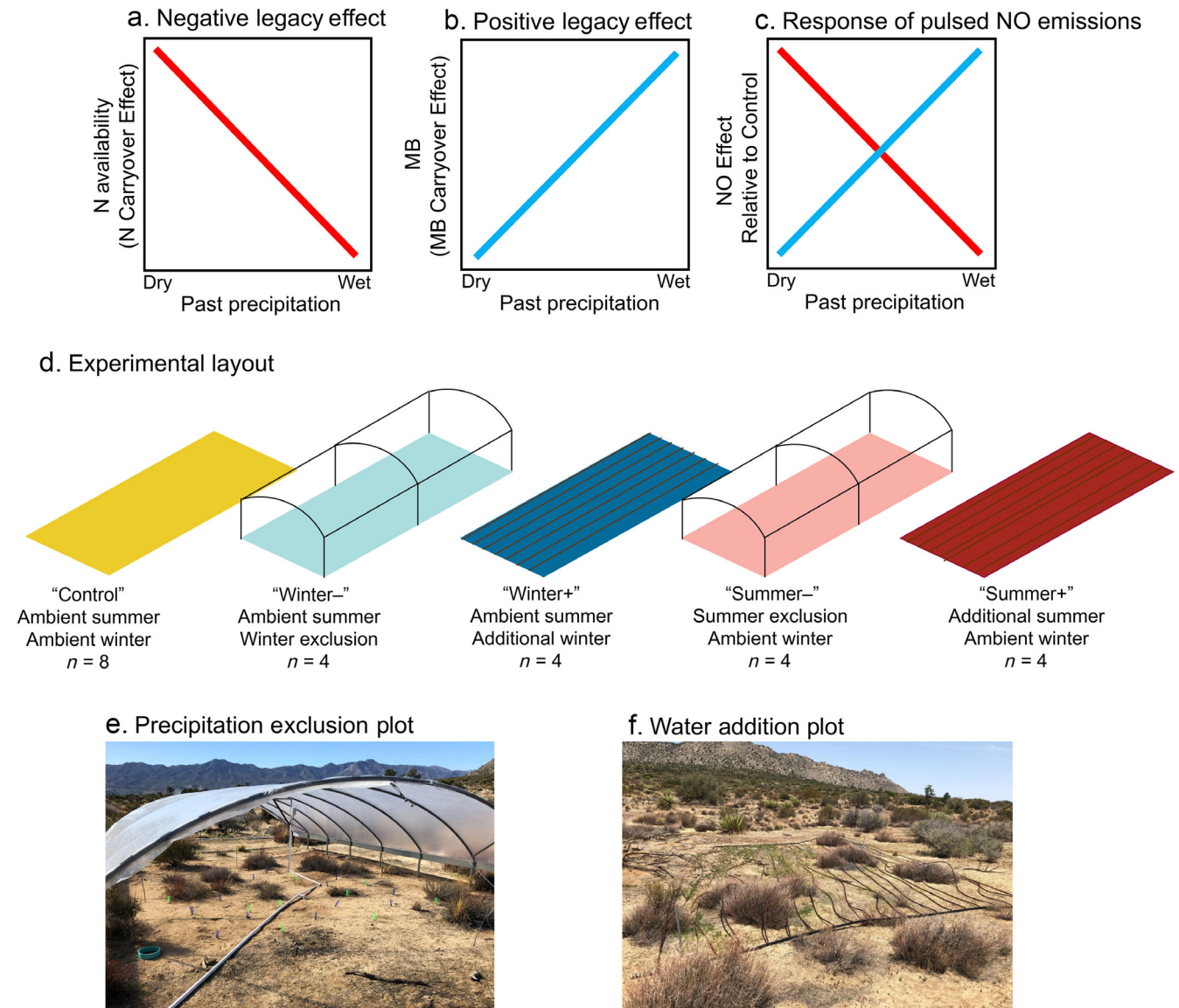
FIGURE 1 Conceptual diagram illustrating the N carryover hypothesis (a) and the biomass carryover hypothesis (b), predicted effects of these hypotheses on nitric oxide (NO) pulses (c), layout of the precipitation manipulation experiment (d), and photos of a precipitation exclusion (e) and a water addition plot (f). For (a) through (c), the x-axis represents prior season's rainfall, and the y-axis corresponds to nitrogen (N), microbial biomass (MB), or pulsed NO emissions. In (d), we illustrate the 24 plots and treatments: Control plots were not manipulated; Winter− excluded all winter rainfall; Winter+ roughly doubled water inputs during the winter; Summer− excluded all summer rainfall; and Summer+ roughly doubled water inputs during summer.

(Figure 1; Spasojevic et al., 2022). Precipitation was excluded from "Winter−" plots ($n = 4$) from 11/08/2018–07/23/2019 and 10/22/2019–6/18/2020, and from "Summer−" plots ($n = 4$) from 07/23/2019–10/22/2019 and 6/18/2020–10/07/2020. Precipitation was collected from these plots using a downslope drainage system (polyvinyl chloride tubing; PVC) connected to four 1500-gallon tanks. After precipitation events, water was added to "Winter+" (133 mm in 2019 and 108 mm in 2020) and "Summer+" (29 mm in 2018, 22 mm in 2019, and 0 mm in 2020) plots ($n = 4$) by pumping water from the tanks and distributing using 17 mm drip tubing

(Netafim Irrigation, Inc., Fresno, CA). Control plots ($n = 8$) received ambient precipitation (194 mm in 2018, 400 mm in 2019, and 189 mm in 2020).

We measured soil NO emissions from each plot in the winter (February), early summer (June), and late summer (September) of 2020 in response to wetting soils within each plot independent from the seasonal precipitation manipulation treatments. One PVC gas sampling collar (20 cm diameter × 10 cm height; inserted 5 cm into the ground) was installed in each plot in January 2020. Emissions were measured when no precipitation had fallen in the prior 2 weeks. Soil NO emissions were

measured prior to wetting and 15 min, 3 h, and 24 h after wetting soils within each collar with 500 ml of deionized water. This water addition corresponds to ~7 mm of rainfall, which is within the range of historical rain events (https://deepcanyon.ucnrs.org/weather-data/). Prior to wetting, we collected 50 g soil (0–10 cm depth) within 50 cm of the collars to measure soil moisture and inorganic N. Separate soil cores were collected in February, May, and August to measure microbial biomass. Concomitant with microbial biomass, we measured in situ net N mineralization rates and net nitrification rates using intact core incubations (Appendix S1: Section S1.1).

Field NO emissions

We measured NO emissions from each plot using a PVC chamber system and a Scintrex LMA-3 chemiluminescent NO_x analyzer (Eberwein et al., 2020; Appendix S1: Section S2.1). Fluxes of NO were calculated as the linear change in gas concentration over the last 90 s of each incubation using custom script (Andrews & Krichels, 2022). Cumulative NO emissions for each plot were calculated using trapezoidal integration in R version 3.6.1 ("trapz" function; R Core Team, 2019).

Soil inorganic N, moisture, microbial biomass C (MBC), and NH_3-oxidizing gene abundance

We measured extractable NO_3^-, NH_4^+, and gravimetric water content (GWC) from soil samples collected within 50 cm of each collar whenever we measured soil NO emissions. Soil GWC was measured by drying soils at 104°C for 24 h. NO_3^- and NH_4^+ were measured by extracting 3 g of soil in 30 ml of 2 M KCl. This solution was shaken for 1 h and was then filtered (Whatman 42; 2.5 μm pore size) and frozen until analysis. Colorimetric assays were used to measure extractable NO_3^- (SEAL method EPA-129-A) and NH_4^+ (SEAL method EPA-126-A).

Microbial biomass C was measured from homogenized soils collected in February, May, and August using a chloroform slurry extraction (Fierer & Schimel, 2002). Briefly, 10 g of soil was extracted in either K_2SO_4 (40 ml, 2 M) or 2 M K_2SO_4 with 0.5 ml chloroform. Samples were filtered (Whatman 42; 2.5 μm pore size) and analyzed for total organic carbon (TOC; Shimadzu TOC-V). Microbial biomass C was calculated as the difference in TOC between the K_2SO_4 extraction and the K_2SO_4 plus chloroform extraction. We did not account for extraction efficiency and our measurements represent a flush of C rather than the total microbial biomass. To specifically target the

microbial communities responsible for NO emissions, we measured ammonia oxidizing gene abundance from bacteria and archaea (Appendix S1: Section S3.1).

Statistical analyses

All statistics were run using R version 3.6.1 (R Core Team, 2019). We used analysis of variance (ANOVA) to test for differences in cumulative NO emissions, soil moisture, inorganic N, and MBC at each sampling period ("car" package; Fox & Weisberg, 2011) after assessing for normality using Shapiro-Wilkes tests and applying log transformations when appropriate. Treatment was included as a predictor variable and cumulative NO emissions, soil moisture, or soil N were included as response variables. If the ANOVA detected a significant treatment effect ($p < 0.05$), then we compared each treatment to the control using a Dunnett's test ("lsmeans" package; Lenth, 2016). We also ran the Dunnett's test when $p < 0.1$ but acknowledge greater uncertainty with these results.

RESULTS

Field NO emissions

Manipulating winter precipitation altered cumulative NO emissions in the winter ($F_{4,19} = 22.3$, $p < 0.001$), which were over 18× higher in the Winter− plots (1002 ± 450 μg N-NO m^{-2}; mean ± SD) compared to the Control plots (53.6 ± 11.1 μg N-NO m^{-2}; Figure 2d). In the Winter− plots, instantaneous NO emissions increased from −0.07 ± 0.08 ng N-NO m^{-2} s^{-1} at field moisture to 20.17 ± 7.94 ng N-NO m^{-2} s^{-1} 24 h after wetting (Figure 2a). In contrast, NO emissions in the Control plots never rose above 0.77 ± 0.17 ng N-NO m^{-2} s^{-1}.

Both excluding and adding winter precipitation increased pulsed NO emissions early in the summer ($F_{4,19} = 5.80$, $p = 0.003$; Figure 2e), which was 1 month after the last winter rain event. In the early summer, cumulative NO emissions were greater in both the Winter− plots (2750 ± 972 μg N-NO m^{-2}, $p = 0.008$) and Winter+ plots (2449 ± 408 μg N-NO m^{-2}, $p = 0.048$) compared to Control plots (1506 ± 397 μg N-NO m^{-2}). The legacy of winter precipitation on cumulative NO emissions dissipated by the late summer when no treatments differed from the control ($p \geq 0.28$; Figure 2f). Cumulative NO emissions were higher in Control plots in the late summer (4889 ± 956 μg N-NO m^{-2}, $F_{2,14} = 187$, $p < 0.001$) compared to the early summer (1506 ± 397 μg N-NO m^{-2}) or winter (53.6 ± 11.1 μg N-NO m^{-2}).
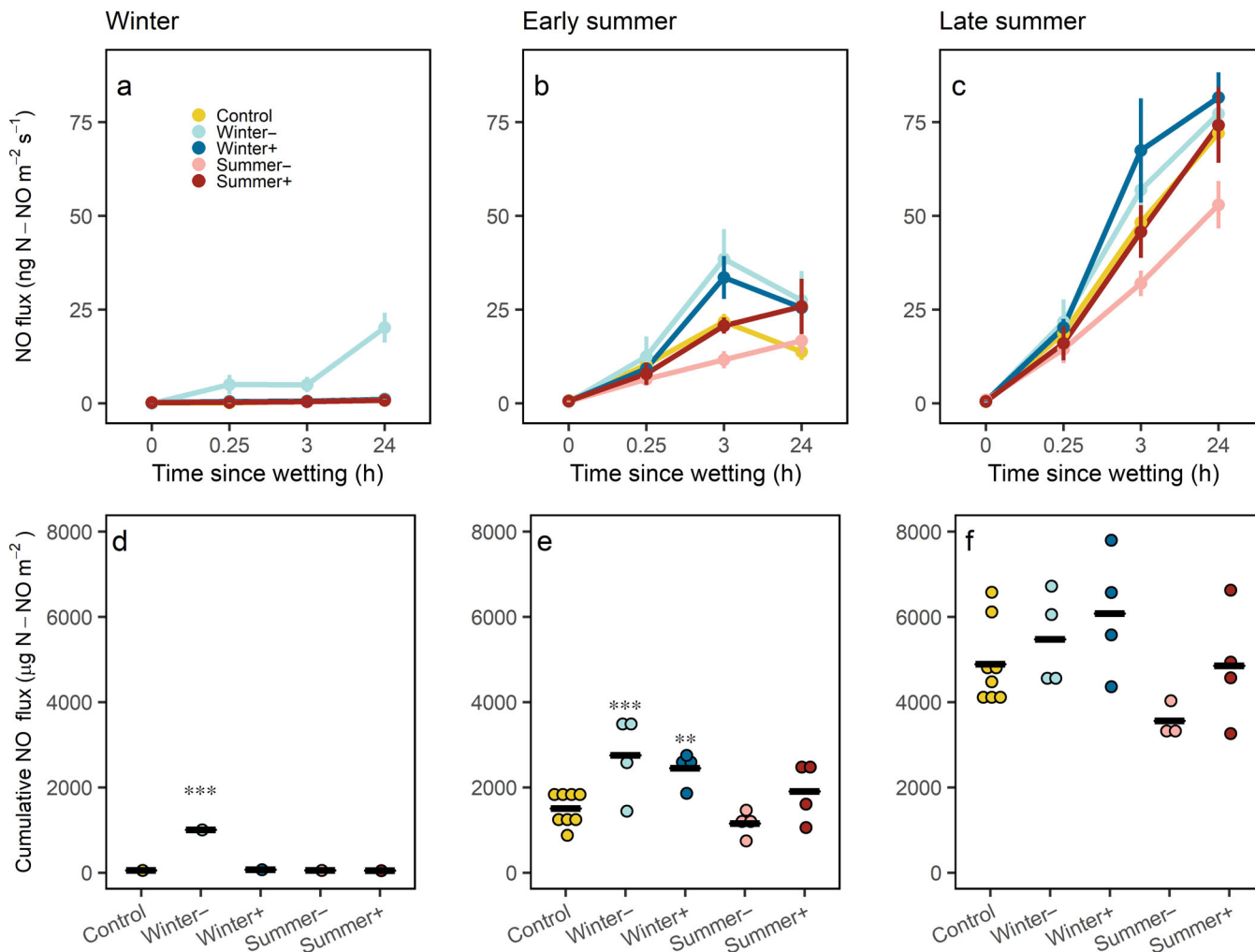
FIGURE 2 Instantaneous (a–c) and cumulative (d–f) soil nitric oxide (NO) emissions in the winter (a, d), early summer (b, e), and late summer (c, f) 2020. Instantaneous measurements are reported prior to wetting and at 15 min, 3 h, and 24 h after wetting soils. For the instantaneous measurements, dots represent mean NO emissions from each treatment ($n = 4$ for treatments, $n = 8$ for Control) and error bars represent standard error of the mean. For the cumulative emissions (d–f), horizontal lines represent the mean cumulative NO emissions ($n = 4$ for treatments, $n = 8$ for Control) and dots represent individual measurements. Asterisks indicate if cumulative NO emissions differ from Control plots (*$p < 0.10$, **$p < 0.05$, ***$p < 0.01$).

Soil moisture, inorganic N, and MBC

Manipulating winter precipitation affected soil moisture in the winter ($F_{4,19} = 16.7$, $p < 0.001$) with drier Winter− soils ($0.86\% \pm 0.13\%$ GWC, $p < 0.001$) compared to Control plots ($5.40\% \pm 1.27\%$ GWC) (Figure 3a). We did not detect an effect of manipulating seasonal precipitation on soil moisture in the early summer ($F_{4,19} = 0.13$, $p = 0.97$, Control GWC $= 0.49\% \pm 0.24\%$) or late summer ($F_{4,19} = 0.66$, $p = 0.63$, Control GWC $= 0.51\% \pm 0.08\%$)— it did not rain from May through October 2020, allowing soils in all plots to dry out.

While we did not detect an effect of manipulating winter precipitation on soil NH_4^+ in the winter ($F_{4,19} = 0.72$, $p = 0.59$), it likely affected the carryover of NH_4^+ into the early ($F_{4,19} = 2.85$, $p = 0.052$; Figure 3b) and late summer ($F_{4,19} = 2.77$, $p = 0.057$). In the early summer, NH_4^+ was $2.6\times$ higher in Winter− plots (6.53 ± 2.88 µg N-NH_4^+ g^{-1}, $p = 0.018$) than in the Control (2.52 ± 1.19 µg N-NH_4^+ g^{-1}). In the late summer, NH_4^+ was $1.7\times$ higher in Winter− plots (4.29 ± 2.50 µg N-NH_4^+ g^{-1}) than in the Control (2.55 ± 1.58 µg N-NH_4^+ g^{-1}; $p = 0.10$). Winter precipitation manipulation affected NO_3^- in the winter ($F_{4,19} = 5.54$, $p < 0.01$) and the carryover of NO_3^- into the early ($F_{4,19} = 24.0$, $p < 0.001$) and late summer ($F_{4,19} = 44.15$, $p < 0.001$; Figure 3c) with NO_3^- always highest in the Winter− plots ($p < 0.01$).

We did not detect an effect of manipulating winter precipitation on net N mineralization nor net nitrification rates ($p > 0.1$; Appendix S1: Figure S1). Similarly,
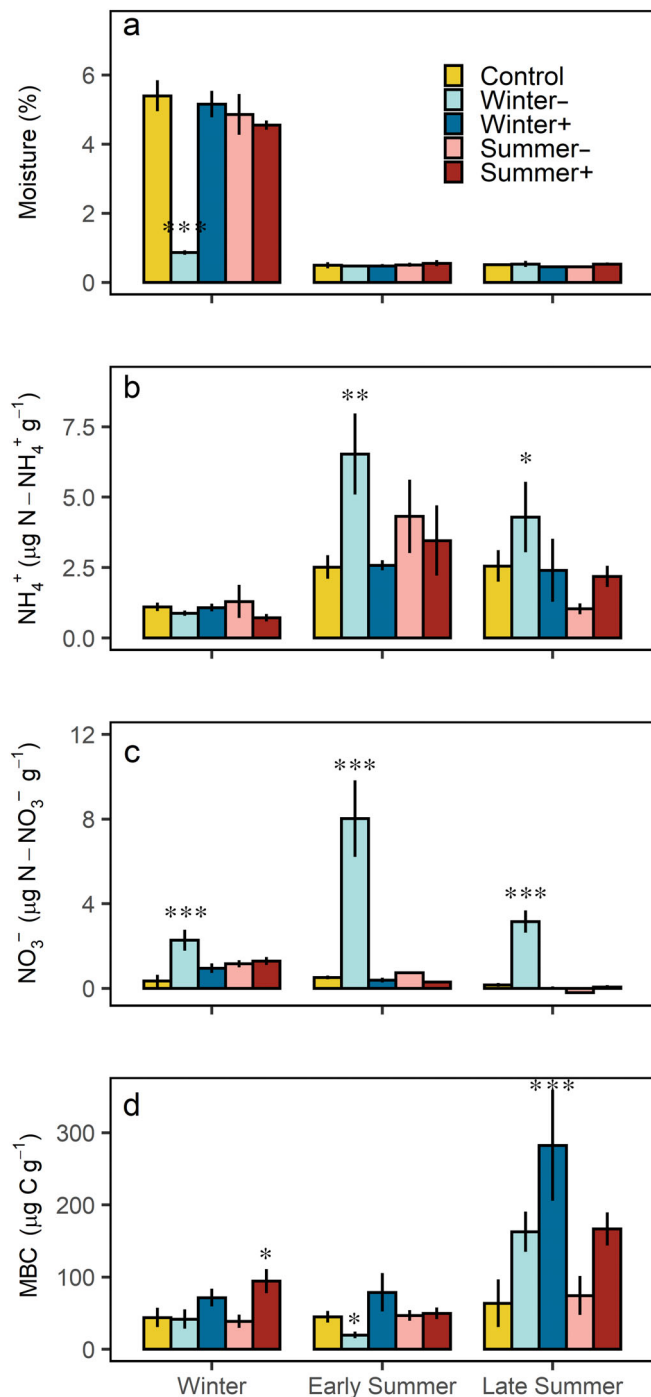
FIGURE 3 Gravimetric soil moisture (%) (a), NH_4^+ (μg N g^{-1} dry soil) (b), NO_3^- (μg N g^{-1} dry soil) (c), and microbial biomass C (MBC) (μg C g^{-1} dry soil) (d) in the winter, early summer, and late summer of 2020. Bars represent the mean from each treatment ($n = 4$ for treatments, $n = 8$ for Control) and error bars show standard error of the mean. Asterisks indicate if the mean in each treatment differs from Control plots (*$p < 0.10$, **$p < 0.05$, ***$p < 0.01$).

soil NO_2^- concentrations were not affected by manipulating winter precipitation ($p > 0.1$; Appendix S1: Figure S2).

Manipulating winter precipitation affected the carryover of MBC into the early ($F_{4,19} = 3.70$, $p = 0.02$) and late summer ($F_{4,17} = 4.9$, $p = 0.008$; Figure 3d). In the early summer, MBC was 2.3$\times$ lower in Winter$-$ plots (19.7 ± 8.91 μg C g^{-1}) compared to Control plots (44.9 ± 22.9 μg C g^{-1}; $p = 0.051$). While MBC was almost 2$\times$ higher in Winter$+$ plots (78.7 ± 53.3 μg C g^{-1}) than in the Control in the early summer (44.9 ± 22.9 μg C g^{-1}), this difference was not significant ($p = 0.39$). The carryover of MBC in response to more winter precipitation lasted into the late summer, when MBC was 4.5$\times$ higher in Winter$+$ plots (282 ± 133 μg C g^{-1}, $p = 0.003$) than in the Control (63.3 ± 87.6 μg C g^{-1}).

We did not detect an effect of manipulating winter precipitation on the abundance of ammonia oxidizing genes from bacteria or archaea ($p > 0.1$; Appendix S1: Figure S4).

DISCUSSION

Using a seasonal precipitation manipulation experiment, we found that the legacy of previous seasonal precipitation influenced pulsed NO emissions after wetting dry soils: both adding and excluding winter precipitation increased NO pulses early the following summer. In support of the N carryover hypothesis—dry conditions during the previous season increase soil available N to stimulate NO the following season—we found that soil N was higher in the Winter$-$ treatment compared to the Control in the early summer. In partial support of the biomass carryover hypothesis—increasing precipitation during the previous season increases soil microbial biomass and produces more NO the following season—we found that adding extra water in the Winter$+$ treatment increased NO emissions in the early summer, and that while microbial biomass did not concurrently increase, it began trending upward in the early summer, becoming greater than the Control by late summer. These findings suggest that while well-established factors such as water, temperature and N availability directly control soil NO emissions, precipitation legacies can influence the magnitude of NO pulses.

Decreased winter precipitation can stimulate pulsed NO emissions early in the summer by increasing the carryover of soil N between seasons, consistent with a negative winter precipitation legacy (Figure 1a). This negative legacy likely originated from a N carryover effect, since soil moisture was similar among treatments in summer, but NH_4^+ and NO_3^- accumulated after excluding winter precipitation (Figure 3b,c), likely easing N limitation of NO pulses (Eberwein et al., 2020; Krichels et al., 2022). Soil N may have accumulated because plant N

assimilation decreased under drought—rainfall exclusion decreased plant biomass (Spasojevic et al., 2022)—especially considering that excluding winter precipitation did not affect in situ net N mineralization or nitrification, a common finding across ecosystems (e.g., Homyak, Allison, et al., 2017; Appendix S1: Figure S1). Furthermore, during the winter, NO emissions were only observed in the Winter− plots, suggesting that reduced plant N assimilation in dry soils allowed microbial and/or abiotic processes to produce NO (e.g., nitrification, chemodenitrification, nitrifier denitrification; Homyak et al., 2016; Homyak, Kamiyama, et al., 2017; Zhong et al., 2014). Since baseline winter rainfall (189 mm) was higher than the historical mean (154 mm), our results suggest that abnormally dry winter periods can establish legacy effects that support pulsed NO emissions in the summer.

Increasing winter precipitation may also stimulate pulsed NO emissions early in the summer by increasing the carryover of microbial biomass between seasons, consistent with a positive legacy effect (Figure 1b). This positive legacy could have been driven by the biomass carryover hypothesis despite microbial biomass not increasing above control plots in the winter after adding extra water (Winter+ plots) as we had hypothesized. Instead, microbial biomass in Winter+ plots began to trend upward in early summer, becoming larger than in Control plots by late summer (Figure 3d), offering partial support for the hypothesis. Since baseline winter precipitation (189 mm) was only slightly higher than normal (154 mm historical average), it is possible that wetter winters—and associated larger water additions to the Winter+ plots—are necessary to further stimulate carryovers of microbial biomass. Although nitrifying microorganisms are thought to produce NO in drylands (Homyak et al., 2016; Krichels et al., 2022), we also did not observe a treatment effect on the size of archaeal or bacterial nitrifier communities (Appendix S1: Figure S4). Rather, greater microbial biomass may have enhanced inorganic N supply via rapid N mineralization following wetting, or stimulated conversion of N to NO via microbial denitrification (Austin et al., 2004). Still, our results suggest that elevated winter precipitation can establish positive legacies the following summer, increasing NO emissions.

The legacies of winter precipitation on NO emissions ended by late summer when no rain had fallen in over 6 months. This 6-month dry period is also consistent with the lack of legacy effects detected in the late summer from manipulating early summer precipitation; summer legacies were not established because it did not rain. Still, soil N in the late summer was highest after excluding winter precipitation (Winter−; Figure 3b,c) and microbial biomass was highest in the late summer after adding more winter precipitation (Winter+; Figure 3d), suggesting

N and microbial biomass carryovers did persist. It is possible these carryovers stimulated other N-limited processes (Evans & Burke, 2013; Shen et al., 2016) without affecting NO emissions. For example the smaller difference in soil N among treatments in the late, relative to the early summer, may not have been enough to stimulate differences in NO pulses. Furthermore, warm temperatures may have increased nitrification rates across all treatments regardless of microbial biomass, explaining the high NO emissions in the late summer without evidence of a legacy effect (Figure 2; Tourna et al., 2008). While winter precipitation legacies on soil NO pulses may only last a few months, they can still amplify ecosystem N losses during the early summer.

In conclusion, both increasing and decreasing winter precipitation increased soil NO emissions through both positive and negative legacy effects. Excluding winter precipitation established negative legacies on NO emissions likely by increasing inorganic N. On the other hand, adding extra winter precipitation established positive legacies on NO emissions. While NO emissions did not concurrently increase with microbial biomass, microbial biomass did trend upwards during summer, suggesting that biomass carryover effects may contribute to this positive legacy effect. Our results suggest soil NO emissions are part of the large number of ecological processes affected by precipitation legacy effects. Despite appearing short lived, these legacies can amplify NO emissions and may exacerbate ecosystem N limitation in response to more extreme precipitation regimes.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
All data (Krichels, 2022) are available in Dryad at https://doi.org/10.6086/D1MH4B. Code used to process flux data (Andrews & Krichels, 2022) is available in Zenodo at https://doi.org/10.5281/zenodo.7246428.

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REFERENCES

Andrews, H. M., and A. H. Krichels. 2022. "Handr003/TraceGasArray: v1.1 (v1.1)." Zenodo. https://doi.org/10.5281/zenodo.7246428.

Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. "Water Pulses and Biogeochemical Cycles in Arid and Semiarid Ecosystems." *Oecologia* 141: 221–35.

Dai, A. 2013. "Increasing Drought under Global Warming in Observations and Models." *Nature Climate Change* 3: 52–8.

Davidson, E. A., P. M. Vitousek, P. A. Matson, R. Riley, G. García-Méndez, and J. M. Maass. 1991. "Soil Emissions of Nitric Oxide in a Seasonally Dry Tropical Forest of México." *Journal of Geophysical Research* 96: 15439.

Dijkstra, F. A., M. He, M. P. Johansen, J. J. Harrison, and C. Keitel. 2015. "Plant and Microbial Uptake of Nitrogen and Phosphorus Affected by Drought Using ^{15}N and ^{32}P Tracers." *Soil Biology and Biochemistry* 82: 135–42.

Eberwein, J. R., P. M. Homyak, C. J. Carey, E. L. Aronson, and G. D. Jenerette. 2020. "Large Nitrogen Oxide Emission Pulses from Desert Soils and Associated Microbiomes." *Biogeochemistry Letters* 149: 239–50.

Evans, S. E., and I. C. Burke. 2013. "Carbon and Nitrogen Decoupling under an 11-Year Drought in the Shortgrass Steppe." *Ecosystems* 16: 20–33.

Fierer, N., and J. P. Schimel. 2002. "Effects of Drying-Rewetting Frequency on Soil Carbon and Nitrogen Transformations." *Soil Biology and Biochemistry* 34: 777–87.

Fox, J., and S. Weisberg. 2011. *An R Companion to Applied Regression*, 2nd ed. Thousand Oaks, CA: Sage.

Homyak, P. M., S. D. Allison, T. E. Huxman, M. L. Goulden, and K. K. Treseder. 2017. "Effects of Drought Manipulation on Soil Nitrogen Cycling: A Meta-Analysis." *Journal of Geophysical Research: Biogeosciences* 122: 3260–72.

Homyak, P. M., J. C. Blankinship, K. Marchus, D. M. Lucero, J. O. Sickman, and J. P. Schimel. 2016. "Aridity and Plant Uptake Interact to Make Dryland Soils Hotspots for Nitric Oxide (NO) Emissions." *Proceedings of the National Academy of Sciences of the United States of America* 113: E2608–16.

Homyak, P. M., M. Kamiyama, J. O. Sickman, and J. P. Schimel. 2017. "Acidity and Organic Matter Promote Abiotic Nitric Oxide Production in Drying Soils." *Global Change Biology* 23: 1735–47.

Homyak, P. M., J. O. Sickman, A. E. Miller, J. M. Melack, T. Meixner, and J. P. Schimel. 2014. "Assessing Nitrogen-Saturation in a Seasonally Dry Chaparral Watershed: Limitations of Traditional Indicators of N-Saturation." *Ecosystems* 17: 1286–305.

Hudman, R. C., N. E. Moore, A. K. Mebust, R. V. Martin, A. R. Russell, L. C. Valin, and R. C. Cohen. 2012. "Steps towards a Mechanistic Model of Global Soil Nitric Oxide Emissions: Implementation and Space Based-Constraints." *Atmospheric Chemistry and Physics* 12: 7779–95.

Krichels, A. H. 2022. "Data for: Precipitation Legacies Amplify Ecosystem Nitrogen Losses from Nitric Oxide Emissions in a Pinyon-Juniper Dryland." Dryad, dataset. https://doi.org/10.6086/D1MH4B.

Krichels, A. H., P. M. Homyak, E. L. Aronson, J. Sickman, H. Shulman, S. Piper, H. Andrews, and G. D. Jenerette. 2022. "Rapid Nitrate Reduction Contributes to Pulsed NO and N_2O Emissions Following Rewetting of Dryland Soils." *Biogeochemistry* 158: 233–50.

Lenth, R. C. 2016. "Least-Square Means: The R Package Lsmeans." *Journal of Statistical Software* 69: 1–33.

McCulley, R. L., I. C. Burke, and W. K. Lauenroth. 2009. "Conservation of Nitrogen Increases with Precipitation across a Major Grassland Gradient in the Central Great Plains of North America." *Oecologia* 159: 571–81.

Ogle, K., J. J. Barber, G. A. Barron-Gafford, L. P. Bentley, J. M. Young, T. E. Huxman, M. E. Loik, and D. T. Tissue. 2015. "Quantifying Ecological Memory in Plant and Ecosystem Processes." *Ecology Letters* 18: 221–35.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reichmann, L. G., O. E. Sala, and D. P. C. Peters. 2013. "Precipitation Legacies in Desert Grassland Primary Production Occur through Previous-Year Tiller Density." *Ecology* 94: 1–9.

Sala, O. E., L. A. Gherardi, L. Reichmann, E. Jobbágy, and D. Peters. 2012. "Legacies of Precipitation Fluctuations on Primary Production: Theory and Data Synthesis." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 3135–44.

Sha, T., X. Ma, H. Zhang, N. Janechek, Y. Wang, Y. Wang, L. Castro García, G. D. Jenerette, and J. Wang. 2021. "Impacts of Soil NO_x Emission on O_3 Air Quality in Rural California." *Environmental Science and Technology* 55: 7113–22.

Shen, W., G. D. Jenerette, D. Hui, and R. L. Scott. 2016. "Precipitation Legacy Effects on Dryland Ecosystem Carbon Fluxes: Direction, Magnitude and Biogeochemical Carryovers." *Biogeosciences* 13: 425–39.

Soper, F. M., T. W. Boutton, P. M. Groffman, and J. P. Sparks. 2016. "Nitrogen Trace Gas Fluxes from a Semiarid Subtropical Savanna under Woody Legume Encroachment." *Global Biogeochemical Cycles* 30: 614–28.

Spasojevic, M. J., P. M. Homyak, G. D. Jenerette, M. L. Goulden, S. McFaul, T. Madison-McQueen, L. Schauer, and M. Solis. 2022. "Altered Seasonal Precipitation Has Asymmetric Impacts on Plant Communities in Warm and Cool Growing Seasons." *Elementa* 10: 00014.

Tourna, M., T. E. Freitag, G. W. Nicol, and J. I. Prosser. 2008. "Growth, Activity and Temperature Responses of Ammonia-Oxidizing Archaea and Bacteria in Soil Microcosms." *Environmental Microbiology* 10: 1357–64.

Veach, A. M., and L. H. Zeglin. 2020. "Historical Drought Affects Microbial Population Dynamics and Activity during Soil Drying and Re-wet." *Microbial Ecology* 79: 662–74.

Vitousek, P. M., K. K. Treseder, R. W. Howarth, and D. L. Menge. 2022. "A "Toy Model" Analysis of Causes of Nitrogen Limitation in Terrestrial Exosystems." *Biogeochemistry* 160: 381–94.

Vourlitis, G. L., C. Defotis, and W. Kristan. 2015. "Effects of Soil Water Content, Temperature and Experimental Nitrogen Deposition on Nitric Oxide (NO) Efflux from Semiarid Shrubland Soil." *Journal of Arid Environments* 117: 67–74.

Wang, B., and S. D. Allison. 2021. "Drought Legacies Mediated by Trait Trade-Offs in Soil Microbiomes." *Ecosphere* 12: e03562.

Zhong, Y., W. Yan, J. Chen, and Z. Shangguan. 2014. "Net Ammonium and Nitrate Fluxes in Wheat Roots under Different Environmental Conditions as Assessed by Scanning Ion-Selective Electrode Terchnique." *Scientific Reports* 4: 7223.

SUPPORTING INFORMATION

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