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Large nitrogen oxide emission pulses from desert soils and associated microbiomes

Jennifer R. Eberwein · Peter M. Homyak · Chelsea J. Carey · Emma L. Aronson · G. Darrel Jenerette

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Abstract Nitrogen (N) trace gas emission pulses produced after wetting dry soils may be important pathways of ecosystem N loss. However, the rates and mechanisms controlling these emissions remain unclear. We tested whether changes in microbial community structure and increased rates of atmospheric N deposition could explain N emissions at two desert sites differing in atmospheric N deposition by ~ six fold. We measured peak NO_x (sum of nitric oxide and nitrogen dioxide) emissions 12 h post-wetting. NO_x emissions remained elevated over 24 h and increased after adding N. In contrast, we measured the highest nitrous oxide (N_2O) emissions within only 15 min post-wetting. N_2O emissions decreased within 12 h, were insensitive to adding N, and were among the highest reported globally. Microbial communities at the high N deposition site were less diverse with higher 16S nitrifier and bacterial *amoA* gene abundances relative to the low N deposition site, suggesting an increased capacity for nitrification. Nevertheless, N emissions were lower at the high N deposition site. While microbial communities changed after wetting, these changes were not correlated with N emissions. We conclude that desert soils can produce substantial NO_x and N_2O emission pulses, but that these emissions do not appear directly governed by changing microbial community characteristics or higher atmospheric N inputs. These findings highlight the importance of gaseous N loss pathways from dryland ecosystems that may contribute to sustained N limitation, with implications for atmospheric chemistry and Earth's climate.

Keywords Nitrous oxide · Nitric oxide · NO_x · N_2O · Drying-rewetting · Nitrogen deposition

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Introduction

Soil emissions of nitrous oxide (N_2O) and NO_x (the sum of nitric oxide [NO] and nitrogen dioxide [NO_2]) are key components of ecosystem nitrogen (N) budgets; they are pathways for ecosystem N loss and contribute to N limitation (von Sperber et al. 2017). In drylands, theory and measurements suggest limited water and N availability constrain N emissions (Hartley and Schlesinger 2000; Meixner and Yang 2006; Hall et al. 2012; Oerter et al. 2018). However, wetting dry soils can increase metabolic activity (Jenerette and Chatterjee 2012) and produce large emission "pulses" of NO_x and N_2O over relatively short periods (i.e. hours to days; Hartley and Schlesinger 2000; Hall et al. 2008; Oikawa et al. 2015; Homyak et al. 2016; Soper et al. 2016). While short-lived, N emissions can be substantial and are hypothesized to represent $\sim$ 77% of the N inputs to a desert ecosystem (Peterjohn and Schlesinger 1990). Because some drylands experience among the highest rates of atmospheric N deposition in the world (up to $\sim$ 71 kg N ha^{-1} yr^{-1}; Fenn et al. 2008), soil N availability may be increasing with unknown consequences for N emissions. Determining how changes in N availability may control dryland N emissions is critical from a N mass balance perspective, but also because NO_x can adversely affect regional air quality (Crutzen 1979) and N_2O is a powerful greenhouse gas and primary driver of stratospheric ozone depletion (Conrad et al. 1996; Ravishankara et al. 2009).

Soil NO_x and N_2O emissions are primarily controlled by nitrification and denitrification, but it remains unclear what mechanisms control N emission pulses when dry soils wet up (Davidson et al. 2000). Ammonia (NH_3) oxidation, the first and rate-limiting step of nitrification where NH_3 is first oxidized to hydroxylamine (NH_2OH) and then to nitrite (NO_2^-), is primarily performed by a phylogenetically constrained group of obligate chemoautotrophic *Proteobacteria* (ammonia-oxidizing bacteria; AOB) and *Thaumarchaetoa* (ammonia-oxidizing archaea; AOA) (Hayatsu et al. 2008). In contrast, denitrification is a phylogenetically broad facultative process carried out by a consortium of bacteria, archaea, and fungi (Schimel and Gulledge 1998) and generally correlates with microbial diversity metrics (Graham et al. 2016). This suggests that microbial community structure, including composition and diversity (Graham et al. 2016; Philippot et al. 2013; Cavigelli and Robertson 2000), as well as activity or dormancy (Blagodatskya and Kuzyakov 2013) can influence soil N emissions. Assessing changes in microbial community structure (composition and diversity) may help characterize N emission pulses and their potential response to increasing atmospheric N inputs (Hall et al. 2018).

One way to assess changes in microbial community structure is through DNA amplicon sequencing of universal genes such as the 16S rRNA gene for bacteria and archaea. This approach can capture broad-scale taxonomic changes in microbial community structure, including changes in richness and relative abundance of particular taxa of interest. Assessing functional gene abundance may also help characterize N emission pulses and their response to atmospheric N inputs. The *amoA* functional gene encodes the α-subunit of the ammonia monooxygenase enzyme in AOA and AOB, and is used for molecular assessment of these chemoautotrophic taxa (Leininger et al. 2006). Atmospheric and experimental N inputs to soils generally increase *amoA* functional gene abundance, often favoring AOB over AOA (Carey et al. 2016). Since AOB produce significantly more NO (Mushinski et al. 2019) and N_2O (Liu et al. 2017) than AOA, soil N emissions may increase under chronic N inputs. However, long-term N enrichment in one desert ecosystem increased AOA over AOB with associated increases in NH_3 oxidation (Marusenko et al. 2015). Soil microbial activity and composition also differ within hours to days after wetting dry soils, which may also affect N cycling (Placella et al. 2012; Šťovíček et al. 2017). How microbial community structure and functional gene abundance respond to both increasing N deposition and wetting may help explain the magnitude of N emission pulses.

Quantifying how chronic N inputs alter N emissions through changes in microbial community structure and function remains challenging, especially because increasing N availability may also influence N emissions through other mechanisms. For example, experimentally adding N often increases N_2O (Aronson and Allison 2016; Aronson et al. 2019; Gu et al. 2019) and NO emissions (Hartley and Schlesinger 2000; Vourlitis et al. 2015). However, adding N may also acidify soils (Vitousek et al. 1997) and increase plant biomass (Rao and Allen 2010), both of which can constrain the mechanisms producing N gases (Homyak et al. 2016; Li et al. 2018). To address some

of the uncertainties governing dryland N emissions following wetting and responses to atmospheric N deposition we ask: (1) What is the magnitude of NO_x and N_2O emission pulses after wetting dry desert soils? (2) Are the pulses related to changes in microbial community structure? And (3) do chronic atmospheric N inputs produce higher soil N emissions?

To answer these questions, we conducted field experiments in two desert sites 30 km apart but differing in atmospheric N deposition by ~ sixfold. At each site, we wetted dry soils with and without experimentally adding N, and measured NO_x and N_2O emission pulses, changes in microbial community composition and richness, and *amoA* gene copy numbers. We hypothesized that: (1) pulses of N trace gas emissions would be large; (2) chronic N deposition would reduce microbial species richness, increase the relative abundance of nitrifier communities, and favor AOB over AOA; and (3) emissions would be limited by N and increase with *amoA* gene copy numbers, nitrifier relative abundance, microbial diversity, and rates of atmospheric N deposition. Field tests of these hypotheses will help quantify N trace gas emission rates from desert soils, a key uncertainty in desert N budgets (Peterjohn and Schlesinger 1991), and inform how increasing rates of atmospheric N deposition in drylands may affect soil microbiomes and N emissions with implications for ecosystem function, air quality, and climate.

Materials and methods

Study sites

We selected two desert sites along a gradient of atmospheric N deposition generated by the Los Angeles, CA, USA metropolis. The Low N deposition site is located in Boyd Deep Canyon Desert Research Center (BDC), a part of the University of California Natural Reserve System (UCNRS) near Palm Desert, CA. The High N deposition site is located in Oasis de los Osos, another site in the UCNRS located at the north face of the San Jacinto Mountains. Both sites are located within the Colorado Desert, with hot summers and occasional precipitation occurring primarily during winter. Soils at the Low N site are classified as hyperthermic Typic Torriorthents; they are stony sands mapped within the Carrizo series. Soils at the High N site are classified as thermic Typic Xeropsamments; they are gravelly loamy sands mapped within the Tujunga series. Creosote bush scrub (*Larrea tridentata*) is dominant at both sites with larger shrubs and interspaces between shrubs populated by more extensive annual herbaceous plants at the High N Deposition than at the Low N Deposition site.

Rates of atmospheric N deposition were higher at the High N (12.8 kg N ha^{-1} y^{-1} for throughfall and 2.3 kg N ha^{-1} y^{-1} for bulk deposition; Supplementary Materials 1; Fenn and Poth 2004) than at the Low N deposition site (2.2 kg N ha^{-1} y^{-1} for throughfall and 1.5 kg N ha^{-1} y^{-1} for bulk deposition; *t*-test $p < 0.001$). At both sites, N deposition was higher under the canopy (throughfall) of *Larrea tridentata* than in the interspaces (bulk) between shrubs ($p < 0.0001$) and was roughly composed of equal parts of ammonium (NH_4^+) and nitrate (NO_3^-; $p > 0.05$). In contrast to N deposition between sites, total soil C and N was similar between the High and Low N deposition sites with no significant differences detected (Table 1; $p > 0.05$). Soil inorganic N (sum of NO_2^- and $NO_3^- + NH_4^+$) was not significantly different between the High (67.2 μg g^{-1} winter; 34.5 μg g^{-1} summer) than at the Low (77.8 μg g^{-1} winter; 12.1 μg g^{-1}) N deposition site. These differences were observed in summer ($p > 0.05$, although sample size was limited at Low N deposition, $n = 3$) when inorganic N was 34.5 μg g^{-1}at the High and 12.5 μg g^{-1} at the Low N deposition site. Nitrate was the dominant form of soil inorganic N at both sites during both winter and summer. Soil pH differed between the two sites ($p = 0.004$) and was more acidic at the High (6.6 pH) than the Low N deposition site (8.0 pH).

Experimental design

Field experiments were conducted in July 1–15, 2014, months before the onset of the wet season (Oct – Apr), and when daily peak air temperature exceeded 40 °C. At both sites we established six replicate plots under the canopy of creosote bushes (*Larrea tridentata*) to capture N dynamics in soils known to be active "hot spots" of biogeochemical cycling. At each plot, four PVC collars (30 cm diameter by 15 cm height) were spaced ~ 20 cm apart from each other and driven ~

Table 1 Site differences (mean, standard deviation) for deposition, climate, and soil properties (0–10 cm depth)

	Variable	Low N deposition	High N deposition
N Dep	Throughfall N Deposition (kg N ha^{-1} y^{-1})*	2.2 (0.5)	12.7 (3.3)
Clim	Mean Ann. Max. T (°C)	41.1	40.6
	MAP (mm)	145	139
Soil	Texture	Sand	Loamy Sand
	Total C (mg C g^{-1})	11.4 (5.8)	8.1 (3.4)
	Total N (mg N g^{-1})	1.8 (0.5)	1.5 (0.3)
	Inorganic N (μg g^{-1}) Winter	77.8 (26.8)	67.2 (53.6)
	Inorganic N (μg g^{-1}) Summer	12.1 (9.8)	34.5 (28.1)
	pH*	8.0 (0.3)	6.6 (0.3)

*Denotes significant difference between Low and High N Deposition site ($p<0.05$)

10 cm into the soil approximately two weeks before the start of our measurements. Two of the four collars were irrigated with deionized water to simulate a 2 cm rainfall event, a high intensity rain event but consistent with the range of event totals in the region. The remaining two collars were similarly irrigated but with an additional N enrichment (water + N; 30 kg N ha^{-1}, as H_4NO_3, equivalent to 10.5 kg N ha^{-1}). One collar for each irrigation treatment was used exclusively for trace gas measurements, while the other collar was used to sample soils for microbial characterization (n = 6 for both trace gases and microbial community analyses).

The experiments were initiated at approximately 7 am. Soil trace gas fluxes were measured before wetting ("Pre"), and then at 15 min, 12 h, and 24 h after adding water or water + N. Sampling periods were chosen based on studies showing rapid changes in both N trace gas emissions (Homyak et al. 2016) and microbial community structure (Placella et al. 2012). At each sampling time, soil temperature was recorded at 0–5 cm with a ProCheck Sensor equipped with GS3 probe (Decagon Device, Inc Pullman. WA) and soil moisture was measured from 0–10 cm with a handheld water content probe (HCS620 HydroSense, Campbell Scientific, Inc. Logan, CO) calibrated for our sites.

Microbial community assessments

At each trace gas sampling time, and also at 2 h and 48 h post-wetting, soils were cored (5 cm depth) from replicate collars adjacent to those used to measure N emissions after irrigating with water and water + N. The additional temporal soil samples were collected to improve characterization of microbial community dynamics. In the field, soils were stored in sterile Whirlpak bags (Nasco Inc. Atkinson, WI, USA) and placed inside a cooler with dry ice and then transported to the laboratory where they were frozen at − 20 °C until extraction. We extracted microbial DNA, which was sequenced for the 16S rRNA gene on the Illumina MiSeq platform (Illumina Inc., San Diego, CA, USA) at the UCR Genomics Core Facility (Supplementary Material 2; Klindworth et al. 2013). With the same soil extracts, we used Quantitative Polymerase Chain Reaction (qPCR) to quantify the amount of bacterial and archaeal *amoA* (Supplementary Material 2; Rotthauwe et al. 1997; Beman et al.2008).

Trace gas fluxes

Soil collars were fitted with a custom-made PVC chamber lid with a mixing fan mounted on the inside and reflective tape covering the outside of the chamber (Davidson et al. 1990; Oikawa et al. 2015). A 30 cm diameter by 15 cm tall collar was used for N trace gas measurements. Air was pulled from the chamber top at approximately 1 L min^{-1} and routed sequentially to analyzers to measure concentrations of N_2O and NO. N_2O concentrations were measured with cavity-enhanced laser absorption spectroscopy with a tunable diode laser (Model 908–0014, Los Gatos Research, Inc. Mountain View, CA, USA). The outflow of the N_2O analyzer was routed to a NO monitor (Model 410 and Model 401, 2B Technologies, Boulder CO), where the quantitative depletion of ozone was measured using UV absorbance. This system also uses a molybdenum converter, which converts all nitrogen

dioxide (NO_2) to nitric oxide (NO), before sending sample air to the NO monitor and therefore measurements are expressed as NO_x flux (NO + NO_2). Soil N fluxes were calculated using the rate of increase in NO_x or N_2O concentration, which was quantified by linear regression using $\sim$ 3 min of data to maximize linearity of gas production (Davidson 1990).

Statistical analysis

Microbial communities were annotated bioinformatically using the Quantitative Insights Into Microbial Ecology (QIIME) platform against the Greengenes database (Supplementary Material 2; Price et al. 2009; Caporaso et al. 2010; Edgar 2010; McDonald et al. 2012; Bokulich et al. 2013). To assess alpha diversity of the microbial community, we calculated the number of observed operational taxonomic units (OTUs) for each sample in QIIME and performed a three-way ANOVA including main and interactive effects of site, treatment, and time since wetting. If interactive effects were non-significant, we removed them and re-ran the model. We assessed beta diversity using non-metric multidimensional scaling (NMDS) of the weighted UniFrac distance calculated in QIIME, which incorporates information about phylogenetic distance between pairs of samples using the phylogenetic tree (Lozupone and Knight 2005). Differences in overall microbial community composition across site, treatment, and time points were assessed with permutational multivariate ANOVA (perMANOVA) implemented using the Vegan function 'adonis' in R (999 permutations) (McArdle and Anderson 2001). These steps were conducted twice: once for the overall microbial community (all taxa) and once for nitrifying taxa only (Nitrosomonadales, Nitrospira, Thaumarcheota). To further analyze the nitrifying microbial community, we assessed the overall relative abundance of nitrifying taxa within each sample using an ANOVA approach, same as above. We also used an ANOVA to determine how short and long-term N additions influenced the abundance of AOA and AOB; specifically, we compared amoA gene abundances between sites, treatments, and timepoint (pre-wettup and 48 h only). Combined, these approaches allowed us to determine whether nitrifying microbial communities were significantly affected by any of the factors included in our study.

We related variations in microbial community composition to N fluxes within and across sites by regressing fluxes with the first NMDS axis of the weighted UniFrac distances, nitrifier community abundance, and *amoA* gene abundances to N_2O and NO_x fluxes. The BoxCox family of transformations was used to fulfill assumptions of normality and homoscedacity where necessary. All statistical analysis was performed in R version 3.2.1 (R Development Core Team 2015).

Results

Soil microbial dynamics

Microbial community diversity and composition differed between the High and Low N sites and in response to adding water and water + N. Overall richness of operational taxonomic units (OTUs) was higher at the Low than at the High N deposition site (site, $p < 0.0001$; Fig. 1a). The site effect was more pronounced when comparing across the water + N treatment relative to adding only water (site × treatment interaction, $p = 0.04$; Fig. 1a). For the nitrifier community, OTU richness also differed by site, with the Low N deposition site harboring richer communities (site, $p = 0.04$; Fig. 1b).

In addition to differences in richness, the microbial communities at both sites were distinct in composition. This was true when taking into account all taxa (site, $p < 0.001$; Fig. 1c) or just the nitrifying taxa (site, $p < 0.001$; Fig. 1d). Site also influenced how the microbial community responded to wetting soils with water or water + N (site × treatment interaction, $p = 0.004$), a pattern that was not observed for nitrifiers only (site × treatment interaction, $p > 0.05$). In contrast to nitrifier OTU richness, the relative abundance of nitrifiers was greater at the High than the Low N deposition site ($p = 0.002$; Fig. 1e). The pattern was driven primarily by the higher relative abundance AOB over AOA, as the relative abundance of *Thaumarchaeota* was on average 149% lower at the High than at the Low N deposition site ($p < 0.0001$). The absolute abundance of total *amoA* genes was also greater at the High than at the Low N deposition site ($p = 0.03$). When separating AOA and AOB *amoA* gene abundances, AOA were greatest at the Low N

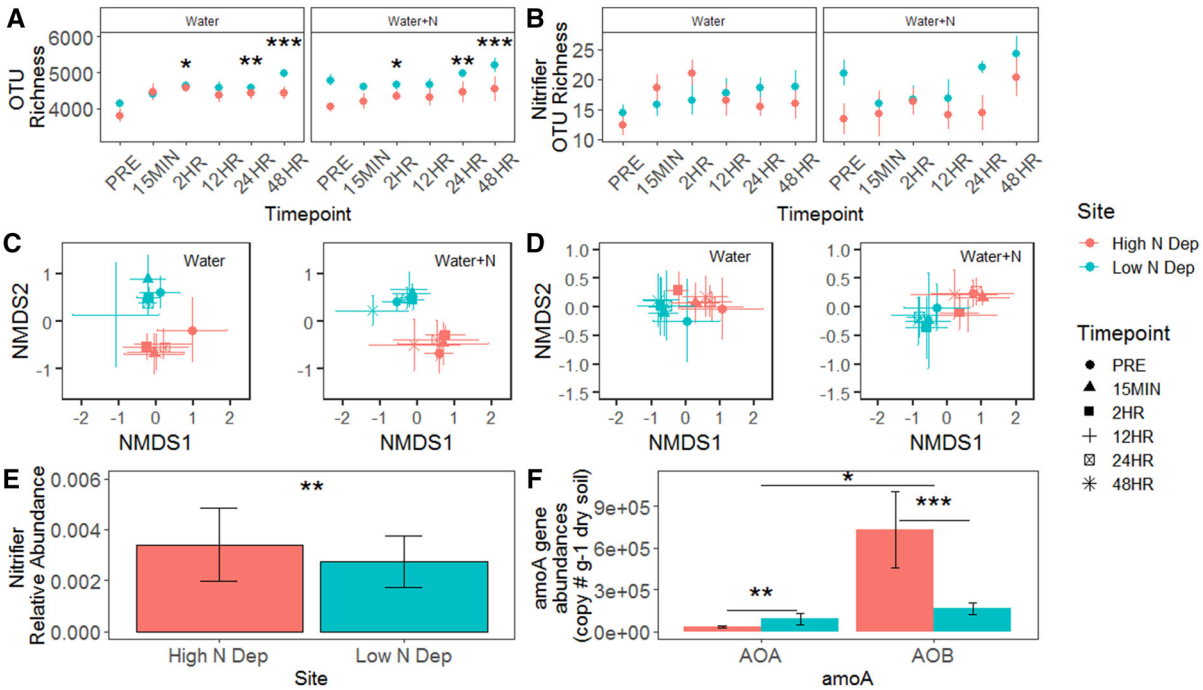

Fig. 1 Microbial community responses to wetting with and without added N across High and Low N deposition sites: **a** overall and **b** nitrifier OTU richness (* denote significant differences compared to pre-wetting samples); NMDS of weighted UniFrac distance for **c** overall and **d** nitrifier community composition; **e** relative abundance of nitrifiers and **f** AOA and AOB amoA gene abundances averaged across time. For **a**, **b**, **e**, and **f** error bars = ± 1 SE of the mean. For **c** and **d**, error bars = 95% confidence intervals. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

deposition site ($p = 0.01$), whereas AOB were greatest at the High N deposition site ($p < 0.001$; Fig. 1f).

The effects of wetting soils on overall OTU richness varied according to site, with richness at the Low N deposition site (but not the High N deposition site) increasing more strongly after adding water + N than after adding water alone (site × treatment interaction, $p = 0.04$). Moreover, while overall OTU richness increased within two hours of wetting (for both water and water + N), and generally remained elevated compared to pre-wetting levels over time (time, $p < 0.001$; Fig. 1a), this was not the case for nitrifier OTU richness (treatment, $p > 0.05$; time, $p > 0.05$; Fig. 1b) or the relative abundance of nitrifiers within the community (treatment, $p > 0.05$, time, $p > 0.05$). *3.2. Soil N emissions.*

NO_x and N_2O emissions were low (0.8 ng NO_x-N m^{-2} s^{-1} and 1.0 ng N_2O-N m^{-2} s^{-1}) in dry soils and did not differ between the Low and High N deposition sites (Fig. 2; $p > 0.05$). However, adding water produced both NO_x and N_2O emission pulses that differed in the amount of N emitted and the timing and duration of peak emissions (Fig. 2). NO_x emission pulses were higher at the Low than at the High N deposition site ($p < 0.0001$); they rose as high as 345 ng NO_x-N m^{-2} s^{-1} within 12 h of wetting and remained elevated for at least 24 h at both sites. Experimentally adding water + N increased NO_x emissions at both the High ($p = 0.003$) and Low ($p = 0.03$) N deposition sites relative to adding water alone. In contrast to NO_x emissions, N_2O emission pulses were short-lived (Fig. 2). Peak N_2O emission rates were measured at the 15-min sampling timepoint post-wetting (up to 1725 ng N_2O-N m^{-2} s^{-1}) and declined within 12 h, although the fluxes after 12 h remained elevated relative to dry soils ($p < 0.0001$). Consistent with NO_x emissions, N_2O emission pulses were lower at the High than at the Low N deposition site ($p < 0.0001$). Unlike NO_x emissions, adding water + N did not change N_2O emissions relative to adding water alone at either the High ($p = 0.49$) or Low ($p = 0.2$) N deposition sites.

We did not detect correlations between the NMDS1 axis and NO_x or N_2O emissions within or across sites

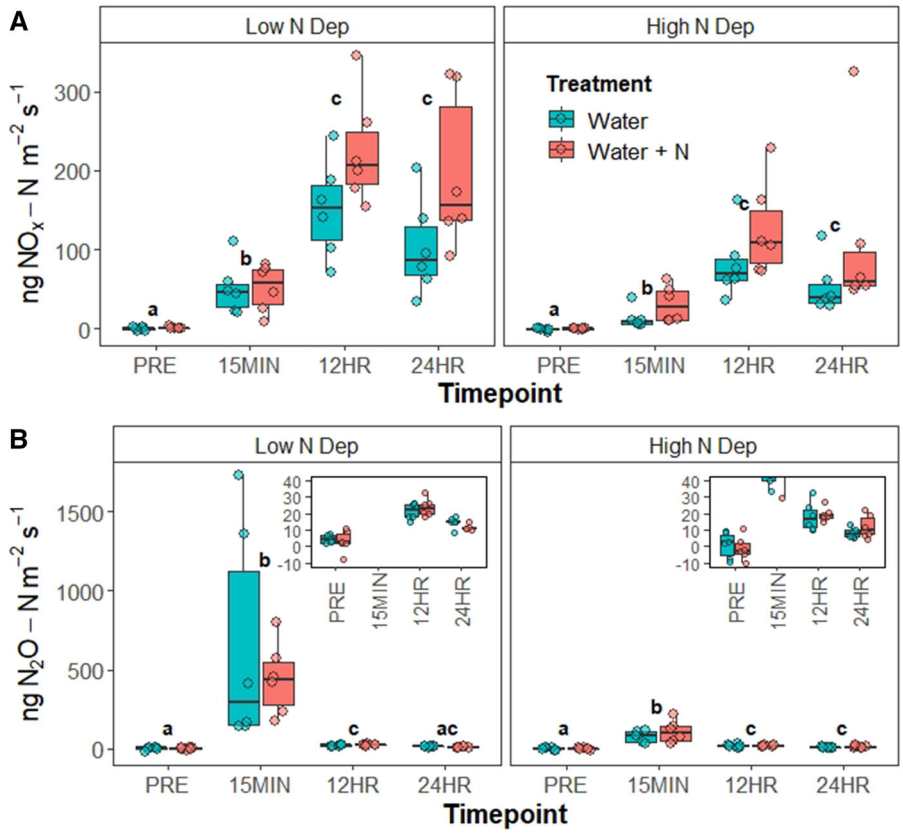

Fig. 2 Soil **a** NO_x and **b** N_2O emissions before ("Pre") and after adding water and water + N at the Low and High N deposition sites. Inset shows the N emissions outside the 15-min peak. Box plots represent the median and interquartile range of our measurements (circles). Letters represent significant differences between time points within a site for both treatments ($p < 0.05$)

nor did we detect correlations between *amoA* gene abundances and NO_x or N_2O emissions ($p > 0.05$).

Discussion

We designed our study to assess the magnitude of desert NO_x and N_2O emission pulses, whether the pulses were related to changes in microbial community diversity and richness, and whether N emissions were stimulated by N deposition. Wetting dry desert soils produced large emission pulses of NO_x and N_2O. These emission patterns could not be explained by the measured microbial metrics, despite strong differences in microbial community structure between sites and in response to wetting. Contrary to our hypothesis that increased N deposition would alleviate N limitation of emissions, we found that both NO_x and N_2O emissions were lower at the High than at the Low N deposition site.

Structural response of the soil microbial community to N deposition

We found support for our hypothesis that chronic N deposition would reduce microbial species richness, favor nitrifier communities, and increase the presence of AOB relative to AOA. In particular, the High N deposition site had lower OTU richness, consistent with a recent meta-analysis demonstrating that high N inputs reduce bacterial richness (Wang et al. 2018). We also observed that communities at the High N site had higher relative abundances of nitrifiers and greater *amoA* gene abundances with an increasing AOB/AOA ratio. Similar patterns have been reported elsewhere (Carey et al. 2016; Ying et al. 2017), and they suggest

an increased capacity for nitrification (Prosser and Nicol 2012) and potential to increase N emissions (Mushinski et al. 2019) with increasing N deposition. However, these differences could be either a direct response to N deposition or an indirect effect of other site differences, such as increased soil acidity that can result from N deposition (Fierer and Jackson 2006; Zeng et al. 2016; Li et al. 2018). While AOA would conceivably be favored at low pH (Zhang et al. 2012), changes in pH can have large and varied effects on microbial communities, including reducing microbial diversity (Zeng et al. 2016). The site-level differences in our study echo previous findings that suggest desert microbial communities are sensitive to N deposition.

Microbial structure also changed after experimentally adding water or water + N. Overall OTU richness increased by an average of 14% after 48 h following wetting. Measuring an increase in OTU richness after adding N is opposite to what we observed under long-term N deposition, and contrary to our hypothesis that N inputs reduce richness (Wang et al. 2018; Šťovíček et al. 2017). Possibly, a one-time 2-cm wetting event with and without 30 kg N ha^{-1} is not a large enough disturbance to cause negative effects, instead releasing microbes from water and N limitation while increasing community richness. Alternatively, changes in richness may not be linear and 48 h may not be enough time to observe effects that emerge over longer time scales (Shade et al. 2012). Treatment-induced increases in richness were accompanied by broadscale shifts in microbial community composition (as shown by ordination and perMANOVA) at both sites, and an increase in AOA *amoA* gene abundances at the High N deposition site. However, in general, changes in community composition with time were not predictable and did not show a clear trend, implying that compositional turnover was not systematically following a trajectory after adding water and N.

Desert N emission responses to experimental wetting and N addition

The timing of peak emissions and response to experimentally adding N suggest different mechanisms governed NO_x and N_2O emission pulses. Two observations suggest microbial processes controlled NO_x emissions following wetting: (1) the timing of peak NO_x emissions occurred 12 h post-wetting, a period consistent with the time required by microbes to recover from dormancy (Blagodatskaya and Kuzyakov 2013) and nitrify (Homyak et al. 2016), and (2) adding NH_4NO_3 stimulated this response. In contrast to NO_x, the nearly instantaneous N_2O emission pulse, and insensitivity to adding NH_4NO_3, suggests processes other than nitrification and/or denitrification, perhaps abiotic, controlled these emissions. Rapid displacement of pore gas space has been suggested for some trace gas emission pulses, but in the sandy soils at our sites, the accumulation of enough N_2O within the pore space to account for emissions is unlikely. Alternatively, chemodenitrification, the abiotic and non-enzymatic production of N trace gases from reactive N intermediates (Heil et al. 2016), can be an important pathway in drylands (Homyak et al. 2017; Wang et al. 2017) and may be responsible for the high rates of N_2O produced within 15 min of wetting and their insensitivity to adding NH_4NO_3. While different mechanisms may have governed the production of NO_x and N_2O, both can be tied to microbial processes that either generate the N emissions directly or through the production of reactive N intermediates.

Although we measured differences in microbial communities between the Low and High N deposition sites and variable changes in microbial community structure within hours post-wetting, we found no correlations relating these community dynamics with NO_x and N_2O emissions. The lack of a relationship between microbial composition and NO_x emissions does not mean the process is not biotically controlled; instead, it may reflect a temporal disconnect between changes in microbial community activity, process rates, and associated community composition, with the latter taking more time to accrue discernable shifts (Bier et al. 2015). In the case of N_2O, this may be because emissions depend on the accumulation of reactive N intermediates (e.g. NO_2^- and NH_2OH), and their abiotic decomposition. Relationships between the dynamics of microbial community structure and N trace gas emissions may also be diluted because of relic and dormant DNA captured by the sequencing technology (Lennon and Jones 2011; Lennon et al. 2018). Evaluating combinations of mRNA expression activities and additional N cycling genes (Graham et al. 2016) may provide a more robust approach for linking microbial processes with N emissions.

N deposition and N emissions: higher emissions at the low N deposition site

We found that N emissions were lower at the High N deposition site. While unexpected because of the general N limitation of dryland ecosystem processes and N emissions in particular, the lack of soil N emission stimulation by increased N inputs is consistent with previous studies showing encroachment by N-fixing trees did not increase N trace gas emissions (Soper et al. 2016). Possibly, differences in plant N uptake, soil pH, and/or microbial N use between sites may constrain N availability and help explain why higher rates of atmospheric N deposition did not translate into higher soil N emissions. The larger shrub cover and understory of herbaceous plants at the High N site, consistent with desert responses to elevated N deposition (Rao and Allen 2010), may have increased plant N uptake relative to the Low N site, lowering soil N availability and N emissions (Homyak et al. 2016). Alternatively, the lower pH at the High N deposition site, also consistent with soil responses to N deposition (Fenn et al. 1998), may reduce the availability of NH_3 and constrain nitrification (Li et al. 2018). Finally, the greater relative abundance of nitrifiers measured at the High N deposition site may imply reactive N intermediates (e.g. NO_2^- and NH_2OH) may be more efficiently transferred between nitrifiers, thereby minimizing their extracellular accumulation in drying soils and their potential to chemodenitrify (Homyak et al. 2017). While N deposition did not stimulate greater N emission pulses, indirect effects of N deposition along with site differences in plant biomass, soil acidity, and efficient transfer of reactive intermediates between nitrifiers may help explain the patterns we observed. A better characterization of N deposition effects on N emissions remains an important research need.

Implications for desert N cycling

Our field measurements are among the largest instantaneous N emission rates observed from soils. Relative to other field studies (Supplementary Material 3), peak emissions of N_2O at our desert sites were greater than in grazing lands (Smith et al. 1994; Teh et al. 2011; Cowan et al. 2015), tropical rain forests (Hall and Matson 2003; Holtgrieve et al. 2006), tropical dry forests (Davidson et al. 1993); grasslands (Leitner et al. 2017; Niboyet et al. 2011), and urbanized ecosystems (Hall et al. 2008; Townsend-Small and Czimczik 2010). The only higher peak emissions of N_2O we identified, were observed from ant refuse mounds in a tropical forest (Soper et al. 2019). Similarly, our peak NO_x emissions exceed those measured in tropical wet forests (Hall and Matson 2003; Holtgrieve et al. 2006), tropical dry forests (Davidson et al. 1991), urban soils (Hall et al. 2008), and grasslands (Leitner et al. 2017), but were exceeded by those measured in the Chihuahuan desert (Hartley and Schlesinger 2000), a chaparral ecosystem (Homyak and Sickman 2014) and especially by those from a high-temperature agroecosystem (Oikawa et al. 2015). These comparisons suggest peak N emissions after wetting dry soils can be substantial in deserts, a finding consistent with large denitrification potentials (Peterjohn and Schlesinger 1991) and NO emissions measured in other drylands (Hartley and Schlesinger 2000; Homyak and Sickman 2014). While it is clear these emissions can be substantial, their implications for ecosystem N budgets remain uncertain.

To assess the potential contribution of NO and N_2O emission pulses to desert N budgets, we used trapezoidal integration to calculate the average mass of N emitted over a 24 h period across our two sites (we excluded the water + N treatment from our calculations). Using this approach, we estimate 7.3 mg NO_x-N m^{-2} and 8.0 mg N_2O-N m^{-2} are emitted over 24 h after wetting dry soils. We then multiplied the mass of N emitted by the average number of precipitations events exceeding 5 mm in a year at our Low N deposition site (6.7 days using a 10-year record; Boyd Deep Canyon Research long-term weather data) yielding 0.049 g NO_x-N m^{-2} yr^{-1} and 0.059 g N_2O-N m^{-2} yr^{-1}. Relative to throughfall N deposition measured at our sites, these potential N emissions represent 49% of atmospheric N inputs at the Low N Deposition site and 9% of atmospheric N inputs at the High N deposition site. Relaxing these criteria by expanding the N emitted from soils to 48 h (and assuming emissions ceased at this time) and using a precipitation threshold of 2 mm, we estimate N emissions could remove 102% of atmospheric N inputs at the High N deposition site and 18% of atmospheric N inputs at the Low N deposition site. Improving this estimate will require better assessment of emissions across seasons, precipitation timing effects, temperature, and N deposition. Nevertheless,

this initial scaling suggests soil N emissions are large components of the desert N cycle consistent with predictions of desert N budgets (Peterjohn and Schlesinger 1990) and highlights the potential for N emissions to help explain widespread N limitation across drylands.

Conclusions

We show that desert soils can produce large NO_x and N_2O emission pulses, and that while microbial communities respond as predicted to elevated N deposition, higher N inputs do not necessarily produce higher soil N emissions. This suggests soil N emissions are predominantly controlled by site-specific factors and not by direct stimulation of long-term N deposition. The site-specific factors (e.g. increased herbaceous plants and lower soil pH) may nevertheless still reflect ecosystem responses to elevated N deposition (Zeng et al. 2016) and complicate predictions of dryland N emissions. How biotic and abiotic processes interact to control N emission pulses is still not well understood and will require new techniques that evaluate the rates and magnitudes that microbes recover from drought stress and process N, as well as better characterizing emission pathways. Regardless of the underlying mechanism, large N emission pulses from dryland ecosystems may contribute to sustained N limitation with potential implications for atmospheric chemistry and Earth's climate.

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References

Aronson EL, Goulden ML, Allison SD (2019) Greenhouse gas fluxes under drought and nitrogen addition in a Southern California grassland. Soil Biol Biochem 131:19–27

Beman JM, Popp BN, Francis CA (2008) Molecular and biogeochemical evidence for ammonia oxidation by marine Crenarchaeota in the Gulf of California. ISME J 2:429–441

Bier RL et al (2015) Linking microbial community structure and microbial processes: an empirical and conceptual overview. FEMS Microbiol Ecol. https://doi.org/10.1093/femsec/fiv113

Blagodatskaya E, Kuzyakov Y (2013) Active microorganisms in soil: Critical review of estimation criteria and approaches. Soil Biol Biochem 67:192–211

Bokulich NA, Subramanian S, Faith JJ, Gevers D, Gordon JI, Knight R, Mills DA, Caporaso JG (2013) Quality-filtering vastly improves diversity estimates from Illumina amplicon sequencing. Nat Methods 10:57–U11

Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK et al (2010) QIIME allows analysis of high-throughput community sequencing data. Nat Methods 7:335–336

Carey CJ, Dove NC, Beman JM, Hart SC, Aronson EL (2016) Meta-analysis reveals ammonia-oxidizing bacteria respond more strongly to nitrogen addition than ammonia-oxidizing archaea. Soil Biol Biochem 99:158–166

Conrad R (1996) Soil microorganisms as controllers of atmospheric trace gases (H-2, CO, CH4, OCS, N2O, and NO). Microbiol Rev 60:609–640

Cowan NJ, Norman P, Famulari D, Levy PE, Reay DS, Skiba UM (2015) Spatial variability and hotspots of soil N2O fluxes from intensively grazed grassland. Biogeosciences 12:1585–1596

Crutzen PJ (1979) Role of NO and NO2 in the Chemistry of the Troposphere and Stratosphere. Annu Rev Earth Pl Sc 7:443–472

Davidson EA, Vitousek PM, Matson PA, Riley R, Garciamendez G, Maass JM (1991) Soil emissions of nitric-oxide in a seasonally dry tropical forest of Mexico. Journal of Geophysical Research-Atmospheres 96:15439–15445

Davidson EA, Keller M, Erickson HE, Verchot LV, Veldkamp E (2000) Testing a conceptual model of soil emissions of nitrous and nitric oxides. Bioscience 50:667–680

Edgar RC (2010) Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26:2460–2461

Fenn ME, Poth MA, Aber JD, Baron JS, Bormann BT, Johnson DW, Lemly AD, McNulty SG, Ryan DE, Stottlemyer R (1998) Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. Ecol Appl 8:706–733

Fenn ME et al (2003) Nitrogen emissions, deposition, and monitoring in the western United States. Bioscience 53:391–403

Fenn ME, Jovan S, Yuan F, Geiser L, Meixner T, Gimeno BS (2008) Empirical and simulated critical loads for nitrogen deposition in Californiamixed conifer forests. Environ Pollut 155:492–511

Fenn ME, Poth MA (2004) Monitoring nitrogen deposition in throughfall using ion exchange resin columns: A field test in the San Bernardino Mountains. J Environ Qual 33:2007–2014

Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. Proc Natl Acad Sci USA 103:626–631

Graham EB et al (2016) Microbes as Engines of Ecosystem Function: When Does Community Structure Enhance Predictions of Ecosystem Processes? Frontiers in Microbiology. https://doi.org/10.3389/fmicb.2016.00214

Gu XY, Wang YH, Laanbroek HJ, Xu XF, Song B, Huo YW, Chen SP, Li LH, Zhang LH (2019) Saturated N2O emission

rates occur above the nitrogen deposition level predicted for the semi-arid grasslands of Inner Mongolia, China. Geoderma 341:18–25
Hall SJ, Matson PA (2003) Nutrient status of tropical rain forests influences soil N dynamics after N additions. Ecol Monogr 73:107–129
Hall SJ, Huber D, Grimm NB (2008) Soil N2O and NO emissions from an arid, urban ecosystem. Journal of Geophysical Research-Biogeosciences. https://doi.org/10.1029/2007jg000523
Hall SJ, Silver WL, Amundson R (2012) Greenhouse gas fluxes from Atacama Desert soils: a test of biogeochemical potential at the Earth's arid extreme. Biogeochemistry 111:303–315
Hall EK et al (2018) Understanding how microbiomes influence the systems they inhabit. Nature Microbiology 3:977–982
Hartley AE, Schlesinger WH (2000) Environmental controls on nitric oxide emissions from northern Chihuahuan desert soils. Biogeochemistry 50:279–300
Hayatsu M, Tago K, Saito M (2008) Various players in the nitrogen cycle: Diversity and functions of the microorganisms involved in nitrification and denitrification. Soil Science and Plant Nutrition 54:33–45
Heil J, Vereecken H, Bruggemann N (2016) A review of chemical reactions of nitrification intermediates and their role in nitrogen cycling and nitrogen trace gas formation in soil. Eur J Soil Sci 67:23–39
Holtgrieve GW, Jewett PK, Matson PA (2006) Variations in soil N cycling and trace gas emissions in wet tropical forests. Oecologia 146:584–594
Homyak PM, Sickman JO (2014) Influence of soil moisture on the seasonality of nitric oxide emissions from chaparral soils, Sierra Nevada, California, USA. J Arid Environ 103:46–52
Homyak PM, Blankinship JC, Marchus K, Lucero DM, Sickman JO, Schimel JP (2016) Aridity and plant uptake interact to make dryland soils hotspots for nitric oxide (NO) emissions. Proc Natl Acad Sci USA 113:E2608–E2616
Homyak PM, Kamiyama M, Sickman JO, Schimel JP (2017) Acidity and organic matter promote abiotic nitric oxide production in drying soils. Glob Change Biol 23:1735–1747
Jenerette GD, Chatterjee A (2012) Soil metabolic pulses: water, substrate, and biological regulation. Ecology 93:959–966
Klindworth A, Pruesse E, Schweer T, Peplies J, Quast C, Horn M, Glockner FO (2013) Evaluation of general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based diversity studies. Nucleic Acids Res. https://doi.org/10.1093/nar/gks808
Leininger S, Urich T, Schloter M, Schwark L, Qi J, Nicol GW, Prosser JI, Schuster SC, Schleper C (2006) Archaea predominate among ammonia oxidizing prokaryotes in soils. Nature. https://doi.org/10.1038/nature04983
Leitner S, Homyak PM, Blankinship JC, Eberwein J, Jenerette GD, Zechmeister-Boltenstern S, Schimel JP (2017) Linking NO and N2O emission pulses with the mobilization of mineral and organic N upon rewetting dry soils. Soil Biol Biochem 115:461–466
Lennon JT, Jones SE (2011) Microbial seed banks: the ecological and evolutionary implications of dormancy. Nat Rev Microbiol 9:119–130
Lennon JT, Muscarella ME, Placella SA, Lehmkuhl BK (2018) How, when, and where relic DNA affects microbial diversity. mBio 9:e00637–e718. https://doi.org/10.1128/mBio.00637-18
Li YY, Chapman SJ, Nicol GW, Yao HY (2018) Nitrification and nitrifiers in acidic soils. Soil Biol Biochem 116:290–301
Liu S et al (2017) Abiotic conversion of extracellular NH2OH contributes to N2O emission during ammonia oxidation. Environ Sci Technol 51:13122–13132
Lozupone C, Knight R (2005) UniFrac: a new phylogenetic method for comparing microbial communities. Appl Environ Microbiol 71:8228–8235
Marusenko, Y., F. Garcia-Pichel, S.J. Hall. (2015) Ammonia-oxidizing archaea respond positively to inorganic nitrogen addition in desert soils, FEMS Microbiology Ecology 1–11.
McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82:290–297
McDonald D, Price MN, Goodrich J, Nawrocki EP, DeSantis TZ, Probst A, Andersen GL, Knight R, Hugenholtz P (2012) An improved Greengenes taxonomy with explicit ranks for ecological and evolutionary analyses of bacteria and archaea. ISME J 6:610–618
Meixner FX, Yang WX (2006) Biogenic emissions of nitric oxide and nitrous oxide from arid and semi-arid land. In: D'Odorico P, Porporato A (eds) Dryland Ecohydrology. Springer, Netherlands, Dordrecht, pp 233–255
Mushinski RM, Phillips RP, Payne ZC, Abney RB, Jo I, Fei SL, Pusede SE, White JR, Rusch DB, Raff JD (2019) Microbialmechanisms and ecosystem flux estimation for aerobic NOy emissions from deciduous forest soils. Proc Nat Acad Sci USA 116:2138–2145
Niboyet A, Brown JR, Dijkstra P, Blankinship JC, Leadley PW, Le Roux X, Barthes L, Barnard RL, Field CB, Hungate BA (2011) Global Change Could Amplify Fire Effects on Soil Greenhouse Gas Emissions. PLoS ONE. https://doi.org/10.1371/journal.pone.0020105
Oerter E, Mills JV, Maurer GE, Lammers LN, Amundson R (2018) Greenhouse gas production and transport in desert soils of the southwestern United States. Global Biogeochem Cycles 32:1703–1717
Oikawa PY, Ge C, Wang J, Eberwein JR, Liang LL, Allsman LA, Grantz DA, Jenerette GD (2015) Unusually high soil nitrogen oxide emissions influence air quality in a high-temperature agricultural region. Nature Communications. https://doi.org/10.1038/ncomms9753
Peterjohn WT, Schlesinger WH (1990) Nitrogen loss from deserts in the Southwestern United-States. Biogeochemistry 10:67–79
Peterjohn WT, Schlesinger WH (1991) Factors controlling denitrification in a Chihuahuan desert ecosystem. Soil Sci Soc Am J 55:1694–1701
Philippot L, Spor A, Henault C, Bru D, Bizouard F, Jones CM, Sarr A, Maron PA (2013) Loss in microbial diversity affects nitrogen cycling insoil. ISME Jl 7:1609–1619
Placella SA, Brodie EL, Firestone MK (2012) Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. Proc Natl Acad Sci USA 109:10931–10936

Prosser JI, Nicol GW (2012) Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. Trends Microbiol 20:523–531

Price MN, Dehal PS, Arkin AP (2009) FastTree: Computing Large Minimum Evolution Trees with Profiles instead of a Distance Matrix. Mol Biol Evol 26:1641–1650

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rao LE, Allen EB (2010) Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. Oecologia 162:1035–1046

Ravishankara AR, Daniel JS, Portmann RW (2009) Nitrous oxide (N2O): the dominant ozone-depleting substance emitted in the 21st century. Science 326(5949):123–125

Rotthauwe JH, Witzel KP, Liesack W (1997) The ammonia monooxygenase structural gene amoA as a functional marker: Molecular fine-scale analysis of natural ammonia-oxidizing populations. Appl Environ Microbiol 63:4704–4712

Schimel JP, Gulledge J (1998) Microbial community structure and global trace gases. Glob Change Biol 4:745–758

Shade A, Peter H, Allison SD, Baho DL, Berga M, Bürgmann H, Huber DH, Langenheder S, Lennon JT, Martiny JBH, Matulich KL, Schmidt TM, Handelsman J (2012) Fundamentals of microbial community resistance and resilience. Frontiers in Microbiology 3:417–417

Soper FM, Boutton TW, Groffman PM, Sparks JP (2016) Nitrogen trace gas fluxes from a semiarid subtropical savanna under woody legume encroachment. Global Biogeochem Cycles 30:614–628. https://doi.org/10.1002/2015GB005298

Soper FM, Sullivan BW, Osborne BB, Shaw AN, Philippot L, Cleveland CC (2019) Leaf-cutter ants engineer large nitrous oxide hot spots in tropical forests. Proceedings of the Royal Society B: Biological Sciences 286:20182504

Smith KA, Clayton H, Arah JRM, Christensen S, Ambus P, Fowler D, Hargreaves KJ, Skiba U, Harris GW, Wienhold FG, Klemedtsson L, Galle B (1994) Micrometeorological and chamber methods for measurement of nitrous-oxide fluxes between soils and the atmosphere – an overview and conclusions. J Geophys Res-Atmos 99:16541–16548

Šťovíček A, Azatyan A, Soares MIM, Gillor O (2017) The Impact of Hydration and Temperature on Bacterial Diversity in Arid Soil Mesocosms. Frontiers in Microbiology. https://doi.org/10.3389/fmicb.2017.01078

Teh YA, Silver WL, Sonnentag O, Detto M, Kelly M, Baldocchi DD (2011) large greenhouse gas emissions from a temperate peatland pasture. Ecosystems 14:311–325

Townsend-Small A, Czimczik CI (2010) Carbon sequestration and greenhouse gas emissions in urban turf. Geophys Res Lett. https://doi.org/10.01029/02009gl041675

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: Sources and consequences. Ecol Appl 7:737–750

Vourlitis GL, DeFotis C, Kristan W (2015) Effects of soil water content, temperature and experimental nitrogen deposition on nitric oxide (NO) efflux from semiarid shrubland soil. J Arid Environ 117:67–74

von Sperber C, Chadwick OA, Casciotti KL, Peay KG, Francis CA, Kim AE, Vitousek PM (2017) Controls of nitrogen cycling evaluated along a well-characterized climate gradient. Ecology 98:1117–1129

Wang B, Lerdau M, He YL (2017) Widespread production of nonmicrobial greenhouse gases in soils. Glob Change Biol 23:4472–4482

Wang C, Liu D, Bai E (2018) Decreasing soil microbial diversity is associated with decreasing microbial biomass under nitrogen addition. Soil Biol Biochem 120:126–133

Ying JY, Li XX, Wang NN, Lan ZC, He JZ, Bai YF (2017) Contrasting effects of nitrogen forms and soil pH on ammonia oxidizing microorganisms and their responses to long-term nitrogen fertilization in a typical steppe ecosystem. Soil Biol Biochem 107:10–18

Zeng J, Liu XJ, Song L, Lin XG, Zhang HY, Shen CC, Chu HY (2016) Nitrogen fertilization directly affects soil bacterial diversity and indirectly affects bacterial community composition. Soil Biol Biochem 92:41–49

Zhang LM, Hu HW, Shen JP, He JZ (2012) Ammonia-oxidizing archaea have more important role than ammonia-oxidizing bacteria in ammonia oxidation of strongly acidic soils. ISME J 6:1032–1045

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