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REVIEW

Microbial Biogeochemical Cycling of Nitrogen in Arid Ecosystems

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SUMMARY Arid ecosystems cover ~40% of the Earth's terrestrial surface and store a high proportion of the global nitrogen (N) pool. They are low-productivity, low-biomass, and polyextreme ecosystems, i.e., with (hyper)arid and (hyper)oligotrophic conditions and high surface UV irradiation and evapotranspiration. These polyextreme conditions severely limit the presence of macrofauna and -flora and, particularly, the growth and productivity of plant species. Therefore, it is generally recognized that much of the primary production (including N-input processes) and nutrient biogeochemical cycling (particularly N cycling) in these ecosystems are microbially mediated. Consequently, we present a comprehensive survey of the current state of knowledge of biotic and abiotic N-cycling processes of edaphic (i.e., open soil, biological soil crust, or plant-associated rhizosphere and rhizosheath) and hypo/endolithic refuge niches from drylands in general, including hot, cold, and polar desert ecosystems. We particularly focused on the microbially mediated biological nitrogen fixation, N mineralization, assimilatory and dissimilatory nitrate reduction, and nitrification N-input processes and the denitrification and anaerobic ammonium oxidation (anammox) N-loss processes.

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We note that the application of modern meta-omics and related methods has generated comprehensive data sets on the abundance, diversity, and ecology of the different N-cycling microbial guilds. However, it is worth mentioning that microbial N-cycling data from important deserts (e.g., Sahara) and quantitative rate data on N transformation processes from various desert niches are lacking or sparse. Filling this knowledge gap is particularly important, as climate change models often lack data on microbial activity and environmental microbial N-cycling communities can be key actors of climate change by producing or consuming nitrous oxide (N_2O), a potent greenhouse gas.

KEYWORDS biogeochemistry, desert, drylands, soils, biological soil crusts, lithobiont, diazotrophy, nitrogen cycling

INTRODUCTION

Drylands represent ~40% of the Earth's terrestrial surface, occur on all continents, and are expanding with climate change (1). Drylands are arid environments, i.e., they present an overall deficiency in water availability. The aridity index (AI), which is the ratio of precipitation (P) to potential evapotranspiration (PET), is used to subcategorize them into hyperarid (AI $<$ 0.05), arid (0.05 $<$ AI $<$ 0.2), semiarid (0.2 $<$ AI $<$ 0.5), and dry subhumid (0.5 $<$ AI $<$ 0.65) drylands (Fig. 1). Drylands with an AI of $<$0.65 encompass various ecosystems such as scrublands, shrublands, grasslands, savannas, semideserts, and true deserts. In this context, it must be noted that most of the studies used in this review were conducted in environments ranging from semiarid to hyperarid zones. Deserts further can be subdivided into three distinct categories depending on their global climatic conditions: hot (mean annual temperature $>$ 18°C), cold (mean annual temperature $<$ 18°C), or polar (warmest month mean temperature $<$ 10°C) deserts.

Drylands are typically characterized by (i) low water availability, (ii) extreme diel and seasonal temperature ranges and fluctuations, (iii) high UV radiation, and (iv) low nutrient status (i.e., oligotrophy) (2). Due to these polyextreme conditions, microbial communities are most prevalent in islands of fertility, i.e., in specialized shielded niches such as biological soil crusts (BSCs), plant-associated environments (e.g., rhizospheres and rhizosheath/root systems), and lithic habitats, i.e., hypoliths and (chasmo/crypto)endoliths, which are microbial communities found under the ventral surface of translucent rocks or within the fissures and pores of rocks, respectively (3–6). Furthermore, since plant productivity is both temporally and spatially limited in arid ecosystems, microbial communities are the principal drivers of primary production and nutrient cycling (4, 5, 7, 8).

Nitrogen (N) is an element essential for life. Yet, despite amounting to some 4×10^{18} kg N in the form of dinitrogen (N_2) in the atmosphere (i.e., 78% of the total mean mass of the atmosphere, which has been estimated to represent 5.148×10^{18} kg) (9), nitrogen is often a limiting factor for terrestrial and aquatic ecosystem productivity (10, 11). Oceans contain approximately 1 Tg (1×10^9 kg) of N, 94% as biounavailable N_2 and much of the rest as bioavailable nitrate (NO_3^-) (12). The N lithospheric content has been estimated to range between 133×10^3 and 140×10^3 Tg N in the top 100 cm of the terrestrial surface (13). Deserts have been estimated to store 95×10^3 Tg of N (14), i.e., more than half of the terrestrial N pool. Recent evidence suggests that drylands store an even greater amount of N in large subterranean nitrate (NO_3^-) pools, representing ~10^4 kg N ha^{-1} (15, 16). Extrapolated to the global desert pavement surface area, this would represent a 5-fold increase in total N storage in desert soils. Consequently, models suggest that 80% of the global nitrate pool (i.e., 460 Tg) is stored in deserts (17). However, due to the combination of water scarcity and high soil salinity, much of this pool is unavailable to productive guilds, i.e., plants and microbial communities (16). In drylands, N is considered the second most important limiting factor after water; i.e., it is the most limiting nutrient (18–20).

As in other environments, the arid land microbial communities are critical for the completion of the biogeochemical N cycle, as specific taxa are the sole mediators of key processes that control the quantities of bioavailable ammonium/ammonia (NH_4^+/NH_3)

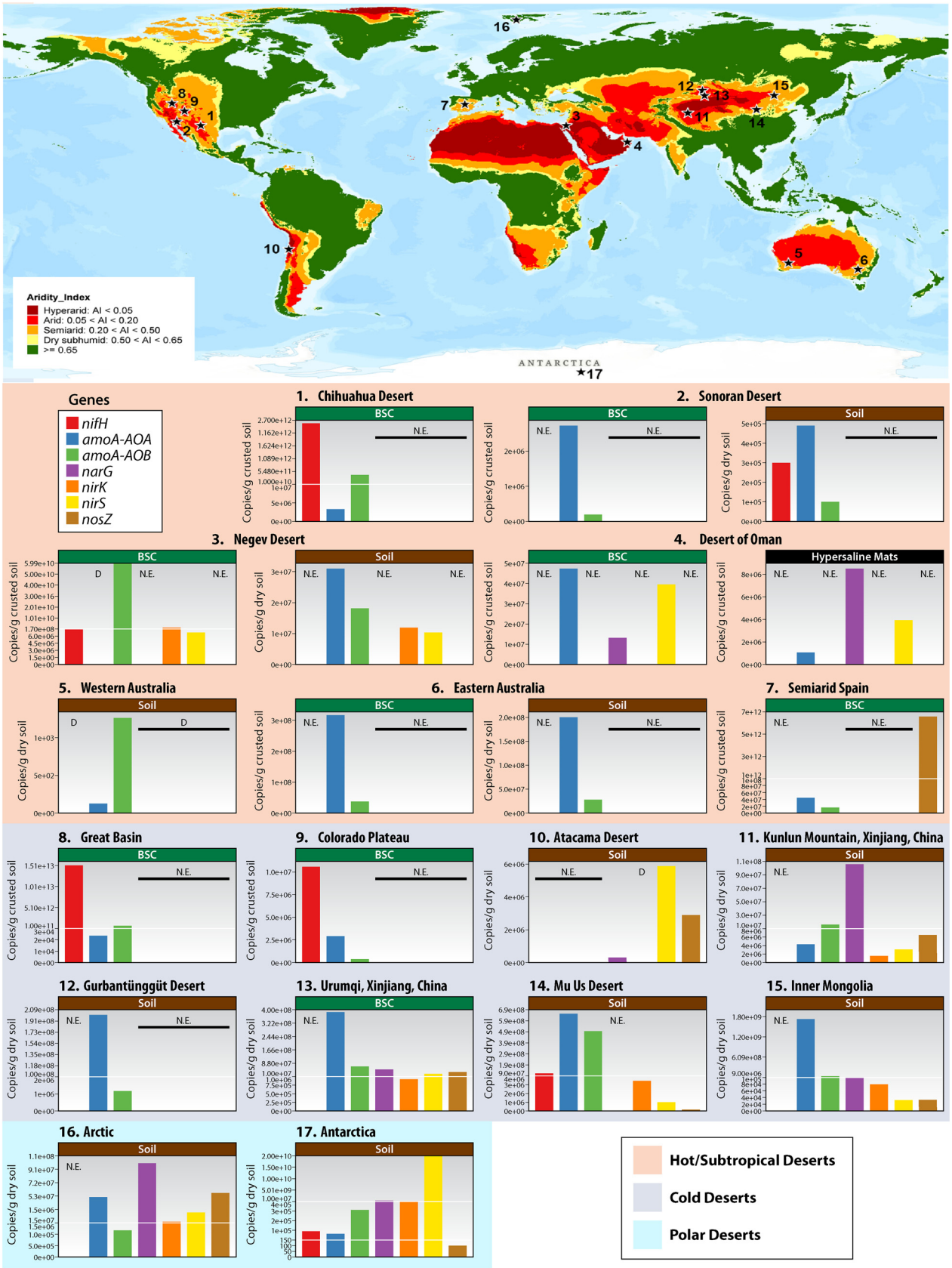

FIG 1 Global aridity index (AI) map and microbial N-cycling gene abundances in various desert niches. The AI map (Esri grid) was obtained from the Food and Agriculture Organization of the United Nations (FAO, 10 arc min; https://data.apps.fao.org/map/catalog/srv/eng/catalog.search#/metadata/221072ae-2090-48a1-be6f-5a88f061431a) and was visually represented with ArcGIS Pro. The AI classification is shown in the key on

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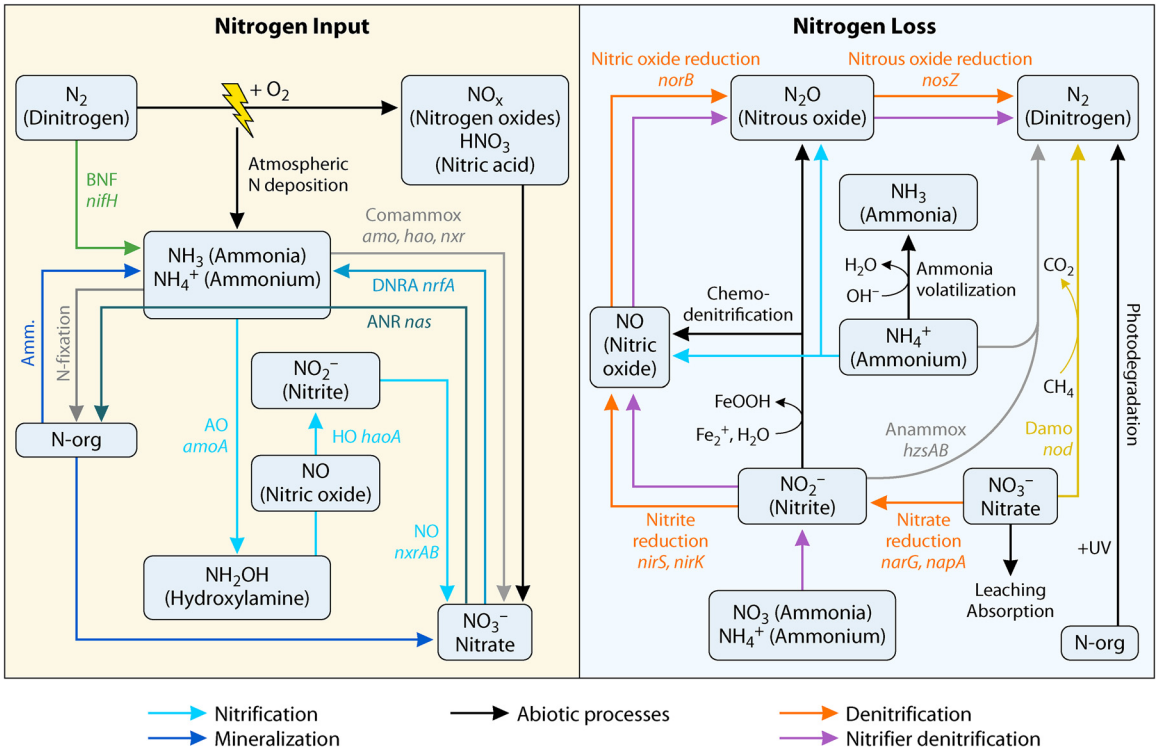

FIG 2 Biogeochemical cycle of nitrogen. Denitrification encompasses the nitrate, nitrite, nitric oxide, and nitrous oxide reduction reactions, and nitrification encompasses the aerobic ammonia, hydroxylamine, and nitrite oxidation reactions. Amm., ammonification; AO, ammonia oxidation; BNF, biological nitrogen fixation; DNRA, dissimilatory nitrate reduction to ammonium; HO, hydroxylamine oxidation; NO, nitrate oxidation; anammox, anaerobic ammonium oxidation; comammox, complete ammonia oxidation; Damo, denitrifying anaerobic methane oxidation. Microbial genes relevant to each process are indicated. N-Org, organic nitrogen. The NH_4^+/NH_3 equilibrium in the environment is controlled by many parameters. Ammonia volatilization has notably been positively correlated to soil pH, $CaCO_3$, and salt contents and negatively to soil cation exchange capacity, organic matter, and clay contents (323).

and nitrate (NO_3^-). These include biological N fixation (BNF) and nitrification, which are processes by which N is added to the environment (Fig. 2), and denitrification, a process by which N is lost and which can lead to the production of the greenhouse gas nitrous oxide (N_2O) (Fig. 2). Global annual terrestrial microbial production of N_2O has been estimated to amount to 7.2 to 13.2 Tg N year^{-1}, of which drylands contribute 3×10^{-12} to 49×10^{-12} Tg N ha^{-1} year^{-1} (21). With drylands covering ~6 billion hectares globally (22), this represents 1.8×10^{-5} to 2.94×10^{-3} Tg N year^{-1}.

The inherent oligotrophy of dryland ecosystems makes them particularly vulnerable to the alterations of the global N cycle by anthropogenic activities and global climate change (23). As the acceleration of desertification processes is an inevitable consequence of current anthropogenic activities (24), it becomes increasingly important to understand the global functioning of arid ecosystems. Here, we describe and discuss the abiotic and microbial processes that contribute to N cycling in the various niches of arid environments.

NITROGEN INPUT PROCESSES IN ARID ENVIRONMENTS

Nitrogen is the principal limiting factor in the net primary productivity (NPP) of most terrestrial ecosystems (19), the exception being arid ecosystems, where water

FIG 1 Legend (Continued)
the figure. Hot, cold, and polar deserts where quantification of microbial cycling genes has been performed are indicated by numbers. Quantitative expression (qPCR) levels of functional genes involved in N cycling were collected from available sources (Table 3), and the average expression per gene (as copies g^{-1} dry/crusted soil) was calculated for each desert. Note that the *y* axes of the bar plots present different scales. "D" indicates genes detected by metagenomic and/or metatranscriptomic data without available quantitative expressions levels. N.E., not evaluated; BSC, biological soil crusts. References are given in Tables 1, 2, and 3.

availability is the dominant driver of NPP (18–20). In natural ecosystems, as opposed to engineered/man-made ecosystems like wastewater treatment plants or fertilized fields, three processes are responsible for *de novo* nitrogen inputs: (i) atmospheric wet (precipitation) as well as dry gaseous (NO_x, HNO_3, and NH_3) and dust sources, (ii) lightning, and (iii) biological nitrogen fixation (BNF) (Fig. 2) (25–29).

BNF is by far the most dominant process, estimated to be responsible for over 97% of the terrestrial N input in pristine terrestrial systems (27), representing at a global scale from 52 to ~195 Tg N $year^{-1}$ (30, 31). This proportion is also observed in drylands, even though barren lands have the lowest terrestrial BNF globally (31, 32). In desert and arid shrubland ecosystems, BNF has been estimated to contribute 4.8 to 10.8 kg N ha^{-1} $year^{-1}$ and 9.4 to 33.9 kg N ha^{-1} $year^{-1}$, respectively (30). This is significantly higher than BNF in cold boreal forest ecosystems (i.e., 1.5 to 2.0 kg N ha^{-1} $year^{-1}$) (30). This suggests that polar and cold desert BNF is rather low due to lower biological activities (33). Furthermore, it indicates that in dryland ecosystems, BNF is favored in less arid drylands, i.e., increases with vegetation cover. A recent meta-analysis at the Latin American scale confirms this view (34).

Other microbially mediated processes also participate in the input of bioavailable N, particularly through the recycling of the soil N pool via various biogeochemical transformations: ammonification, nitrification, and dissimilatory and assimilatory nitrate reduction (Fig. 2). These are particularly important, as organic N represents over 99% of the total N in most environments, including drylands (35).

Abiotic Nitrogen Deposition and Fixation

Atmospheric nitrogen deposition results from three abiotic processes: gaseous (NO_x, NO_2, HNO_3, and NH_3) and dust deposition (dry process), precipitation (wet process), and nitrogen fixation by lightning (30, 36, 37). On a global scale, lightning-derived N fixation, in the form of nitrogen oxides (NO_x), is estimated to be ~7 Tg N $year^{-1}$. This is particularly important around the tropics (36, 38, 39), where most deserts are located. However, satellite data clearly demonstrate that for most deserts, particularly the Sahara and Central Australian deserts, this form of N input is negligible, most probably due to the rarity of storms in such environments (38, 40). For the same reason, atmospheric (wet) N deposition—in the reduced ammonium NH_4^+ and/or oxidized nitrate (NO_3^-) forms—is also temporally limited in drylands but, in contrast to lightning-based N fixation, is not negligible. The wet deposition of ammonium (NH_4^+) in drylands is highly correlated with the magnitude of precipitation events, with concentrations often exceeding those of nitrate (NO_3^-) by up to 50% (41–43). In dryland soils, NH_4^+, rather than being directly taken up by plants, is usually nitrified into nitrate, which can decrease soil pH (44). Ultimately, a large percentage (>40%) of the wet deposited ammonium/nitrate is retained by the vegetation and therefore improves plant biomass production in drylands (43).

Globally, the total N deposition is estimated to range between 125 and 132 Tg N $year^{-1}$ (45) and varies between ~0.5 and ~7.5 kg N ha^{-1} $year^{-1}$ in most drylands (46). However, it is desert/dryland dependent. In the Chihuahan Desert (USA), between 1989 and 2004, atmospheric ammonium and nitrate deposition were positively correlated to precipitation and estimated to represent 1.2 kg ha^{-1} $year^{-1}$ and 0.9 kg ha^{-1} $year^{-1}$, respectively (37). In contrast, in an area spanning the Sonoran and Mojave Deserts (USA), total atmospheric N deposition, which ranged from 2.8 to 14.4 kg N ha^{-1} $year^{-1}$, was not correlated with annual precipitation (47). This apparent dichotomy was also observed at two sites in the Negev Desert (less than 50 km apart) which received similar total N atmospheric inputs (~0.84 kg N ha^{-1} $year^{-1}$). However, one received more atmospheric N deposition during the dry season and the other during the rainy season (48). Together, this clearly demonstrates that local climatic regimes should be monitored when assessing abiotic nitrogen deposition in deserts. For example, the coastal regions of the Atacama (Chile) and Namib (Namibia) Deserts are subjected to regular fog events, with fog water nitrate concentrations ranging from 17.8 to 27.8 mg L^{-1} and 36.2 to 71.2 mg L^{-1}, respectively (46, 49, 50). In the Namib Desert, fog water deposition can range from 3 mm (112 km from the coast)

to 184 mm (33 km inland) annually (51). In the Atacama Desert, fog water deposition is particularly important in the first 10 km from the Pacific Ocean and has been estimated to represent ~25 L m^{-2} (52). Consequently, this provides a significant N input in the form of nitrate deposition, ranging from 1.1 to 2.1 kg ha^{-1} $year^{-1}$ to 66.6 to 131.0 kg ha^{-1} $year^{-1}$ and from 0.5 to 0.7 kg ha^{-1} $year^{-1}$ in the Namib and Atacama Deserts, respectively. As nitrate is deposited with water, it becomes immediately bioavailable, which explains the rather important microbial and vegetation life in the fog-influenced zones of these deserts (53–56).

Human activities have increased the atmospheric N pool by particularly intensifying atmospheric N deposition, thus altering the global N biogeochemical cycle (57). In the Chihuahan Desert, N deposition rates have increased between 1989 and 2004 by 0.049 kg ha^{-1} $year^{-1}$ (37). In this context, the expansion of urban areas in the vicinity of drylands will also locally impact atmospheric N deposition (47, 58). In the Sonoran Desert, atmospheric N deposition rates within metropolitan Phoenix and in the nearby desert have been shown to represent 7.2 ($\pm$0.4) and 6.1 ($\pm$0.3) kg N ha^{-1} $year^{-1}$, respectively, over a 9-year period (2006 to 2015). It is difficult to predict how this increase in N deposition will influence local productivity and microbially mediated N cycling in drylands, since the potential use of N is ultimately linked to the availability of water, which is predicted to remain a scarce resource in most drylands with global climate change (59). Nevertheless, precipitation increases the availability of N in these environments (60, 61). This has been shown to decrease plant community diversity and favor nonnative grass growth (57, 61). Similarly, it certainly will impact the structure and function of dryland (N-cycling) microbial communities, particularly of those interacting with the native plants. This is further supported by a meta-analysis, based on 454 experiments, which suggests edaphic microbial biomass increases in grasslands and decreases in deserts after N addition, whereas fungal biomass decreases in both arid biomes (62). In the Gurbantünggüt Desert (northwestern China), surface soil enzyme activities also varied after N addition (63). Together, this clearly shows that increasing atmospheric N deposition will modify dryland ecosystems' functioning and their N biogeochemical cycling.

Biological Nitrogen Fixation

Prokaryotic N fixers in drylands. The phylogenetic affiliations and abundances of environmental diazotrophic taxa are generally evaluated using the nitrogenase *nifH* gene (Fig. 1 and 2) (64–68). However, for accurate diversity analyses of N-fixing taxa, the use of multiple primer sets and/or a combination of approaches is recommended (68, 69). For example, in a global survey of hypolithic communities, diazotrophic cyanobacteria (e.g., *Nostoc* spp.) were detected using the 16S rRNA gene but not with *nifH* PCR primers known to amplify cyanobacterial *nifH* genes (68). Similarly, nitrogen-fixing genes were marginally detected in shotgun metagenomes from hypolithic and endolithic communities (70, 71), whereas microscopic observations (72) and stable isotope analyses (73) clearly supported the presence of diazotrophic microorganisms in these niche communities.

The capacity for diazotrophy is present in various branches of the bacterial and archaeal domains, particularly within the bacterial phyla *Cyanobacteria*, *Actinomycetota*, *Bacillota*, and *Pseudomonadota* and the *Euryarchaeota* archaeal phylum (30, 74–77). Despite being a highly energy-demanding process (16 ATP molecules and 8 electrons per N_2 molecule reduced) (64), N-fixing representatives from all of these phyla have been detected in hot and cold desert edaphic and cryptic niche communities (Fig. 3; Table 1) (6, 65, 67, 68, 70, 78–84). Environmental N fixation is most commonly quantified using the acetylene reduction assay (ARA), which measures nitrogenase activity via the reduction of acetylene to ethylene (85), and $^{15}N_2$ incorporation rate measurements (86) (Table 1).

Given the strictly anaerobic requirements for nitrogenase functioning, N-fixing bacteria are mainly obligate anaerobes or microaerophilic (i.e., able to live in environments with very low oxygen levels). Multicellular filamentous cyanobacteria have, however, evolved specific cells (heterocysts) which provide the anaerobic conditions suitable for nitrogenase activity in an otherwise aerobic system (87, 88). Over 100 heterocystous cyanobacterial

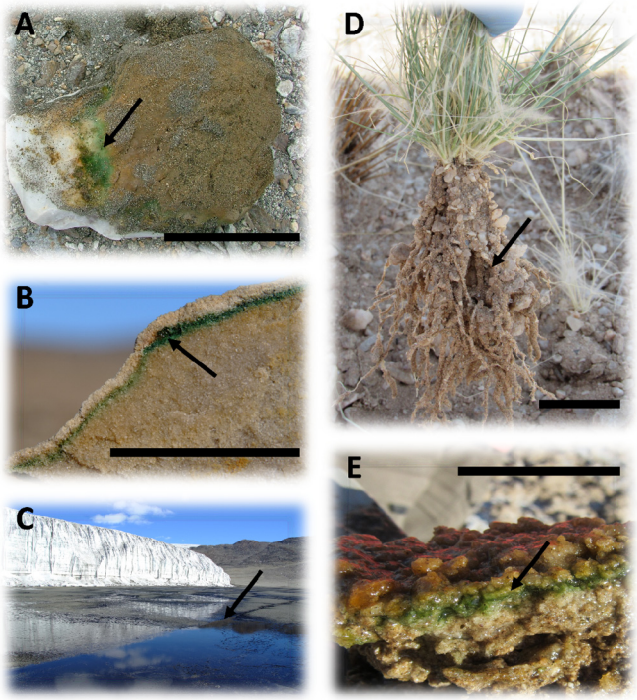

FIG 3 Cryptic and productive desert niches colonized by free-living and symbiotic N fixers. (A) Large quartz hypolith from the McMurdo Dry Valleys (East Antarctica). The ventral surface of the quartz rock shows extensive hypolithic biomass. (B) Cryptoendolithic community in Antarctic Beacon sandstone. The green layer is dominated by *Cyanobacteria*. (C) Antarctic glacial runoff pan with extensive *Nostoc* species growth. (D) Rhizosheath-root structure of *Stipagrostis ciliata* (Namib Desert). (E) Namib Desert stratified salt pan microbial mat. Black bars, 3 cm. Black arrows indicate the productive and N-fixing zone.

genera have already been described (89). The heterocystous cyanobacteria *Nostoc* spp. have been detected in desert niches globally (Fig. 3C; Table 1). Nonheterocystous aerobic cyanobacteria also contribute significantly to N fixation (90). Among these, *Microcoleus* spp., *Chroococcidiopsis* spp., and *Synechococcus* spp. have been shown to be common in hot, cold, and polar desert microbial communities (68, 83, 91, 92) (Table 1). These N-fixing bacteria can be free-living (e.g., *Microvirga* spp.) or symbiotically associated with desert plants such as *Acacia* spp. and *Stipagrostis* spp. (e.g., *Rhizobia*, *Bradyrhizobium*, *Frankia*, and *Azospirillum* spp.) (6, 93). Other symbiotic associations with N-fixing microorganisms found in deserts include cyanolichens and chlorolichens which are obligate symbioses between cyanobacteria and fungi and between green algae and fungi, respectively (94–98) (Table 1).

Biological nitrogen fixation (BNF) in the different dryland niches. (i) Biological soil crusts (BSCs). BSCs are complex microbial assemblages that can cover up to 70% of cold and hot desert soil surfaces (4, 99, 100). Diazotrophic communities associated with BSCs in desert ecosystems have been well characterized (Table 1). BSCs are typically dominated by cyanobacteria, most commonly by members of the diazotrophic genus *Microcoleus*, and include chlorophyte algae, heterotrophic bacteria, fungi, mosses, and lichens (4, 100, 101). BSCs may also contain N-fixing cyanolichens (e.g., *Collema*), chlorolichens (e.g., *Gymnosoma desertorum*), filamentous heterocystous (e.g., *Anabaena* spp., *Nostoc* spp., *Scytonema* spp.) and nonheterocystous (e.g., *Microcoleus* spp., *Chroococcidiopsis* spp.) cyanobacteria, as well as heterotrophic N-fixing bacteria (e.g., *Azospirillum* spp.) (91, 98, 102–105) (Table 1). BSC microbial assemblages and diazotrophic communities have been shown to vary spatially and temporally, depending on aridity and their developmental stages (100, 105–107). BSCs in hyperarid desert regions, which are characterized by very high evapotranspiration rates, typically do not contain either mosses or lichens (100, 106).

With both photosynthetic and diazotrophic capacities, BSCs constitute the dominant

TABLE 1 Microbial nitrogen fixation in hot and cold dryland/desert habitats[a]

Habitat type	Desert	Reference	Acetylene reduction assay rates	*nifH* detection and/or abundances	Diversity of diazotrophs
Biological soil crust	Canyonlands, Utah	280	Light crust: 0.13 ± 0.05 μmol m^{-2} h^{-1}	NE	NE
			Dark crust: 0.86 ± 0.26 μmol m^{-2} h^{-1}	NE	NE
	Chihuahuan Desert	309	~40–100 μmol m^{-2} h^{-1}	NE	*Scytonema* sp., *Microcoleus steenstrupii*, *Microcoleus vaginatus*, *Pseudanabaena* sp.
		324	Early successional crust: ~3–20 μmol C_2H_4 m^{-2} day^{-1}	NE	NE
			Late successional crust: ~10–100 μmol C_2H_4 m^{-2} day^{-1}	NE	NE
		130	0.04–12.69 nmol C_2H_4 m^{-2} h^{-1}	NE	NE
			20 nmol C_2H_4 cm^{-2} h^{-1}	NE	NE
		131	Lichen crust: ~0–100 μmol N m^{-2} h^{-1}	5.13 × 10^{12} copies g^{-1}	*Nostoc* spp., *Tolypothrix* spp., *Scytonema* spp.
			Light crust: ~0–50 μmol N m^{-2} h^{-1}	2.52 × 10^{12} copies g^{-1}	*Nostoc* spp., *Tolypothrix* spp., *Scytonema* spp.
		106	Poorly developed crust (*Microcoleus* spp. dominated): ~5 μmol m^{-2} h^{-1}	1.8 × 10^6 copies g^{-1} soil	*Microcoleus steenstrupii*, *Microcoleus vaginatus*
			Mature crust (mixed cyanobacteria, lichen, and moss): ~12 μmol m^{-2} h^{-1}	3.4 × 10^7 copies g^{-1} soil	*Microcoleus steenstrupii*, *Chrococcidiopsis* sp., *Scytonema* sp.
		103	NE	D	*nifH* clusters S1 (29/121; *Scytonema* sp.), S2 (7/121; *Scytonema hyalinum*), T2 (4/121; *Tolypothrix* sp.), U1 (13/121), and U2 (52/121), other cyanobacterial *nifH* sequences (8/121), other bacterial *nifH* sequences (8/121)
		131	Lichen crust: ~0–100 μmol N m^{-2} h^{-1}	5.13 × 10^{12} copies g^{-1}	*Nostoc* spp., *Tolypothrix* spp., *Scytonema* spp.
			Light crust: ~0–60 μmol N m^{-2} h^{-1}	2.52 × 10^{12} copies g^{-1}	*Nostoc* spp., *Tolypothrix* spp., *Scytonema* spp.
	Colorado Plateau	309	~30–50 μmol m^{-2} h^{-1}	NE	*Scytonema* sp., *Microcoleus steenstrupii*, *Microcoleus vaginatus*, *Pseudanabaena* sp.
		324	Early successional crust: ~3–76 μmol C_2H_4 m^{-2} day^{-1}	NE	NE
			Late successional crust: ~18–107 μmol C_2H_4 m^{-2} day^{-1}	NE	NE
		325	Lichen crust: 11.0 ± 5.7–57.9 nmol C_2H_4 cm^{-2} h^{-1}	NE	NE
		326	Cyanobacteria-dominated crust: ~15–30 nmol C_2H_4 m^{-2} h^{-1}	NE	*Microcoleus vaginatus*, *Scytonema myochrous*
			Lichen crust: ~10–90 nmol C_2H_4 m^{-2} h^{-1}	NE	*Collema tenax* (*Nostoc* sp. as N-fixing phycobiont)
		91	Light cyanobacterial crust: 0–0.80 nmol cm^{-2} h^{-1}	NE	*Microcoleus vaginatus*
			Dark cyanobacterial crust: 0–5 nmol cm^{-2} h^{-1}	NE	*Nostoc commune*, *Scytonema myochrous*
			Colema crust: 0–13 nmol cm^{-2} h^{-1}	NE	*Collema* sp.
		103	NE	D	*nifH* clusters S1 (69/473; *Scytonema* sp.), S2 (62/473; *Scytonema hyalinum*), N1 (134/473; *Nostoc* sp.), N2 (28/473; *Nostoc commune*), and T1 (128/473; *Spirirestis* sp.), other cyanobacterial *nifH* sequences (17/473), other bacterial *nifH* sequences (83/473)
		106	Poorly developed crust (*Microcoleus* spp. dominated): ~2.5 μmol m^{-2} h^{-1}	1.1 × 10^6 copies g^{-1} soil	*Microcoleus steenstrupii*, *Phormidium murrayii*, *Phormodium* sp., *Microcoleus vaginatus*
			Mature crust (mixed cyanobacteria, lichen, and moss): ~20 μmol m^{-2} h^{-1}	2.0 × 10^7 copies g^{-1} soil	*Microcoleus steenstrupii*, *Microcoleus sociatus*, *Phormidium* spp., *Scytonema* sp.
		178	Dark crust: 48.00 ± 9.31 μmol C_2H_2 reduced m^{-2} h^{-1}	NE	NE
			Light crust: 6.53 ± 1.87 μmol C_2H_4 m^{-2} h^{-1}	NE	NE
		98	*Collema*-dominated biocrusts: 1.6 nmol C_2H_2 cm^{-2} h^{-1}	NE	*Collema* spp.
			Squamarina lentigera-dominated biocrust: 0.2 nmol C_2H_2 cm^{-2} h^{-1}	NE	*Squamarina lentigera*
			Gyalolechia desertorum-dominated biocrust: 0.4 nmol C_2H_2 cm^{-2} h^{-1}	NE	*Gyalolechia desertorum*
	Great Basin Desert	326	~15–90 nmol C_2H_4 cm^{-2} h^{-1}	NE	NE
		327	Ungrazed: 0.37–2.54 g N ha^{-1} h^{-1}	NE	NE
		132	4.3–72.2 nmol C_2H_4 m^{-2} s^{-1}	NE	NE
		328	10.5–84.0 nmol C_2H_4 m^{-2} s^{-1}	NE	NE
		131	Light crust: ~0–200 μmol N m^{-2} h^{-1}	3.94 × 10^{12} copies g^{-1}	*Nostoc* spp., *Tolypothrix* spp., *Scytonema* spp.
			Dark crust: ~0–370 μmol N m^{-2} h^{-1}	2.63 × 10^{13} copies g^{-1}	*Nostoc* spp., *Tolypothrix* spp., *Scytonema* spp.
	Gurbantunggut Desert	110	Cyanobacterial crust: 2.26–9.81 × 10^3 nmol C_2H_4 m^{-2} h^{-1}	NE	NE
			Lichen crust: 6.54 × 10^2–9.06 × 10^3 nmol C_2H_4 m^{-2} h^{-1}	NE	NE
			Moss crust: 6.38 × 10^2–2.03 × 10^3 nmol C_2H_4 m^{-2} h^{-1}	NE	NE
	Kalahari Desert	329	0.6–6.8 nmol C_2H_4 nmol m^{-2} h^{-1}	NE	NE

(Continued on next page)

TABLE 1 (Continued)

Habitat type	Desert	Reference	Acetylene reduction assay rates	*nifH* detection and/or abundances	Diversity of diazotrophs
	Mojave Desert	309	~30–200 μmol m^{-2} h^{-1}	NE	*Scytonema* sp., *Microcoleus steenstrupii*, *Microcoleus vaginatus*, *Pseudanabaena* sp.
		135	Lichen crust: 11.3 ± 7.7–25.2 ± 11.7 μmol C_2H_4 m^{-2} h^{-1}	NE	NE
			Nonlichen crust: 0–27.0 ± 26.3 μmol C_2H_4 m^{-2} h^{-1}	NE	NE
	Negev Desert	330	34 nmol C_2H_4 cm^{-2} h^{-1}	NE	NE
		331	Cyanobacterial crust: 1.0–1.2 g N m^{-2} yr^{-1}	NE	NE
		332	Cyanobacterial crust (n = 4): NE	6.7 × 10^7–3.4 × 10^8 copies cm^{-2}	*Microcoleus vaginatus* (4/4), *Scytonema* sp. (3/4), *Phormidium* sp. (1/4), *Nostoc* sp. (1/4)
			Moss crust (n = 1): NE	1.6 × 10^8 copies cm^{-2}	*Microcoleus vaginatus*, *Nostoc* sp.
	Omani Desert	104	58.5 ± 2.6 mmol C_2H_4 reduced m^{-2} h^{-1} (or 183–258 mg N m^{-2} h^{-1})	NE	*Microcoleus vaginatus*, *Nostoc* sp., *Scytonema* sp., *Brasilonema* sp., *Petalonema* sp.
	Sahel Desert	133	0.001–4.2 nmol C_2H_4 cm^{-2} h^{-1}	NE	*Nostoc* sp., *Scytonema javancum*
	Sonoran Desert	309	~50–100 μmol m^{-2} h^{-1}	NE	*Scytonema* sp., *Microcoleus steenstrupii*, *Microcoleus vaginatus*, *Pseudanabaena* sp.
		333	78 nmol C_2H_4 cm^{-2} h^{-1}	NE	NE
		107	NE	NE	*Synechococcus* sp., *Microcoleus vaginatus*, *Microcoleus steenstrupi*, *Chroococcidiopsis* sp., *Cylindrospermum* sp., *Scytonema hyalinum*
	Tengger Desert	111	Cyanobacterial-algal crust: 16.6 mmol C_2H_4 m^{-2} h^{-1}	NE	NE
			Lichen crust: 6.9 mmol C_2H_4 m^{-2} h^{-1}	NE	NE
			Moss crust: 2.6 mmol C_2H_4 m^{-2} h^{-1}	NE	NE
		334	Moss and bacterial BSC: NE	Moss (n = 6): 0.0021 ± 0.0007	NE
				Bacterial (n = 6): 0.0060 ± 0.0031	NE
Soil	Roxby Downs, Australia	125	NE	6.4% (±1.2%) total predicted genes in metagenomes (n = 8) and 3.4% (±2.5%) in metatranscriptomes (n = 2)	*Archaea* ("*Candidatus* Methanoperedens sp.," *Methanobacterium* sp., *Methanolobus* sp., *Methanosarcina* spp.); *Bacillota* (*Sporobacer* sp., *Clostridum* spp., *Eubacterium* sp., *Marvinbryantia* spp., *Lachnoclostridium* spp., *Paenibacillus* sp., *Carboxydocella* spp., *Desulfotomaculum* sp., *Propionispira* sp., *Desulfitobacterium* spp., *Butyrivibrio* spp.); *Spirochaetota* (*Treponema* sp.); *Alphaproteobacteria* (*Skermanella* sp., *Neorhizobium* sp., *Azospirillum* spp., *Phaeospirillum* sp., *Bradyrhizobium* sp., *Rhizobium* spp., *Nitrospirillum* sp., *Sphingomonas* sp., *Methylocapsa* sp., *Rhodopila* sp., *Rhodovulum* sp., *Rhodopseudomonas* sp., *Aurantimonas* sp., *Komagataeibacter* sp., *Methylocella* sp.); *Betaproteobacteria* (*Derxia* sp., *Dechloromonas* sp., *Rubrivivax* sp., *Herbaspirillum* spp.), *Gammaproteobacteria* (*Alteromonadales*, *Beggiatoa* sp., *Neiella* sp., *Halorhodospira* sp., *Methylovulum* sp., *Agarivorans* sp., *Pseudomonas* sp., *Solimonas* sp.); *Deltaproteobacteria* (*Geothermobacter* sp., *Desulfuromusa* sp., *Dissulfuribacter* sp., *Anaeromyxobacter* sp.); *Bacteroidota* (*Draconibacterium* sp., *Labilibacter* sp.); *Chloroflexota* (*Oscillochloris* sp., *Roseiflexus* sp.); *Cyanobacteria* (*Trichormus* sp., *Nostoc* spp., *Calothrix* sp., *Chlorogloeopsis* sp., *Cylindrospermum* sp., *Fischerella* spp., *Cylindrospermopsis* sp., *Nodularia* sp., *Tolypothrix* sp., *Kamptonema* sp.); *Actinomycetota* (*Propionibacterium* sp.)
	Gobi Desert		NE	1.8% total predicted genes	*Archaea* ("*Candidatus* Methanoperedens sp."); *Bacillota* (*Sporobacer* sp., *Clostridum* spp., *Eubacterium* sp., *Marvinbryantia* sp., *Lachnoclostridium* spp., *Carboxydocella* spp., *Moorella* sp., *Megasphaera* sp., *Butyrivibrio* spp., *Acetobacterium* sp.); *Alphaproteobacteria* (*Rhodoblastus* sp., *Cohaesibacter* sp.), *Betaproteobacteria* (*Rhodocyclales* spp.); *Gammaproteobacteria* (*Succinivibrio* sp., "*Candidatus* Contendobacter sp.," *Ectothiorhodospira* sp., *Halorhodospira* sp.)
	Mojave Desert		NE	2.4% total predicted genes	*Bacillota* (*Sporobacer* sp., *Clostridum* spp., *Eubacterium* sp., *Marvinbryantia* sp., *Lachnoclostridium* spp.); *Planctomycetota*

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TABLE 1 (Continued)

Habitat type	Desert	Reference	Acetylene reduction assay rates	*nifH* detection and/or abundances	Diversity of diazotrophs
					(*Blastopirellula* sp.); *Gammaproteobacteria* (*Allochromatium* sp., *Ectothiorhodospira* sp., *Halorhodospira* sp.)
	Northeastern desert region of Egypt	335	NE	2.51×10^4 copies g^{-1} soil	*Alphaproteobacteria* (*Rhizobium* sp., *Bradyrhizobium* sp.), *Betaproteobacteria* (*Ideonella* sp., *Derxia* sp., *Dechloromonas* sp., *Zoogloea* sp.), *Gammaproteobacteria* (*Azomonas* sp.), *Bacilli* (*Paenibacillus* sp.)
	Gurbantunggut Desert	171	NE	NE	*Microcoleus* sp., *Chroococcidiopsis* sp., *Phormidium* sp., *Nostoc* spp.
	Namib Desert	79	NE	D	*Pseudomonadota*
		123	NE	NE	*Nostocales*
		124	NE	D	NE
		125	NE	2.9% total predicted genes	*Archaea* ("*Candidatus* Methanoperedens sp.," *Methanobacterium* sp.); *Bacillota* (*Clostridum* spp., *Eubacterium* sp., *Marvinbryantia* sp., *Lachnoclostridium* spp., *Carboxydocella* spp., *Dethiosulfatibacter* sp., *Butyrivibrio* sp.); *Spirochaetota* (*Treponema* sp.); *Alphaproteobacteria* (*Sphingomonas* sp.); *Betaproteobacteria* (*Rhodocyclales* spp.), *Gammaproteobacteria* (*Marichromatium* sp., *Nitrincola* sp., *Agarivorans* sp., *Thiorhodospira* sp.); *Cyanobacteria* (*Trichormus* sp.)
	Mu Us Desert	336	NE	1.3×10^7–2.0×10^8 copies g^{-1} soil	NE
	Sonoran Desert	337	Undisturbed site: 2.4 ± 0.05 nmol C_2H_4 soil g^{-1} day^{-1}	3.02×10^5 copies g^{-1} soil	*Azospirillum* sp., *Rhizobium* sp., *Pseudomonas* sp.
	Tengger Desert	67	Control site: 0.025 ± 0.008 mmol C_2H_4 m^{-2} h^{-1}	NE	*Alphaproteobacteria* (*Mesorhizobium* sp.), *Epsilonproteobacteria* (*Arcobacter* sp.), *Cyanobacteria* (*Plectonema* sp.), *Verrucomicrobiota*, *Bacillota*
	King Sejong Station and Cape Burk area (Antarctica)	257	NE	4.0×10^4–1.4×10^5 copies g^{-1} soil	NE
	Miers Valley (Antarctica)	65	ND (0/14)	NE	NE
		83	NE	D	*Archaea*, *Actinomycetota*, *Alpha-*, *Beta-*, *Delta-*, *Gamma-*, and *Epsilonproteobacteria*, *Chlorobiota*, *Chloroflexota*, *Cyanobacteria*, *Bacillota*, *Spirochaetota*, *Bacteroidota*, *Fusobacteriota*
	Anchorage Islands (Antarctica)	103	NE	D	NE
	Anvers Island (Antarctica)	338	12.31–59.32 μmol N m^{-2} h^{-1}	NE	NE
	McKelvey Valley (Antarctica)	78	NE	D	*Archaea*, *Actinomycetota*, *Cyanobacteria*, *Bacillota*, *Alpha-*, *Beta-*, *Delta-*, *Gamma-*, and *Epsilonproteobacteria*, *Spirochaetota*
	18 Antarctica soils	120	NE	6 *nif* hits in 3/18 shotgun metagenomes	*Cyanobacteria*
Hypolith	Namib Desert	71	NE	D	*Cyanobacteria*, *Alphaproteobacteria*
	Qaidam Basin	114	NE	ND	*Chroococcidiopsis* sp., *Phormidium* sp., *Micrococcus* sp.
	Taklimakan Desert	114	NE	ND	*Chroococcidiopsis* sp., *Phormidium* sp.
		68	NE	D	*nifH*: *Alphaproteobacteria* (*Rhodospirillales*, *Rhizobiales*), *Gammaproteobacteria* (*Pseudomonadales*)/16S rRNA: 14.6% of the sequences, including *Chroococcidopsis* sp. and *Phormidium* sp.
	Tibetan Plateau	68	NE	D	*nifH*: *Alphaproteobacteria* (*Rhodospirillales*, *Rhizobiales*), *Betaproteobacteria* (*Burkholderiales*)/16S rRNA: 18.4% of the sequences, including *Chroococcidopsis* sp. and *Phormidium* sp.
	Turpan Depression	114	NE		*Chroococcidiopsis* sp.
	McKelvey Valley (Antarctica)	78	NE	D	*Archaea*, *Actinomycetota*, *Cyanobacteria*, *Bacillota*, *Nitrospirota*, *Alpha-*, *Beta-*, *Delta-*, *Gamma-*, and *Epsilonproteobacteria*, *Spirochaetota*

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TABLE 1 (Continued)

Habitat type	Desert	Reference	Acetylene reduction assay rates	*nifH* detection and/or abundances	Diversity of diazotrophs
	Miers Dry Valley (Antarctica)	65	0.02–0.174 nmol N g^{-1} h^{-1} (6/12)	D	*Cyanobacteria*, *Pseudomonadota*
		83	NE	D	*Archaea*, *Actinomycetota*, *Alpha-*, *Beta-*, *Delta-*, *Gamma-*, and *Epsilonproteobacteria*, *Chlorobiota*, *Chloroflexota*, *Cyanobacteria*, *Bacillota*, *Spirochaetota*, *Verrucomicrobiota*
	McMurdo Dry Valleys (Antarctica)	68	NE	D	*nifH*: *Alphaproteobacteria* (*Rhizobiales*), *Betaproteobacteria* (*Burkholderiales*)/16S rRNA: 5.3% of the sequences, including *Phormidium* sp.
	Arctic	68	NE	ND	16S rRNA: 13.8% of the sequences, including *Chroococcidopsis* sp. and *Phormidium* sp.
Endolith	7 hot and 41 cold deserts	112	Detected (1 Antarctic/48)	NE	NE
	Al-Jafr Basin Desert	113	NE	NE	*Chroococcidiopsis* sp.
	Mojave Desert	113	NE	NE	*Chroococcidiopsis* sp.
	Atacama Desert	113	NE	NE	*Chroococcidiopsis* sp.
		70		NE	ND
		119		ND	NE
		339		NE	*Chroococcidiopsis* sp.
	McKelvey Valley	78	NE	D	*Archaea*, *Actinomycetota*, *Cyanobacteria*, *Bacillota*, *Nitrospirota*, *Alpha-*, *Beta-*, *Delta-*, *Gamma-*, and *Epsilonproteobacteria*, *Spirochaetota*
	McMurdo Dry Valleys	88	Aerobic 20°C: 0.095–1.2 mol C_2H_4 μg Chl*a*$^{-1}$ g rock^{-1} h^{-1}	NE	*Chroococcidiopsis* sp.
			Aerobic 5°C: 0.099–2.1 mol C_2H_4 μg Chl*a*$^{-1}$ g rock^{-1} h^{-1}	NE	*Chroococcidiopsis* sp.
			Anaerobic 20°C: 1.07–2.24 mol C_2H_4 μg Chl*a*$^{-1}$ g rock^{-1} h^{-1}	NE	*Chroococcidiopsis* sp.
			Anaerobic 5°C: 1.5-2.95 mol C_2H_4 μg Chl*a*$^{-1}$ g rock^{-1} h^{-1}	NE	*Chroococcidiopsis* sp.

[a]D, detected; ND, not detected; NE, not evaluated.

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primary producers in plant-free desert ecosystems (108). Globally, desert BSCs show one of the highest N fixation rates of all terrestrial ecosystems, at around 7.6 kg N ha^{-1} $year^{-1}$ and representing a global total of 107 Tg N $year^{-1}$ (108, 109). As shown in Table 1, desert BSC N-fixing capacities vary widely, depending on location, developmental stage, and composition (91, 110, 111). This is particularly exemplified by a study on lichen-dominated Colorado Plateau BSCs, which have even been found to fix N_2 at different rates depending on the dominant lichen (98). Using surface coverage metrics, the annual N fixation flux contributions for each lichen-dominated BSC species in the Colorado Plateau were estimated to be 1.17, 0.08, 0.06, and 0.04 kg ha^{-1} $year^{-1}$ for *Collema* spp., *Psora decipiens*, *Gyalolechia desertorum*, and *Squamarina lentigera*, respectively (98).

(ii) Lithic communities. In arid environments, diazotrophic microbial communities colonizing lithic environments, such as hypoliths and endoliths, are dominated by cyanobacteria (particularly *Chroococcidiopsis*) but also contain alpha-, beta-, and gammaproteobacterial diazotrophs (4, 5, 68, 70, 84, 92, 112–116) (Table 1). GeoChip microarray analyses have indicated that N-fixing phylotypes of Antarctic lithic communities included *Delta-*, *Epsilon-*, and *Gammaproteobacteria*, *Chlorobiota*, *Chloroflexota*, *Spirochaetota*, *Bacillota*, *Verrumicrobiota*, and *Nitrospirota* (78, 83) (Table 1). Interestingly, metatranscriptomics data from Namib Desert hypoliths, analyzed using cooccurrence networks, demonstrated that low-abundance alphaproteobacterial taxa of the N-fixing *Rhizobiales* order were central to the community structure, as indicated by their module hub and module connector positions in the network topology (117).

Perhaps because of their visible dominance as macroscopic biological assemblages (Fig. 3), these cryptic refuge lithic niches are widely assumed to act as productivity hot spots in otherwise depauperate desert soil ecosystems (4, 92). Stable isotope analyses have clearly demonstrated that hypoliths are positioned at the base of the N productivity web in the hyperarid central Namib Desert and are therefore considered to be critical elements of NPP in this desert ecosystem (73). However, very few quantitative data are available to support this conclusion, with ARA data available only from Antarctic Dry Valley hypoliths (0.02 to 0.174 nmol N g^{-1} h^{-1}) (65) and endoliths (0.097 to 2.95 mol C_2H_4 produced μg chlorophyll *a* (Chl*a*)$^{-1}$ g $rock^{-1}$ h^{-1}) (Table 1) (88). This highlights a substantial knowledge gap in global desert nitrogen biogeochemistry, as hypoliths may cover up to 50% of dryland surfaces (2) and quartz rock colonization rates can reach ~100% in hot desert pavements (118). There are suggestions that diazotrophy may be absent from the most hyperarid deserts. No nitrogenase-encoding genes were detected in shotgun metagenomes of Atacama Desert halite endolithic communities (70, 119), suggesting that these communities may obtain sufficient bioavailable N via nitrate reduction (see "Assimilatory and Dissimilatory Nitrate Reduction" below) and/or from atmospheric wet deposition (i.e., fog).

(iii) Soils and plant-associated environments. Desert diazotrophic communities and N-fixing capacities from open soils have been little studied, compared to those of BSCs and lithic communities (Table 1). Antarctic Dry Valley soils have been shown to present diverse, but rare, *nifH* gene sequences (78, 83, 120). In contrast, the isolation of desert soil diazotrophs (e.g., see references 121 and 122) and their detection in metatranscriptomes and metaproteomes from hyperarid Namib Desert soils and the metatranscriptomes of Australian desert soils (79, 123–125) suggest that desert soil communities contribute to the N fixation budget of hot deserts. Recent shotgun metagenomics even suggest a very high diversity of diazotrophs in desert soils globally (125) (Table 1).

Given the hyperoligotrophy of many desert soils and the sessile nature of plants, plant growth-promoting bacteria (PGPB), which increase nutrient acquisition, are thought to be crucial for desert plant growth and fitness (126). These microorganisms are recruited from the surrounding soils and colonize structures such as root nodules and rhizosheaths (127). Rhizosheaths are specialized structures coating the roots of xerophytic grasses from the Poaceae and Haemodoraceae families (Fig. 3D) (6, 127). Several N fixers have been isolated from rhizosheaths, including *Bacillus* spp., *Enterobacter* spp., *Serratia* spp., *Pseudomonas* spp., *Klebsiella* spp., *Agrobacterium*

radiobacter, and *Gluconacetobacter diazotrophicus* (128). An in-depth analysis of rhizosheath microbial communities associated with three Namib Desert dune grass species (*Stipagrostis sabulicola*, *Stipagrostis seelyae*, and *Cladoraphis spinosa*) showed that a sequence variant (SV) affiliated with the N-fixing *Microvarga* genus was abundant and was identified as a keystone taxon in the cooccurrence networks from the three grass species studied (6). This indicates that microbial N fixation represents a key metabolic capacity recruited by desert plants to improve their fitness.

(iv) Factors controlling BNF in dryland ecosystems. Both the duration and rate of nitrogenase activity in desert soil communities are largely controlled by the availability of water (91, 129–131). Under hyperarid conditions, soil diazotrophs are mainly inactive (124), but nitrogenase activity is initiated within a few hours of a wetting event (104, 132, 133). Diazotrophy may also be stimulated by increased net primary production after wetting, which provides organic substrates (used as energy sources) for the energy-expensive N fixation process (134). This suggestion is corroborated by the observation that the addition of external carbon sources (e.g., readily available sugars) enhances nitrogenase activity in soils (130, 135). However, prolonged wetting, despite increasing microbial community biomass, may reduce N fixation rates due to a shift from water to nutrient limitation (130, 136). An excess of bioavailable N, such as solubilized nitrate and/or ammonium ions, reduces biological N fixation but without limiting the growth of diazotrophic microorganisms (121).

N fixation rates in desert soils are temperature dependent and optimal between 20°C and 30°C (7, 91, 110). Consequently, BNF shows seasonal maxima and is limited by low temperatures in desert BSCs (91, 110, 131, 137). Furthermore, BNF is favored during daylight hours, although it has been shown in BSCs to persist for 4 to 6 h in the dark if sufficient C is available (91). The temperature dependence of BNF in the hottest hyperarid desert soils is largely unknown. Given that surface soils in hot hyperarid deserts (such as the Namib Desert) exceed 50°C on a daily basis for much of each year (138) and wetting periods are restricted to a few days per annum, an integrated annual value of soil N fixation is not a simple estimation. Nevertheless, the determination of such values is particularly important, given projected climate change-related increases in both mean temperatures and temperature maxima (139). With the current paucity of quantitative N fixation data and the limited information on temperature and water availability dependence, it is currently not possible to predict how biological nitrogen fixation processes may be affected by future climate change effects in arid ecosystems.

Nitrogen Mineralization

Nitrogen mineralization encompasses all the processes converting organic nitrogen to assimilable inorganic nitrogen (N-org $\rightarrow$ NH_4^+, NO_3^-) (Fig. 2). It therefore comprises ammonification, which leads only to the formation of ammonium (N-org $\rightarrow$ NH_4^+) (Fig. 2). This process is carried out by a cohort of heterotrophic prokaryotes and microeukaryotes (78, 83, 140) and is particularly important, as organic N can represent over 99% of total N in desert soils (35). In a cross-biome analysis, soil N mineralization was positively correlated with soil moisture (primary factor) and negatively with soil C/N ratio (secondary factor) (141). The overall lack of water therefore explained why drylands displayed the lowest N mineralization rates (141).

Soil leucine aminopeptidase (LAP; which degrades peptides) and β-*N*-acetylglucosaminidase (NAG; which degrades chitin) activities have been used as proxies for soil N mineralization capacity in various desert soils (142–146). Soil N mineralization in Antarctic Dry Valley soils was found to be either undetectable (when measuring NAG activity as a proxy for N mineralization) or strongly influenced by temperatures (when measuring LAP activity), ranging from 0 to 15 nmol h^{-1} g^{-1} at 0°C to 15 to 50 nmol h^{-1} g^{-1} at 15°C (146). Hot desert microbial ammonification varied according to soil type (143), vegetation cover (144), and precipitation (145). By using GeoChip technologies, diverse ammonifying microbial communities were detected in Antarctic Dry Valley edaphic, hypolithic, and endolithic communities, comprising numerous archaeal, bacterial, and fungal taxa (78, 83). In contrast, shotgun metagenomic analyses

suggested that N mineralization in Namib Desert hypolithic communities involved only *Actinobacteria* and *Deltaproteobacteria*, based on metabolic pathway reconstructions (71). These apparently inconsistent results are probably the result of the different methodologies used and/or are related to the environment studied (hot versus polar desert).

Assimilatory and Dissimilatory Nitrate Reduction

Assimilatory and dissimilatory nitrate reductions are biological processes by which nitrate is reduced, via a nitrite intermediate, to the more assimilable ammonium ions, which are either excreted (dissimilatory nitrate reduction to ammonium [DNRA]) or incorporated into biomass (assimilatory nitrate reduction [ANR]) (Fig. 2). DNRA and ANR processes have been largely unstudied in arid environments, despite the existence of phylogenetic markers that can be used to infer the relative abundances of the key genes and the phylogenetic affiliations of the host taxa (Fig. 2) (78, 83, 125). DNRA is controlled mainly by the C/N and NO_2^-/NO_3^- ratios (147), i.e., is favored in nitrate-limited and high-C-content soils. Furthermore, this process has been shown to rather occur in soils in anoxic (when nitrate and nitrite are used as terminal electron acceptors rather than oxygen) and flooded states (148). These do not correspond to typical desert conditions and therefore may explain why this process remains understudied. Nevertheless, cross-biome comparative analyses clearly showed that DNRA is a ubiquitous terrestrial process, even occurring, but at the lowest rates, in desert soils (141). This strongly suggests that DNRA is generally an overlooked terrestrial process in studies of the fate of environmental N.

In Antarctica, DNRA and ANR communities have been ubiquitously detected, i.e., observed in edaphic, hypolithic, and chasmo- and crypotendolic niches (78), and have displayed niche differentiation, with, for example, soil communities showing significantly higher ANR and DNRA gene abundances than hypolithons (83). Furthermore, in all these niches, the DNRA- and ANR-performing taxa were very diverse and belonged to numerous prokaryotic and some fungal phyla (78, 83). More specifically, *Halobacteria*, *Betaproteobacteria*, and *Deltaproteobacteria* with the capacity to perform ANR were more abundant in Antarctic soils than in hypolithons, while hypolithic ANR communities were enriched in *Bacteroidota*, *Bacillota*, *Planctomycetota*, and *Verrumicrobiota* in comparison to edaphic samples. The Antarctic DNRA community was also found to be niche dependent, as soil communities were richer in *Actinobacteria*, *Alphaproteobacteria*, and *Deferribacterota* and hypolithic communities were richer in *Bacteroidota*, *Deltaproteobacteria*, and *Bacillota* (83).

The detection of *nrfA* genes in shotgun metagenomes from Namib Desert, Mojave Desert, and Australian hot desert soils and in the cold Gobi Desert (125) further suggests that all desert edaphic communities can perform DNRA. This is further emphasized by their detection in Australian desert soil metatranscriptomes (125) and the detection of DNRA activity in Californian desert soils (141). It was particularly noted that the Australian and Mojave Desert soil metagenomes showed significantly more *nrfA* read hits than those of the Namib and Gobi Deserts, which may suggest that temperature and/or aridity may positively select for DNRA (125). However, more studies are necessary to confirm this. Furthermore, as for Antarctic soils, DNRA community members from hot desert soils belonged to many prokaryotic groups and essentially to the *Deltaproteobacteria* (*Archangium* spp., *Myxococcus* spp., *Sorangium* spp., *Vulgatibacter* spp., *Anaeromyxobacter* spp., *Bdellovibrio* spp., *Geobacter* spp.), *Nitrospirota* ("*Candidatus* Nitrospira inopinata"), *Verrumicrobiota* (*Chthoniobacter* spp., *Lacunisphaera* spp.), *Planctomycetota* ("*Candidatus* Brocadia sínica," "*Candidatus* Jettenia caeni," *Rhodopirellula* spp.), and *Acidobacteriota* (*Geothrix* spp., *Propionibacterium* spp.) phyla.

It is worth noting that "*Candidatus* Brocadia sínica" and "*Candidatus* Jettenia caeni," which have been detected in Gobi, Namib, Mojave, and Australian desert soils (125), are also capable of the anaerobic ammonium oxidation (anammox) reaction (Fig. 2). Similarly, reads assigned to the *nrfA* genes of the euryarchaeote "*Candidatus* Methanoperedens nitroreducens," which is capable of the denitrifying anaerobic methane oxidation process (149), were detected in soils from the Gobi, Mojave, and

Australian deserts (Fig. 1) (125). Together, this suggests that certain microorganisms, depending on substrate availability, may participate in both N-input and N-loss processes. The threshold(s) governing how and when these switch to the one or the other process remains a knowledge gap to be filled to improve arid land N biogeochemical cycling models.

Nitrification

Nitrification (Fig. 2) ($NH_3/NH_4^+ \rightarrow NO_3^-$) is the principal process determining the fate of biologically fixed N in the environment (150). While both NH_3 and NH_4^+ can be oxidized to nitrate, NH_4^+ predominates the inorganic forms of N in soil and is rapidly converted to NO_3^- (151, 152). Also, NH_4^+ exists as exchangeable and soluble cations and does not easily leach from soil (151). In contrast, NH_3 exists in gas form, which can easily escape from soil surfaces to the air, especially at higher pH range (151). The effect of substrate availability supply on nitrification can be found elsewhere (152, 153).

Nitrification is performed by a group of chemolithoautotrophic prokaryotes and by chemoorganoheterotrophic bacteria and fungi, all of which oxidize various N compounds (e.g., ammonia, hydroxylamine, N organics, and/or nitrite) (154, 155). Despite being a critical component of N biogeochemical cycling (154), to the best of our knowledge, heterotrophic nitrification has never been quantified in arid soil environments. The detection of methanotrophs (i.e., presence of the *pmoA* gene marker sequence) in soil metagenomes from the Negev, Gobi, Mojave, Namib, and Australian deserts and in soil metatranscriptomes of Australian desert soils (125, 156) suggests that this guild may compete with chemoautotrophic nitrifiers and therefore may influence the fate of N in desert ecosystems (154).

Aerobic ammonia oxidation. Aerobic ammonia oxidation consists of three sequential aerobic microbially mediated steps: (i) ammonia oxidation, (ii) hydroxylamine oxidation, where both hydroxylamine and NO act as obligate intermediates (157), and (iii) nitrite oxidation (Fig. 2). All ammonia oxidizers can oxidize ammonia to hydroxylamine, and most can continue the process to form nitrite (155). Hydroxylamine oxidation to nitrite ($NH_2OH \rightarrow NO_2^-$) is catalyzed by hydroxylamine dehydrogenase, encoded by the *haoA* gene. However, to our knowledge, no data on the diversity or frequency of this gene in desert soils have been published.

The oxidation of ammonia to nitrite is the rate-limiting step of nitrification and is performed by chemolithoautotrophic ammonia-oxidizing bacteria (AOB) and archaea (AOA). AOB belong to the *Beta-* and *Gammaproteobacteria* classes (particularly the *Nitrosospira* genus, in arid environments) (158–160), and AOA belong to the *Nitrososphaerota* phylum (e.g., *Nitrososphaera* sp.) (Table 2) (155, 161). The *amoA* gene, which encodes ammonia monooxygenase, is commonly used to study the abundance and diversity of ammonia oxidizers in the environment (Fig. 1 and 2) (160), and both AOA and AOB have been frequently detected in hot and cold desert soils, BSCs, and lithic habitats (e.g., see references 71, 78, 83, 159, 160, and 161–168) (Table 2).

Ammonia-oxidizing communities in soils are globally dominated by AOA over AOB (169), and this has also been observed in most desert soil studies (164, 166, 170–172) (Table 2). The high AOA/AOB ratio observed in desert ecosystems is thought to be related to the higher resilience of AOA in more extreme environmental conditions (e.g., higher temperature and aridity) (164, 170, 173). Exceptions to this trend, where AOB dominated, include Great Basin BSCs and Negev Desert arid and semiarid soils, semiarid Australian surface soils, and some (but not all) hyperarid Antarctic Dry Valley soils (Fig. 1; Table 2) (160, 165, 170, 174). The observation that the edaphic AOB/AOA ratios varied in different Antarctic soils was interpreted as the influence of microenvironmental conditions in structuring the ammonia-oxidizing community (165). This was supported by observations that the AOB/AOA ratio in soils varied across an aridity gradient (175), where AOA abundances increased with increasing aridity, independently of the edaphic microenvironment, while AOB abundances were significantly dependent on soil carbon and ammonium content. The fact that not all arid lands present higher AOA/AOB ratios further supports the hypothesis that local environmental

TABLE 2 Microbial nitrification in hot and cold dryland/desert habitats[a]

Habitat type	Desert	Reference(s)	Potential ammonia oxidation rate	*amoA* detection and/or abundances	Diversity of ammonia oxidizers and/or nitrifiers
Biological soil crust	Arid and semiarid Eastern Australia	175	NE	*amoA*-AOB: ~3.72×10^7 copies g^{-1} soil *amoA*-AOA: ~3.16×10^8 copies g^{-1} soil	NE
	Chihuahuan Desert	131	Lichen crust: ~0–500 μmol N m^{-2} h^{-1} Light crust: ~0–210 μmol N m^{-2} h^{-1}	*amoA*-AOB: 9.80×10^{11} copies g^{-1} *amoA*-AOB: 5.92×10^{11} copies g^{-1}	NE
		170	NE	*amoA*-AOA: 1.5×10^3–6.7×10^6 copies g of crusted $soil^{-1}$ *amoA*-AOB: 8.7×10^4–5.0×10^5 copies g crusted $soil^{-1}$	*Nitrososphaera* sp.
		309	~20–100 μmol m^{-2} h^{-1}	NE	NE
	Colorado Plateau	170	NE NE	*amoA*-AOA: 2.0×10^3–5.8×10^6 copies g crusted $soil^{-1}$ *amoA*-AOB: 9.2×10^4–5.9×10^5 copies g crusted $soil^{-1}$	*Nitrososphaera* sp.
		309	~40–50 μmol m^{-2} h^{-1}	NE	NE
		178	Dark crust: 41.98 ± 21.08 μmol m^{-2} h^{-1} Light crust: 53.38 ± 28.08 μmol m^{-2} h^{-1}	7.93 ± 5.65×10^3 AOB cells g^{-1}[b] 6.69 ± 6.20×10^3 AOB cells g^{-1}[b]	NE NE
	Great Basin	170	NE NE	*amoA*-AOA: 5.4×10^1–4.8×10^4 copies g crusted $soil^{-1}$ *amoA*-AOB: 2.2×10^4–5.0×10^6 copies g crusted $soil^{-1}$	*Nitrososphaera* sp.
		132	Dark crust: ~0–400 μmol N m^{-2} h^{-1} Light crust: ~0–840 μmol N m^{-2} h^{-1}	*amoA*-AOB: 1.99×10^{12} copies g^{-1} *amoA*-AOB: 7.43×10^{11} copies g^{-1}	NE NE
	Mojave Desert	309	~40–260 μmol m^{-2} h^{-1}	NE	NE
	Negev Desert	332	Cyanobacterial crust: NE	*amoA*-AOB: ~3.16×10^{10}–6.31×10^{10} copies cm^{-2} *amoA*-AOA: ~1×10^3–1.58×10^3 copies cm^{-2} *Nitrobacter* sp: ~7.94×10^3–2×10^4 copies cm^{-2}	*Nitrosospira* sp. Distantly related to *Nitrososphaera* sp. *Nitrobacter* sp.
			Moss crust: NE	*amoA*-AOB: ~7.95×10^{10} copies cm^{-2} *amoA*-AOA: ~2×10^4 copies cm^{-2} *Nitrobacter* sp.: 2.51×10^5 copies cm^{-2}	*Nitrosospira* sp. Distantly related to *Nitrososphaera* sp. *Nitrobacter* sp.
	Omani Desert	163	Cyanobacterial crust: 15 ± 2 μmol N m^{-2} h^{-1}	*Betaproteobacteria*: 1.3 ± 0.1 × 10^6 copies g^{-1} crust *Gammaproteobacteria*: 2.9 ± 0.1 × 10^7 copies g^{-1} crust *amoA*-AOA: 9.3 ± 13.1 × 10^7 copies g^{-1} crust	NE
			Lichen crust: 11 ± 5 μmol N m^{-2} h^{-1}	*Betaproteobacteria*: 1.6 ± 0.1 × 10^7 copies g^{-1} crust *Gammaproteobacteria*: 2.0 ± 1.4 × 10^8 copies g^{-1} crust *amoA*-AOA: 2.6 ± 2.6 × 10^6 copies g^{-1} crust	NE
	Semiarid Spain (Aranjuez Exptl Station)	180	NE	Low biocrust cover: *amoA*-AOB: 1.5–~1.9 × 10^7 copies g^{-1} soil; *amoA*-AOA: 1.6 × 10^6–~1.4 × 10^8 copies g^{-1} soil High biocrust cover: *amoA*-AOB: 1.7–~1.85 × 10^7 copies g^{-1} soil; *amoA*-AOA: 1.2 × 10^7–~1.5 × 10^8 copies g^{-1} soil	NE NE
	Sonoran Desert	309	~50–100 μmol m^{-2} h^{-1}	NE	NE
		170	NE	*amoA*-AOA: 2.8×10^3–5.5×10^6 copies g of crusted $soil^{-1}$ *amoA*-AOB: 3.9×10^3–3.7×10^5 copies g of crusted $soil^{-1}$	*Nitrosospira* sp.
	Tengger Desert	334	Moss and bacterial BSC: NE	Moss ($n = 6$): 0.0034 ± 0.0010 Bacterial ($n = 6$): 0.0066 ± 0.0022	NE
Soil	Arid region, Xinjiang, China	340	NEA: ~0.4–0.58 μg NO_3-N+NO_2-N g^{-1} h^{-1}	*amoA*-AOA: 12–60 × 10^7 copies g^{-1} soil *amoA*-AOB: ~4–11 × 10^7 copies g^{-1} soil	NE NE
	Arid-semiarid region (Kunlun Mountain), Xinjiang, China	341	NEA: ~0.06–0.1 μg NO_3-N+NO_2-N g^{-1} h^{-1}	*amoA*-AOA: ~1.7–8.4 × 10^6 copies g^{-1} soil *amoA*-AOB: ~1–40 × 10^6 copies g^{-1} soil	NE NE
	Atacama Desert	159, 162	NE	NE	*Nitrosospira* sp.
	Semiarid Western Australia	342	NE	*amoA*-AOB: ~1.26×10^3 copies g^{-1} soil *amoA*-AOA: ~1.26×10^2 copies g^{-1} soil	NE NE
	Arid and semiarid Eastern Australia	175	NE	*amoA*-AOB: ~2.63×10^7 copies g^{-1} soil *amoA*-AOA: ~2.00×10^8 copies g^{-1} soil	NE NE
	Australian Desert	125	NE	1.8% (±0.4%) total predicted genes in metagenomes ($n = 8$) and 0.4 (±0.5) in metatranscriptomes ($n = 2$) (AOA/B)	*Nitrososphaera* sp., Candidatus *Nitrosocosmicus* sp., *Nitrosococcus* sp., *Nitrospira* sp., Candidatus *Nitrosoglobus* sp.
	Gobi	125	NE	0.7 % total predicted genes (AOA)	*Nitrososphaera* sp., Candidatus *Nitrosocosmicus* sp.
	Gurbantunggut Desert	171	NE	*amoA*-AOB: 1.17×10^4–2.36×10^6 copies g^{-1} soil *amoA*-AOA: 3.55×10^5–4.02×10^8 copies g^{-1} soil	*Nitrososphaera* sp.

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TABLE 2 (Continued)

Habitat type	Desert	Reference(s)	Potential ammonia oxidation rate	*amoA* detection and/or abundances	Diversity of ammonia oxidizers and/or nitrifiers
	Inner Mongolia Desert	176	~1.8 mg NO_2-N kg^{-1} dry soil day^{-1}	*amoA*-AOB: 1.6×10^7–1.6×10^8 copies g^{-1} dry soil *amoA*-AOA: 9×10^9–1×10^{10} copies g^{-1} dry soil	*Nitrososphaerea* sp.
		172	~0,36 μg NO_2-N g^{-1} h^{-1}	*amoA*-AOA: 2.5×10^5 copies g^{-1} soil *amoA*-AOB: 0.2×10^5 copies g^{-1} soil	NE
		343	0- to 2-cm depth: 1.2 ± 0.64 mg N kg^{-1} dry soil day^{-1} 2- to 5-cm depth: ~2.8 mg N kg^{-1} dry soil day^{-1} 5- to 10-cm depth: ~2.8 mg N kg^{-1} dry soil day^{-1}	*amoA*-AOB: ~1.78×10^6 copies g^{-1} soil *amoA*-AOA: ~3.16×10^7 copies g^{-1} soil *amoA*-AOB: ~1.00×10^6 copies g^{-1} soil *amoA*-AOA: ~5.0×10^7 copies g^{-1} soil NE	*Nitrospira* sp., *Nitrosomonas* sp., *Nitrosovibrio* sp. *Nitrososphaera* sp. *Nitrospira* sp., *Nitrosomonas* sp., *Nitrosovibrio* sp. *Nitrososphaera* sp.
		344	NE	*amoA*-AOA: $1.5-4.9 \times 10^7$ copies g^{-1} soil *amoA*-AOB: $1-\sim 8.5 \times 10^5$ copies g^{-1} soil	NE NE
	Mojave Desert	125	NE	2.4% total predicted genes (AOA)	*Nitrososphaera* sp., "*Candidatus* Nitrosocosmicus sp."
	Mu Us Desert	336	NE	*amoA*-AOA: 3.6×10^6–1.3×10^9 copies g^{-1} soil *amoA*-AOB: 5.2×10^6–9.8×10^8 copies g^{-1} soil	NE
	Namib Desert	168	NE	NE	*Nitrososphaera* sp.
		125		1.4% total predicted genes (AOA)	*Nitrososphaera* sp., "*Candidatus* Nitrosocosmicus sp."
	Negev Desert	158	0–20 μM NO_2-N	NE	*Nitrospira* sp., *Nitrosomonas* sp.
		164	Dry: 86 ± 17–120 ± 24 μg N kg^{-1} soil h^{-1}	Dry: *amoA*-AOB: ~3.16×10^5–1.58×10^7 copies g^{-1} soil; wet, ~1.00×10^5–6.31×10^5 copies g^{-1} soil	NE
			Wet: 102 ± 24–140 ± 31 μg N kg^{-1} soil h^{-1}	Dry: *amoA*-AOA: ~1.26×10^5–2.51×10^6 copies g^{-1} soil; wet, 5.01×10^5–2.51×10^6 copies g^{-1} soil	NE
		345	NE	*amoA*-AOB: 6.25×10^6–2.47×10^7 copies g^{-1} soil *amoA*-AOA: 1.36×10^7–1.37×10^8 copies g^{-1} soil	NE
		160	83 (±10)–115 (±20) μg N kg^{-1} soil h^{-1}	Arid, winter: *amoA*-AOB: ~$2.5–5.0 \times 10^7$ copies g^{-1} soil Semiarid, winter: *amoA*-AOB: ~$2.5–\sim 3.2 \times 10^7$ copies g^{-1} soil Arid, summer: *amoA*-AOB: ~7.9×10^6–2.8×10^7 copies g^{-1} soil Semiarid, summer: *amoA*-AOB: ~7.9×10^6–2.8×10^7 copies g^{-1} soil Arid, winter: *amoA*-AOA: ~6.3×10^6–1.3×10^7 copies g^{-1} soil Semiarid, winter: *amoA*-AOA: ~$1.3–2.0 \times 10^7$ copies g^{-1} soil Arid, Summer: *amoA*-AOA: ~8.9×10^7–1.3×10^8 copies g^{-1} soil Semiarid, summer: *amoA*-AOA: $5.6–6.3 \times 10^7$ copies g^{-1} soil	*Nitrosospira* sp., *Nitrosophaera* sp.
		346	NE	Sand: *amoA*-AOA: ~3.98×10^5 copies g^{-1} soil; *amoA*-AOB: ~8.91×10^4 copies g^{-1} soil Loess: *amoA*-AOA: ~4.47×10^5 copies g^{-1} soil; *amoA*-AOB: ~4.41×10^6 copies g^{-1} soil	NE NE
	Sonoran Desert	166	0.3–3 μg NO_2-N g^{-1} h^{-1}	*amoA*-AOB: ~1×10^5 copies g^{-1} soil *amoA*-AOA: ~4.4×10^5–5.4×10^5 copies g^{-1} soil	*Nitrosomonas* sp., *Nitrosospira* sp. *Nitrosopharea* sp.
	King Sejong Station and Cape Burk area (Antarctica)	257	NE	*amoA*-AOB: 1.9×10^4–2.5×10^4 copies g^{-1} soil *amoA*-AOA: $1.0 \times 10^{-4}-2.9 \times 10^{-2}$ copies g^{-1} soil	NE
	Anvers Island (Antarctica)	338	0.11–2.47 μmol N m^{-2} h^{-1}	NE	NE
	McMurdo Dry Valleys (Antarctica)	189	NE	NE	*Nitrospira* sp.
	Upper Wright Valley in McMurdo Dry Valleys (Antarctica)	165	NE	*amoA*-AOB: ~2.8×10^3 copies g^{-1} soil *amoA*-AOA: ~5.0×10^4 copies g^{-1} soil	AOBs distantly related to *Nitrosomonas* sp. and *Nitrosospira* sp. and AOAs distantly related to *Nitrosphaera sp.*
	Beacon Valley in McMurdo Dry Valleys (Antarctica)	165	NE	*amoA*-AOB: ~6.0×10^3 copies g^{-1} soil *amoA*-AOA: ~1.0×10^5 copies g^{-1} soil	AOBs distantly related to *Nitrosomonas* sp. and *Nitrosospira* sp. and AOAs distantly related to *Nitrosphaera* sp.
	Battleship Promontory Valley in McMurdo Dry Valleys (Antarctica)	165	NE	*amoA*-AOB: ~2.3×10^5 copies g^{-1} soil *amoA*-AOA: ~1.0×10^5 copies g^{-1} soil	AOBs distantly related to *Nitrosomonas* sp. and *Nitrosospira* sp. and AOAs distantly related to *Nitrosphaera* sp.
	Miers Valley in McMurdo Dry Valleys (Antarctica)	165	NE	*amoA*-AOB: ~1.38×10^6 copies g^{-1} soil *amoA*-AOA: ~4.0×10^5 copies g^{-1} soil	AOBs distantly related to *Nitrosomonas* sp. and *Nitrosospira* sp. and AOAs distantly related to *Nitrosphaera* sp.

(Continued on next page)

TABLE 2 (Continued)

Habitat type	Desert	Reference(s)	Potential ammonia oxidation rate	*amoA* detection and/or abundances	Diversity of ammonia oxidizers and/or nitrifiers
		173	NE	D	*Nitrososphaera* sp., *Nitrospira* sp.
	Taylor Valley (Antarctica)	146	NE	*amoA*-AOB detected	*Nitrosospira* sp.
	18 Antarctica soils	120	NE	16 hits in 10/18 shotgun metagenomes	*Bacteroidota*, *Cyanobacteria*, *Pseudomonadota*
	Signy Island (Antarctica)	347	NE	Vegetated: *amoA*-AOA: $0.9 \pm 1.6 \times 10^3$ copies g^{-1} soil; *amoA*-AOB: $0.4 \pm 0.3 \times 10^5$ copies g^{-1} soil	NE
				Fell-field: *amoA*-AOA: $15.3 \pm 8.7 \times 10^3$ copies g^{-1} soil; *amoA*-AOB: $3.6 \pm 6.5 \times 10^5$ copies g^{-1} soil	NE
	Anchorage Island (Antarctica)	347	NE	Vegetated: *amoA*-AOA: $0.3 \pm 0.5 \times 10^3$ copies g^{-1} soil; *amoA*-AOB: $3.5 \pm 1.2 \times 10^5$ copies g^{-1} soil	NE
				Fell-field: *amoA*-AOA: $14.4 \pm 11.0 \times 10^3$ copies g^{-1} soil; *amoA*-AOB: $7.8 \pm 3.1 \times 10^5$ copies g^{-1} soil	NE
	Svalbard, Greenland, Siberia (Arctic)	348	*In situ:* ~0.4–50 μg N g^{-1} dry wt soil day^{-1}	*amoA*-AOA: $2 \times 10^6 \pm 3 \times 10^5$–$2 \times 10^8 \pm 2 \times 10^7$ copies g^{-1} soil *amoA*-AOB: $4 \times 10^5 \pm 6 \times 10^4$–$2 \times 10^6 \pm 3 \times 10^5$ copies g^{-1} soil	*Nitrososphaera* sp.,
	Canadian High Arctic	259	NE	*amoA*-AOA: ~0.7×10^5–1.4×10^6 copies g^{-1} soil	NE
Hypolith	Namib Desert	71	NE	ND	*Nitrosomonas* sp., *Nitrobacter* sp., *Nitrospira* sp.
	Antarctica	78, 83	NE	NE	*Archaea* and *Bacteria*
Endolith	Antarctica	78, 83	NE	NE	*Archaea* and *Bacteria*
Hypersaline mat	Omani Desert	349	0.8 ± 0.4 nmol N g^{-1} h^{-1}	*Betaproteobacteria*: $6.7 \pm 1.72 \times 10^6$ copies g^{-1} mat	NE
				Gammaproteobacteria: $7.2 \pm 2.23 \times 10^7$ copies g^{-1} mat	NE
				amoA-AOA: $0.1 \pm 0.10 \times 10^7$ copies g^{-1} mat	NE

[a]D, detected; ND, not detected; NE, not evaluated; AOA, ammonia oxidizing archaea; AOB, ammonia oxidizing bacteria; NEA, nitrifying enzyme activity.
[b]Culture based.

filtering also participates in the structuring of the ammonia-oxidizing community (Fig. 1) (Table 2).

The relative abundances of AOB and/or AOA in a given system do not, however, necessarily reflect their respective contributions to the nitrification process (160, 166). In Negev Desert soils, ammonia oxidation rates were positively correlated with AOB abundances (160), while a similar correlation was observed for AOA in Sonoran and Inner Mongolian desert soils (166, 172) (Table 2). In semiarid Australian and Mongolian steppe soils, it was observed that AOB abundances positively correlated with soil nitrification rates, while those of AOA did not, which supports the view that AOB regulate nitrification in semiarid lands (174, 176).

Ammonia oxidation processes in arid soils are controlled by water availability/aridity, temperature, oxygen supply, and substrate concentrations (131, 160, 166, 176–178). As changes in both water availability and temperature are primary impacts of projected climate change scenarios (1, 24), it is likely that nitrification and other N-input processes (Fig. 2) in arid soils will also change. Recent evidence suggests that rising temperatures may stimulate N mineralization in soils and biocrusts that in turn may promote transformation of N into N_2O (179–182). For example, increasing nitrification (and incomplete denitrification) will enhance N_2O emissions, where nitrification will dominate over denitrification under aerobic conditions in dry soils (182). Also, evidence suggests that the distribution patterns of AOA are more responsive to elevated temperatures than AOB communities in dryland soils (183, 184). However, the effects of climate change on N transformation may vary geographically and latitudinally due to climatic factors (e.g., soil structure, temperature, pH, moisture, and season), suggesting different regional outcomes (180, 181, 183, 185, 186), and should be taken into consideration when evaluating potential future N_2O emissions.

Nitrite oxidation. Nitrite oxidation is particularly important for N conservation in soil ecosystems in the context of climate change, as the balance between nitrite oxidation ($NO_2^- \rightarrow NO_3^-$; N input) or reduction ($NO_2^- \rightarrow NO$; N loss) will determine if the fixed N remains in the ecosystem or is lost to the atmosphere as greenhouse gas (GHG) (Fig. 2) (187).

This process is performed by phylogenetically diverse taxa, collectively termed nitrite-oxidizing bacteria (NOB), catalyzed by nitrite oxidoreductase, and encoded by the *nxrAB* genes (Fig. 2) (187, 188). It remains an understudied step of the nitrogen cycle in desert soil environments.

The dominant NOB in desert soil environments belong to the *Nitrobacter* (*Alphaproteobacteria*) and *Nitrospira* (*Nitrospirota*) genera (Table 2). *Nitrospira* has been frequently detected in Antarctic soils and lithic niches, both by gene-specific PCR (189) and GeoChip-based studies (78, 83). However, recent data suggest that desert soils harbor substantial NOB genetic novelty. A pyrosequencing survey of *Nitrospira nxrB* genes in Namib Desert soils suggested the presence of novel NOB lineages with the identification of three new and distinct *nxrB* clusters (190). A survey comparing the functional diversities of Gobi, Namib, Australian, and Mojave Desert soil microbiomes also showed a high diversity of *nxrA* gene-harboring bacteria (i.e., *Nitrobacter* spp., *Nitrolancea* spp., *Nitrococcus* spp., *Nitrospira* spp., *Thiocapsa* spp., *Nitrospina* spp., "*Candidatus* Nitrospira spp.," "*Candidatus* Nitrospina spp.," "*Candidatus* Nitrotoga spp.") (125).

Complete ammonia oxidation (Comammox). Only members of the chemolithoautotrophic *Nitrospira* lineage II have to date been shown to perform the complete nitrification process, i.e., complete ammonia oxidation (or comammox) to nitrate ($NH_3/NH_4^+ \rightarrow NO_3^-$) (Fig. 2) (191–193). *amoA* gene phylogeny has shown that ~90% of the complete nitrifiers from dryland soils belonged to clade A.2 and ~5% to clades A.1 and B (193). Interestingly, comammox bacteria have been shown to dominate ammonia-oxidizing bacterial communities in dryland soils, with the relative abundances of their *amoA* genes representing ~80% of all AOB *amoA* sequences (193). This observation may be linked to a high affinity for ammonia uptake and growth yields per mole of oxidized NH_4^+ in comparison to incomplete ammonia oxidizers, making comammox bacteria particularly well

adapted to oligotrophic environments such as desert soils (194). Furthermore, it may also explain why in some arid lands, and against globally reported trends, the AOB/AOA ratio is high (Fig. 1; Table 2) (160, 164–166, 170–172, 174). However, the extent to which comammox bacteria actively participate in desert soil N cycling remains unknown, despite their apparent dominance in these habitats (193) (Table 2). Comparing quantitatively the comammox with the various microbially mediated nitrification processes (Fig. 2) would notably enable the assessment of whether comammox bacteria in drylands outcompete incomplete oxidizers. This is particularly relevant in the context of global climate change, as nitrification has been shown to produce the greenhouse gases NO and N_2O (Fig. 2) (195) while comammox bacteria produce NO_x (i.e., nitrous acid [HONO], nitric oxide [NO], and nitrogen dioxide [NO_2]) only at very low yields (196).

NITROGEN LOSS PROCESSES IN ARID ENVIRONMENTS

A clear understanding of the processes involved in environmental nitrogen loss is important, as these can lead to the release of greenhouse gases, nitric (NO) and nitrous (N_2O) oxides, into the atmosphere (Fig. 2) and are of fundamental importance to the nutrient status of an ecosystem. For example, in northern American deserts, N loss has been estimated to represent over 75% of the N fixed (197). Furthermore, while a cross-biome analysis has shown that desert (including polar deserts) and semidesert NO emissions are rather low (i.e., up to 0.5 Tg N $year^{-1}$), the semiarid chaparral/thorn forest biome was found to be the highest NO-emitting biome after the tropical savannas/woodland biome (4.7 versus 7.4 Tg N $year^{-1}$, respectively) (198). Together, this indicates that drylands, due to their global surface, represent important sources of nitrogen gases. Furthermore, with climate change, deserts will become hotter and experience less frequent but higher-magnitude precipitation events (139), which may influence N-loss processes. Desert and dryland N fluxes have notably been shown to vary with plant cover and can increase with water availability and higher temperatures, independently of their aridity (129, 184, 199–205). A multifactorial experiment performed in the temperate Gurbantünggüt Desert (China), however, indicates that soil N content was the most important edaphic factor (over soil temperature and moisture) driving N_2O emissions (206).

N-loss processes include abiotic N gas formation (via chemodenitrification or photodegradation), nitrate leaching and dust aerosol emissions, and microbially mediated processes, including denitrification ($NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$), anaerobic ammonium oxidation (anammox; $NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O$), denitrifying anaerobic methane oxidation ($CH_4 + NO_3^-/NO_2^- \rightarrow CO_2 + H_2O + N_2$), nitrifier denitrification ($NH_3/NH_4^+ \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$), and nitrification ($NH_4^+ \rightarrow NO/N_2O$) (184, 207–214) (Fig. 2). Denitrifying anaerobic methane oxidation is not discussed in this review since, to the best of our knowledge, it has never been studied in desert environments. Furthermore, the fact that it has not been detected in some less-extreme soils (215) suggests that this N-loss process should be marginal in desert soils.

Abiotic N Emissions

While microbial denitrification is an important N-loss process globally (216, 217), in hot deserts, particularly in summer, abiotic processes seem to dominate (201). Indeed, despite the fact that active denitrifiers have been detected in desert soils even during dry periods (e.g., see reference 124), the intensification of N emissions, particularly nitrous oxide species, at temperatures of >50°C favors the hypothesis that abiotic photodegradation and/or photochemical processes, driven by solar radiation, are responsible for hot desert NO_x gas pulses (201, 213). This is further supported by the observation that Arctic and Antarctic snow cover also produces nitrogen oxide gases by photochemical (abiotic) processes (218).

Desert dust-derived N loss has been estimated to range between 4.8 and 84.6 Tg N $year^{-1}$ (197). Desert dust N emissions are particularly important for the surrounding (recipient) environments by acting as a natural fertilizer (219, 220). It has been

estimated that total N dust deposition from deserts amounts to ~0.2 Tg N $year^{-1}$ in the Mediterranean Sea (221).

It should be noted that a very unusual, yet highly productive, abiotic N_2O emission process was discovered in a hypersaline pond in Antarctica, where nitrite/nitrate-rich brine reacts with Fe(II)-rich minerals ($Fe^{2+} + NO_3^-/NO_2^- + H_2O \rightarrow Fe_3O_4 + N_2O$) (222). With fluxes of N_2O comparable to those of fertilized agricultural soils, this process should be evaluated in depth in desert ecosystems, where salt pans, playas, and saline ponds are common features. Increasing evidence demonstrates that chemodenitrification [i.e., abiotic nitrite reduction by Fe(II)] (Fig. 2) is an important source of NO and N_2O emissions in drylands and deserts (223–225), especially upon rewetting of dry soils (224, 225). When dry soils are rewetted, accumulated NO_2^- is rapidly converted to NO and N_2O (204, 224–226). Edaphic factors, such as pH and soil organic matter (SOM), may influence chemodenitrification where acidic conditions and SOM-rich soils with a high concentration of reduced metals favor nitrite reduction (227, 228). However, research suggests that neutral pH soils can also stimulate chemodenitrification, as the latter is a surface-driven process (224, 227). Nitrite accumulates on mineral surfaces and favors nitrite reduction across a wide pH range (226). Conclusively, research to date has demonstrated that chemodenitrification is substantial in arid lands, where drought persists and its contribution to N loss and global N_2O emissions could have been largely underestimated (224, 229, 230).

Photodegradation is the process by which solar irradiance (UV and short-wavelength visible light) directly breaks down organic material (OM), for example, lignin (231, 232) and hemicellulose (233, 234), to release gaseous photoproducts (e.g., CO_2, CO, CH_4, H_2, and N_2O) through either photochemical mineralization (i.e., abiotic) or microbial facilitation (i.e., biotic) (231, 232, 235–238). In drylands, UV-driven photodegradation, in particular UV-B, has been recognized as a main driver of OM degradation and litter mass loss, as these ecosystems are characterized by sparse vegetation and high radiative loads (212, 239). This could be especially important in bare soils and senesced plant litter that are completely sun exposed (212, 240–242), although UV-A and visible light can also contribute to litter decay and gas losses (212, 235, 243). However, some dryland field and laboratory studies have found contradictory results, where mass loss was either not affected or was negatively affected by UV-B radiation (244–246). Moreover, abiotic photodegradation has emerged as a primary factor of CO_2 emissions and C loss in drylands, contributing to 1 to 4 g C m^{-2} $year^{-1}$ (212, 235, 247). It is important to note that litter degradation also releases nitrogen and that direct sunlight may cause the loss of gaseous N (e.g., NO_x and NH_3) from soils (201). Conceptual models and field studies suggest that a combination of abiotic and biotic photodegradation contributes to litter degradation and mass loss in drylands (241, 248), where abiotic processes dominate during daytime and higher rates of microbial degradation occur at night (248). However, the interaction between these two processes is complex and depends on a variety of factors such as soil moisture, temperature, and soil-litter matrix (241, 248). As climate change is predicted to expand and impact drylands globally (24), photodegradation (abiotic and biotic) will likely play a large role in regional and global C cycling and nitrogen gas formation (213, 249). As such, accounting for its impact is fundamental in litter decomposition models to predict how soil and biogeochemical cycles will respond to ongoing climate change (250).

Inevitably, abiotic N loss from deserts is a critical component of the global N biogeochemical cycling model, since this process may (i) play a critical role in maintaining the N-limited status of dryland ecosystems, (ii) enrich, and hence increase the productivity of, neighboring oligotrophic terrestrial and aquatic ecosystems, and (iii) impact the composition and chemistry of the Earth's atmosphere and therefore actively participate in global climate change.

Microbially Mediated N-Loss Processes

Denitrification. Denitrification is an anaerobic/suboxic microbially mediated multistep process in which nitrogen compounds (NO_3^-/NO_2^-) are successively reduced to

gases (nitric oxide [NO], nitrous oxide [N_2O], and dinitrogen [N_2]), encoded by a set of genes (*narG*, *nirS*, *nirK*, *norB* and *nosZ*) (Fig. 1 and 2) (204, 251–253). Of these N gases, NO and N_2O have a large impact on atmospheric chemical composition and, thus, on climate (254). In the atmosphere, NO can react with tropospheric ozone (i.e., ozone [O_3] in the innermost layer of Earth's atmosphere) to form nitrogen dioxide (NO_2), a nitrogen oxide (NO_x in Fig. 2) pollutant. Tropospheric ozone is further produced by a series of complex reactions between nitrogen dioxide (NO_2) and volatile organic compounds (VOCs) in the presence of heat and sunlight. The resultant ozone is regarded as a secondary pollutant, and levels are generally higher during hot, dry months (255). Nitrous oxide (N_2O) is a potent greenhouse gas that promotes stratospheric ozone (ozone in the second-lowest layer of Earth's atmosphere) depletion (254, 256).

Desert denitrifiers belong to a phylogenetically diverse group of bacteria and fungi, including members of *Actinomycetota*, *Bacteroidota*, *Cyanobacteria*, *Nitrospirota*, *Pseudomonadota*, Ascomycota, and Basidiomycota (78, 125, 163, 257–260) (Table 3). It has been shown that fungi dominate denitrification processes during the dry seasons in arid and semiarid ecosystems, contributing to >50% of the total soil N_2O emissions (184, 261–264). The fungal denitrification system is characterized by a copper-containing NO_2^- reductase and a cytochrome P450 NO reductase that reduces NO_2^- to N_2O (265). However, fungal denitrifiers generally lack the gene encoding N_2O reductase (*nosZ*) to further reduce N_2O to N_2, thereby generating N_2O as the end product (266). A summary of N_2O-producing fungi and associated N_2O production processes can be found elsewhere (265). Increasing evidence suggests that AOB (e.g., *Nitrosospira* or *Nitrosomonas*) and AOA have the capacity to perform denitrification in low-pH (e.g., polar desert soils) and N-limited environments (267–269). This is particularly relevant to Arctic desert soils, which have pH values ranging from ~4.4 to ~8 (270, 271). As AOA usually outnumber AOB in N-depleted soils and oligotrophic environments, it is reasonable to suggest that AOA are an important N_2O source (269). Nevertheless, current knowledge on the denitrification dynamics of AOA and AOB in desert environments is still limited, and further experimental investigation is clearly required.

Globally, denitrification significantly contributes to terrestrial N loss, ranging from ~120 Tg N $year^{-1}$ (252) to ~200 Tg N $year^{-1}$ (272). In terms of deserts, estimates of denitrification rates are highly variable, ranging from 0.4 to 10 kg N ha^{-1} $year^{-1}$ in hot deserts and BSCs (e.g., Chihuahuan, Sonoran, and Negev Deserts) (199, 273) to 19 kg N ha^{-1} $year^{-1}$ in cold deserts (Colorado Plateau) (163, 274, 275). Denitrification genes also show highly variable abundances in hot and cold desert soils and BSCs (Fig. 1). For example, *nirS* gene abundances have been shown to range from ~9.89×10^6 to ~2.00×10^{10} copies g^{-1} dry soil in the Negev Desert and Antarctica, respectively (Fig. 1). Although denitrification estimates are available for a number of deserts, it remains an understudied process in extreme environments in comparison to nitrogen fixation and nitrification. Abundances for denitrification genes (*narG, nirK*, *nirS*, *norB*, and *nosZ*) in deserts are mostly available for soils and limited to *narG*, *nirK*, *nirS*, and, rarely, *nosZ* (Fig. 2; Table 3). Given that denitrification contributes to more than 30% of N loss from terrestrial ecosystems, the need for information on denitrification at ecosystem, landscape, regional, and global scales is pressing (276).

Desert soil N emissions were found to be independent of microbial community composition (204), while those of BSCs were influenced by crust type (e.g., light, dark, chlorolichen, and moss biocrusts) (277) (Table 3). Denitrification rates in deserts have also been shown to be affected by multiple variables, including elevated soil surface temperatures, precipitation, C and N supply, vegetation, and pH (10, 253, 278–281). Denitrifying enzymes in hot desert soils show optimal activities between 30°C and 40°C (282, 283). Conversely, in the cold Arctic and Antarctic soils, denitrification potentials based on the presence of *narG, nirK*, *nirS*, *norB*, and *nosZ* genes and denitrification activity based on *in situ* and laboratory measurements of N_2O fluxes suggest that denitrification can occur from −4°C to +25°C, especially in soils with higher moisture content (281, 284–286). This clearly demonstrates a niche adaptation of the desert denitrifying guilds (287, 288).

TABLE 3 Microbial denitrification in hot and cold dryland/desert habitats[a]

Habitat type	Desert	Reference	Denitrification rates	Denitrification gene detection and/or abundances	Diversity of denitrifiers
Biological soil crust	Chihuahan Desert	309	~1 μmol m^{-2} h^{-1}	NE	NE
	Mojave Desert		~0.7–1 μmol m^{-2} h^{-1}	NE	NE
	Sonoran Desert		~1 μmol m^{-2} h^{-1}	NE	NE
	Colorado Plateau		~1 μmol m^{-2} h^{-1}	NE	NE
		275	38 ng N m^{-2} s^{-1}; 0.7 kg N ha^{-1} yr^{-1}	NE	NE
	Canyonlands, Utah	280	Light crust: 48 μg N m^{-2} day^{-1}	NE	NE
			Dark crust: 418 μg N m^{-2} day^{-1}	NE	NE
	Negev Desert	289	0.01 N_2O-N kg $soil^{-1}$ h^{-1}	NE	NE
		332	Cyanobacterial crust: 0.8– 1.3 mg N_2O m^{-2} day^{-1}	*nirK*: 2× 10^8–8 × 10^8 copies cm^{-2}	NE
				nirS: ~5.0 × 10^6–7.9 × 10^6 copies cm^{-2}	NE
			Moss crust: 1.4–2.4 N_2O mg m^{-2} day^{-1}	*nirK*: 20 × 10^8 copies cm^{-2}	NE
				nirS: ~7.94 × 10^6 copies cm^{-2}	NE
	Omani Desert	163	Lichen crust: 58 ± 20 μmol N m^{-2} h^{-1} (total denitrification; N_2O + N_2)	Nitrate reducers (*narG*): (2.2 ± 0.9) × 10^7 copies g^{-1} crust	
				Nitrate reducers (*napA*): (9.6 ± 4.1) × 10^7 copies g^{-1} crust	
				Nitrite reducers (*nirS*): (2.0 ± 0.1) × 10^7 copies g^{-1} crust	*nirS*: *Paracoccus denitrificans*
			Cyanobacterial crust: 584 ± 101 μmol N m^{-2} h^{-1} (total denitrification; N_2O + N_2)	Nitrate reducers (*narG*): (4.5 ± 2.2) × 10^6 copies g^{-1} crust	
				Nitrate reducers (*napA*): (8.9 ± 1.7) × 10^6 copies g^{-1} crust	
				Nitrite reducers (*nirS*): (6 ± 1.4) × 10^7 copies g^{-1} crust	*nirS*: *Cyanobacteria*; *Paracoccus denitrificans*; *Azospirillum* sp.
	Semiarid Spain (Aranjuez exptl Station)	181	Control low biocrust cover: ~10 μg N_2O m^{-2} day^{-1}	Control low biocrust cover: *nosZ*: ~3.16 × 10^{12} copies g^{-1} soil	NE
			Control high biocrust cover: ~20 μg N_2O m^{-2} day^{-1}	Control high biocrust cover: *nosZ*: ~1 × 10^{13} copies g^{-1} soil	NE
	Soebatsfontein, Succulent Karoo	350	Cyanobacterial crust: 208 ± 15 ng NO-N m^{-2} s^{-1}	NE	NE
			Lichen crust: 94.85 ng NO-N m^{-2} s^{-1}	NE	NE
			Moss crust: 47.61 ng NO-N m^{-2} s^{-1}	NE	NE
	Tengger Desert	334	Moss and bacterial BSC: NE	Moss: *narG*: 0.0455 ± 0.0067; *nirS*: 0.0013 ± 0.0008; *nirK*: 0.0278 ± 0.0027; *norB*: 0.0562 ± 0.0084; *nosZ*: 0.0110 ± 0.0020	NE
				Bacterial: *narG*: 0.0344 ± 0.0048; *nirS*: 0.0007 ± 0.0003; *nirK*: 0.0283 ± 0.0030; *norB*: 0.0549 ± 0.0058; *nosZ*: 0.0057 ± 0.0012	NE
Soil	Arid region, Xinjiang, China	351	−0.3–4.5 g N ha^{-1} day^{-1}	NE	NE
		340	4.30 ± 0.59 g N_2O-N ha^{-1} day^{-1}	*narG*: ~30 × 10^6−70 × 10^6 copies g^{-1} soil	NE
				nirS: 10−52 × 10^6 copies g^{-1} soil	NE
				nirK: 7.5−22 × 10^5 copies g^{-1} soil	NE
				nosZ: 10− 81× 10^6 copies g^{-1} soil	NE
		352	45.6–235 μg N_2O-N m^{-2} h^{-1}	*nirS*: ~1.8 × 10^4 copies g^{-1} soil	
				nirK: ~1.3 × 10^4 copies g^{-1} soil	*nirK*: *Sphingomonas* sp., *Chloroflexus* sp., *Frankia* sp., *Rhizobium* sp., *Arthrobacter* sp., *Sphingobium* sp., *Curvibacter* sp., *Comamonas* sp., *Bordetella* sp., *Azoarcus* sp., *Streptoalloteichus* sp.
				nosZ: ~4.1 × 10^3 copies g^{-1} soil	*nosZ*: *Nitrospirillum* sp., *Pseudomonas* sp., *Sinorhizobium* sp., *Shinella* sp., *Aeromonas* sp., *Acidovorax* sp., *Comamonas* sp., *Maritimibacter* sp., *Thioalkalivibrio* sp., *Sulfitobacter* sp., *Bordetella* sp., *Azospirillum* sp.
	Arid-semiarid region (Kunlun Mountain), Xinjiang, China	341	244 ± 20 g N_2O-N ha^{-1}	*narG*: 13−225 × 10^6 copies g^{-1} soil	NE
				nirK: ~0.7 × 10^6, 0.7 × 10^6, 2.3 × 10^6, 1.7 × 10^6, 2.2 × 10^6, 2.5 × 10^6 copies g^{-1} soil	NE
				nirS: 1.5−4.5 × 10^6 copies g^{-1} soil	NE
				nosZ: 1.8−15.0 × 10^6 copies g^{-1} soil	NE

(Continued on next page)

TABLE 3 (Continued)

Habitat type	Desert	Reference	Denitrification rates	Denitrification gene detection and/or abundances	Diversity of denitrifiers
	Atacama Desert	258	Semiarid soil: 1.81 ± 0.41 ng N_2O g^{-1} h^{-1}	*nirK*: 31 clones (semiarid soils) and 43 clones (arid soils)	*nirK*: *Bradyrhizobium* sp., *Nitrosomonas* sp., *Alcaligenes* sp., *Acidovorax* sp., *Paracoccus* sp., *Enterococcus* sp., *Chryseobacterium* sp., *Brucella suis*, *Pseudomonas* sp., *Rhizobium hedysari*
			Arid soil: ND	*nirS*: 40 clones (semiarid soils)	*nirS*: *Corynebacterium* sp., *Pseudomonas* sp., *Alcaligenes* sp., *Azoarcus* sp., *Dechloromonas* sp., *Paracoccus* sp., *Azospirillum brasilense*, *Simplicispira psychrophila*
		353	NE	A1042: *napA*: ~2.51×10^5; *narG*: ~7.94×10^4; *nirS*: ~6.31×10^6; *cnorB*: ~1.58×10^6; *qnorB*: ~7.94×10^5; *nosZ*: ~3.98×10^6 copies g^{-1} soil A1243: *napA*: ~6.31×10^5; *narG*: ~6.31×10^5; *nirS*: ~5.01×10^6; *cnorB*: ~1×10^6; *qnorB*: ~6.31×10^6; *nosZ*: ~1.26×10^6 copies g^{-1} soil A1700: *napA*: ~5.01×10^5; *narG*: ~7.94×10^4; *nirS*: ~3.98×10^6; *cnorB*: ~1.26×10^6; *qnorB*: ~1.58×10^6; *nosZ*: ~1.58×10^6 copies g^{-1} soil A2029: *napA*: ~1.58×10^6; *narG*: ~5.01×10^5; *nirS*: ~1×10^7; *cnorB*: ~2.51×10^6; *qnorB*: ~4.47×10^6; *nosZ*: ~5.01×10^6 copies g^{-1} soil A2116: *napA*: ~5.62×10^5; *narG*: ~6.31×10^4; *nirS*: ~3.98×10^6; *cnorB*: ~2.51×10^6; *qnorB*: ~2.24×10^6; *nosZ*: ~2.51×10^6 copies g^{-1} soil	
	Roxby Downs, Australia	125	NE	Metagenome: *napA* (29.5% ± 1.6% total predicted genes), *narG* (11.8% ± 0.9%), *nirK* (15.9% ± 0.9%), *nirS* (1.8% ± 0.4%), *norB* (20.6% ± 1.8%), nosZ (8.2% ± 1.5%) Metatranscriptome: *napA* (29.9% ± 5.5% total predicted genes), *narG* (49.5% ± 6.3%), *nirK* (13% ± 0.4%), *nirS* (1.7% ± 0.4%), *norB* (63.3% ± 6.6%), *nosZ* (8.6% ± 2%)	See Reference for full species list associated with the respective genes
	Chihuahuan Desert	282	Bajadas: 9 ng N g^{-1} h^{-1}	NE	NE
			Playas: 192 ng N g^{-1} h^{-1}	NE	NE
		129	Dry soil: <0.1 ng NO-N cm^{-2} h^{-1}	NE	NE
	Colorado Plateau	204	Dry soil: 0.8 ng NO_x-N m^{-2} s^{-1} and 1.0 ng N_2O-N m^{-2} s^{-1}	NE	NE
	Gobi	125	NE	*napA* (13.4% total predicted genes), *narG* (1.5%), *nirK* (5.5%), *nirS* (0.4%), *norB* (1.8%), *nosZ* (0.7%)	See Reference for full species list associated with the respective genes
	Great Basin Desert	274	19 kg N ha^{-1} yr^{-1}	NE	NE
		282	Bajadas: 43 ng N g^{-1} h^{-1}	NE	NE
			Playas: 163 ng N g^{-1} h^{-1}	NE	NE
	Gurbantunggut Desert	206	Control: 1.49 ± 0.61 μg N m^{-2} h^{-1}	NE	NE
	Inner Mongolia Desert	354	Denitrification rates: 0.48–7.64 g N_2O-N ha^{-1} day^{-1}	NE	NE
			N_2O production rates: 0.59–16.02 g N ha^{-1} day^{-1}	NE	NE
		172	Nitrate reduction: 0.34 μg g^{-1} h^{-1}	*nirK*: ~0.8×10^5 copies g^{-1} soil	NE
				nirS: ~3.3×10^4 copies g^{-1} soil	NE
				nosZ: 3.4×10^4 copies g^{-1} soil	NE
		355	Controls: 0.016 ± 0.007 kg N_2O m^{-2} h^{-1}	NE	NE
		344	0.01–0.10 μg N_2O-N g^{-1} soil h^{-1}	*narG*: 2.0−17.5 × 10^6 copies g^{-1} soil	NE
	Namib Desert	124	NE	*nar* & *nir* genes detected	nar (*Nitrospiracea*), nir (*Rubrobaceraceae, Geodermatophilaceae, Frankiaceae, Micrococcaceae, Mycobaceriaceae, Streptomycetaceae*)

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TABLE 3 (Continued)

Habitat type	Desert	Reference	Denitrification rates	Denitrification gene detection and/or abundances	Diversity of denitrifiers
		125	NE	*napA* (14% total predicted genes), *narG* (2%), *nirK* (3.3%), *nirS* (0.2%), *norB* (1.2%), *nosZ* (0.1%)	See Reference for full species list associated with the respective genes
	Mojave Desert	282	Bajadas: 13 ng N g^{-1} h^{-1}	NE	NE
			Playas: 237 ng N g^{-1} h^{-1}	NE	NE
		356	Denitrification: 161 ± 96 μg N m^{-2} day^{-1}	NE	NE
			N_2O fluxes: 30 ± 20 μg N m^{-2} day^{-1}		NE
			Potential DEA: 146 ± 8 mg N m^{-2} day^{-1}		NE
		294	N_2O fluxes (incubations, control soils): 17.5 ± 1.5 mg N_2O-N m^{-2}	NE	NE
			DEA interspace: 0.11 ± 0.08 μg N_2O-N m^{-2} s^{-1}	NE	NE
			DEA under *Larrea tridentata*: 1.10 ± 0.26 μg N_2O-N m^{-2} s^{-1}	NE	NE
			DEA under *Lycium* spp.: 0.76 ± 0.26 μg N_2O-N m^{-2} s^{-1}	NE	NE
			DEA under *Pleuraphis rigida*: 0.43 ± 0.19 μg N_2O-N m^{-2} s^{-1}	NE	NE
		299	DEA controls: 1.23 ± 0.25 μg N_2O-N g^{-1} min^{-1}	NE	NE
		279	Bare soil and soil under grass: 0.6–3.1 ng N g^{-1} soil day^{-1}	NE	NE
			Ant nest soil: 1.6–2.0 ng N g^{-1} soil day^{-1}	NE	NE
		357	Soil under *Larrea tridentata*: 2.39 ± 1.28 ng N_2O-N m^{-2} h^{-1}	NE	NE
			Interspaces: 2.74 ± 1.11 ng N_2O-N m^{-2} h^{-1}	NE	NE
		125	NE	*napA* (15.9% total predicted genes), *narG* (2.5%), *nirK* (5.2%), *nirS* (0.2%), *norB* (4.2%), *nosZ* (1%)	See Reference for full species list associated with the respective genes
	Mu Us Desert	336	NE	*nirS*: ~1 × 10^6 copies g^{-1} soil	NE
				nirK: ~3.5 × 10^6 copies g^{-1} soil	NE
				nosZ: ~1 × 10^5 copies g^{-1} soil	NE
	Negev Desert	315	~25 μg N kg^{-1} h^{-1}	NE	NE
		289	0.04 N_2O-N kg $soil^{-1}$ h^{-1}	NE	NE
		346	Sand: ~0.1–4.5 mg N_2O m^{-2} day^{-1}	Sand: *nirS*: ~3.98 × 10^6 copies g^{-1} soil; *nirK*: ~5.62 × 10^5 copies g^{-1} soil	NE
			Loess: ~0.1–6.0 mg N_2O m^{-2} day^{-1}	Loess: *nirS*: ~1.58 × 10^7 copies g^{-1} soil; *nirK*: ~5.62 × 10^6 copies g^{-1} soil	NE
	Sonoran Desert	273	Wetted soil under *Prosopis* shrubs: 11.6 g N ha^{-1} h^{-1}	NE	NE
			Wetted soil at interspaces: 0.2 g N ha^{-1} h^{-1}	NE	NE
		358	2.4 ± 2.2 ng N_2O-N m^{-2} s^{-1}	NE	NE
		202	Desert site: 3.7–14 μg N_2O-N m^{-2} h^{-1} and 5–16 μg NO-N m^{-2} h^{-1}	NE	NE
	Soebatsfontein, Succulent Karoo	350	9 ± 3 ng NO-N m^{-2} s^{-1}	NE	NE
	18 Antarctica soils	120	NE	*nap*: 2 hits in 1/18 shotgun metagenomes	*Bacteroidota*
				nar: 5 hits in 4/18 shotgun metagenomes	*Actinomycetota*, *Pseudomonadota*
				nor: 86 hits in 14/18 shotgun metagenomes	*Acidobacteria*, *Bacteroidota*, *Chloroflexi*, *Cyanobacteria*, *Pseudomonadota*
				noz: 32 hits in 8/18 shotgun metagenomes	*Actinomycetota*, *Verrucomicrobiota*, *Archaea*

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TABLE 3 (Continued)

Habitat type	Desert	Reference	Denitrification rates	Denitrification gene detection and/or abundances	Diversity of denitrifiers
	University Valley, McMurdo Dry Valleys (Antarctica)	359	NE	*narG*, *nasA*, *napA*: 62 reads of metagenome *nirK*, *nirS*, *nirA*, *nirB*, *nrfA*: 56 reads of metagenome	NE NE
	Anchorage Island (Antarctica)	103	NE	*nir*, *nar*, *nas*, *nos*	NE
	King Sejong Station and Cape Burk area (Antarctica)	257	NE	*narG*: ~1×10^8 copies g^{-1} dry soil *nirS*: ~1×10^{11} copies g^{-1} dry soil *nirK*: ~1×10^5 copies g^{-1} dry soil *norB*: ~1×10^3 copies g^{-1} dry soil *nosZ*: ~1×10^2 copies g^{-1} dry soil	NE
	Anvers Island (Antarctica)	338	0.15–2.38 μmol N m^{-2} h^{-1}	NE	NE
	Signy Island (Antarctica)	347	NE	Vegetated: *nirK*, $(0.1 \pm 0.1) \times 10^7$ copies g^{-1} soil; *nirS*, $(1.1 \pm 0.7) \times 10^7$ copies g^{-1} soil Fell-Field: *nirK*, $(5.6 \pm 8.5) \times 10^7$ copies g^{-1} soil; *nirS*, $(8.6 \pm 9.8) \times 10^7$ copies g^{-1} soil	NE NE
	Anchorage Island (Antarctica)		NE	Vegetated: *nirK*, $(0.1 \pm 0.0) \times 10^7$ copies g^{-1} soil; *nirS*, $(1.4 \pm 1.2) \times 10^7$ copies g^{-1} soil Fell-Field: *nirK*, NA; *nirS*, $(11.6 \pm 11.0) \times 10^7$ copies g^{-1} soil	NE NE
	Rotmoosferner glacier, Ötz Valley (Arctic)	360	NE	*narG*: $7.7 \times 10^7 - 1.9 \times 10^8$ copies g^{-1} soil *nirS*: $4.9 \times 10^6 - 1.1 \times 10^8$ copies g^{-1} soil *nirK*: $7.7 \times 10^6 - 5.7 \times 10^7$ copies g^{-1} soil *nosZ*: $1.3 \times 10^7 - 2.8 \times 10^8$ copies g^{-1} soil	NE NE NE NE
	Zackenberg lowlands, Greenland (High Arctic)	361	Active layer (top soil): 0.01–1.37 μg N_2O-N kg^{-1} h^{-1}	NE	NE
	Russian discontinuous permafrost tundra (Arctic)	362	Cryoturbated: 1.2–1.8 μmol N_2O g^{-1} dry wt	*narG*: $(6.5 \pm 2.0) \times 10^4$ copies ng^{-1} DNA *nirK*: $(5.1 \pm 2.1) \times 10^0$ copies ng^{-1} DNA *nirS*: $(4.6 \pm 1.0) \times 10^3$ copies ng^{-1} DNA *nosZ*: $(1.2 \pm 0.2) \times 10^1$ copies ng^{-1} DNA	*narG*: *Actinomycetota* *nirK*: *Alphaproteobacteria* *nirS*: *Alphaproteobacteria*, *Betaproteobacteria* *nosZ*: *Alphaproteobacteria*
			Unturbated: NA	*narG*: $(6.5 \pm 2.5) \times 10^2$ copies ng^{-1} DNA *nirK*: $(3.5 \pm 1.1) \times 10^1$ copies ng^{-1} DNA *nirS*: $(7.2 \pm 0.9) \times 10^3$ copies ng^{-1} DNA *nosZ*: $(2.7 \pm 1.2) \times 10^0$ copies ng^{-1} DNA	
	Palsa peat Skalluvaara, northwestern Finnish Lapland (Arctic)	363	Vegetated unfertilized palsa peat soil (*in situ*): 0.01–0.02 μmol N_2O m^{-2} h^{-1} Unsupplemented palsa peat soil microcosms, 0–20 cm: 0.4 nmol N_2O g^{-1} dry wt Unsupplemented palsa peat soil microcosms, >20 cm: 1 nmol N_2O g^{-1} dry wt	Unsupplemented palsa peat soil microcosms, 0–20 cm: *narG*: $(1.5 \pm 0.1) \times 10^4$ copies ng^{-1} DNA *nirK*: $(1.4 \pm 0.3) \times 10^0$ copies ng^{-1} DNA *nirS*: $(2.5 \pm 0.3) \times 10^2$ copies ng^{-1} DNA *nosZ*: $(4.3 \pm 0.8) \times 10^1$ copies ng^{-1} DNA Unsupplemented palsa peat soil microcosms, >20 cm: *narG*: $(5.1 \pm 0.2) \times 10^4$ copies ng^{-1} DNA *nirK*: $(8.6 \pm 2.3) \times 10^1$ copies ng^{-1} DNA *nirS*: $(3.7 \pm 0.7) \times 10^1$ copies ng^{-1} DNA *nosZ*: $(8.8 \pm 0.8) \times 10^1$ copies ng^{-1} DNA	*narG*: *Actinomycetota*, *Alphaproteobacteria* *nirK*: *Alphaproteobacteria* *nirS*: *Alphaproteobacteria*, *Betaproteobacteria* *nosZ*: *Alphaproteobacteria*, *Betaproteobacteria*
	Daring Lake, Northwest Territories, (Canadian low Arctic)	364	0.16 nmol N_2O m^{-2} s^{-1}	NE	NE
	McGill Arctic Research Station (MARS) (Canadian high Arctic)	286	Trough soils: 0.291 ± 0.086 mg N_2O m^{-2} day^{-1}	Trough soils (25 cm): *nirS*: -3 $\log_2$ copies	*nirS*: *Nitrosomonadales*, *Acidiferrobacterales*, *Rhodocyclales*, *Xanthomonadales*, *Pseudomonadales*, *Rhodobacterales*, *Burkholderiales*

(Continued on next page)

TABLE 3 (Continued)

Habitat type	Desert	Reference	Denitrification rates	Denitrification gene detection and/or abundances	Diversity of denitrifiers
			Raised polygon soils: 0.121 ± 0.16 mg N_2O m^{-2} day^{-1}	Raised polygon soils (5 cm): *nirS*: −1.1 log2 copies Raised polygon soils (25 cm): *nirS*: −5 log2 copies	*nirS*: *Xanthomonadales*, *Pseudomonadales*, *Acidiferrobacterales*; *Burkholderiales*
Cryptoendolith	University Valley, McMurdo Dry Valleys (Antarctica)	359	NE	*narG*, *nasA*, *napA*: 66 reads in metagenome *nirK*, *nirS*, *nirA*, *nirB*, *nrfA*: 62 reads in metagenome	NE NE
Hypolith	Namib Desert	71	NE	*nar*, *nor*, *nap*	*Actinomycetota*
Hypersaline Mat	Omani desert	349	2.0 ± 1.0 nmol N g^{-1} h^{-1}	*narG*: (8.5 ± 0.7) × 10^6 copies g^{-1} mat *nirS*: (3.9 ± 1.5) × 10^6 copies g^{-1} mat *napA*: (9.3 ± 0.7) × 10^7 copies g^{-1} mat	*nosZ* (*Halomonas koreensis*, *Rhodanobacter* sp., *Pseudomonas* sp., *Marinobacter* sp.), *nirK* (*Rhizobiales*)
Microbial mats	Fildes Peninsula (Maritime Antarctica)	365	NE	*nirK*: 57 phylotypes *nirS*: 29 phylotypes *nosZ*: 79 phylotypes	*nirK*: *Octadecabacter antarcticus* *nirS*: *Rubrivivax gelatinosus*, *Paracoccus denitrificans* *nosZ*: *Rhodopseudomonas palustris*, *Azospirillum lipoferum*, *Pseudomonas* sp., *Rhodoferax ferrireducens*

[a]D, detected; ND, not detected; NE, not evaluated; NA, not available; DEA, denitrification enzyme activity.

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NO and N_2O emissions in drylands are usually highest following precipitation and/or irrigation events (202, 206, 224, 229, 289). Wetting typically causes high soil respiration pulses (290–292), together with the release of intracellular solutes from microbial cells undergoing osmotic stress, resulting in a high flux of nutrients into soils (289, 293). Respiration may be sufficiently rapid to deplete soil oxygen levels, creating anaerobic microsites that allow for anaerobic processes to occur, with substantial release of N_2O (184, 289). In addition, niche separation of N_2O-producing microorganisms is likely to occur with drying-wetting events: fungal denitrifiers and AOA ammonia oxidizers may dominate under dry conditions, while heterotrophic bacteria may be the key mediators of denitrification under wet conditions (184).

Several studies suggest that high levels of labile C and inorganic N promote denitrification in soils (10, 279, 280, 294, 295). As most denitrifying bacteria are heterotrophs, higher concentrations of SOM are likely to increase denitrification by either (i) increasing the energy and electron supply to communities or (ii) enhancing microbial growth and metabolism (associated with high O_2 consumption), thereby forcing heterotrophs to switch from oxic to anoxic metabolism (296–298). Similarly, increased soil NO_3^- concentrations can result in higher denitrification rates and N_2O emissions (294, 297). However, this is subjected to certain conditions, such as O_2 tension and sufficient C availability (297). Soil cover type can strongly influence C and N availability, which affect denitrification rates. Several studies have shown that soils from vegetated areas (e.g., under plant canopies/shrubs) have considerably higher rates of net nitrification and potential denitrification than soils from interspaces (294, 299). These resource hot spots/islands of fertility supply sufficient C and N for increased microbial activity and N cycling. Lastly, the relationship between soil pH and potential denitrification has been well documented (300–303). Generally, denitrification rates increase with increasing pH and organic C content (to an optimum pH of ~7 to 8), with a high N_2/N_2O ratio. In contrast, denitrification activity is low in acidic soils, although the fraction of N_2O produced is high (high N_2O/N_2 ratio) (301).

Although denitrification is performed under anaerobic conditions, recent studies have unequivocally demonstrated that aerobic denitrification (i.e., simultaneous use of both oxygen [O_2] and nitrate [NO_3^-] as electron acceptors) is an active and widespread process in taxa commonly isolated from soils (287, 304). However, this process has rarely been studied in desert ecosystems, and the mechanism of aerobic denitrification, at various molecular levels, warrants further attention.

Anaerobic ammonium oxidation (Anammox). Anaerobic ammonium oxidation (anammox) is an autotrophic anaerobic process leading to the release of N_2 into the atmosphere without the concomitant emission of nitric and nitrous oxides (Fig. 2). This process is performed by members of only six known bacterial genera from the "*Candidatus* Brocadiales" order (*Planctomycetota*) but which are commonly found in many natural and engineered ecosystems (305). Anammox can be quantified with ^{15}N incorporation assays and qualitatively assessed using the phylogenetic diversity and abundances of the *hzsA/hzsB* (hydrazine synthase subunit A/B) genes (306). Globally, the abundance and diversity of anammox bacteria have been shown to be environment specific (i.e., niche partitioned) (305). Anammox activity has been found to be responsible for up to 37% of the N_2 produced in temperate soils and to be influenced by seasonal changes and depth (215, 307). The abundance of anammox bacteria depends strongly on substrate availability, i.e., NO_2^- and NH_4^+, for which many microbial guilds compete to perform their N-input and N-loss processes (Fig. 2) (308), and also water, the main limiting factor (before N) in dryland productivity. Consequently, and although anammox bacteria have been detected in various niches of hot, cold, and polar deserts, their activity was marginal even under wet conditions, suggesting that this process is not particularly important for N loss in drylands (125, 309) (Table 4).

Nitrifier denitrification and nitrification. Nitrifier denitrification and nitrification are microbial processes contributing to the release of gaseous N from ammonium (Fig. 2). Despite the existence of isotopic methods enabling the tracing of N_2O emissions (211),

TABLE 4 Microbial anammox in hot and cold dryland/desert habitats[a]

Habitat type	Desert	Reference	Anammox rate	Annamox genes	Anaerobic ammonia oxidizers
Biological soil crust	Omani Desert	163	Lichen crust: ND	NE	NE
			Cyanobacterial crust: ND	NE	NE
	Mojave Desert	309	D	NE	NE
	Chihuahan Desert	309	D	NE	NE
	Sonoran Desert	309	D	NE	NE
	Colorado Plateau	309	D	NE	NE
Soil	Australia	125	NE	ND	"*Candidatus* Brocadia sp."
	Mojave Desert	125	NE	ND	ND
	Gobi	125	NE	ND	ND
	Namib Desert	125	NE	ND	ND
Hypolith	Namib Desert	71	NE	ND	ND
Hypersaline mat	Omani Desert	349	ND	NE	NE

[a]Anammox, anaerobic ammonium oxidation; D, detected; ND, not detected; NE, not evaluated.

segregating the respective contributions of nitrification or nitrifier denitrification in the release of gaseous N remains difficult (211, 224).

Nitrifier denitrification is essentially performed by ammonia-oxidizing bacteria under water- and nutrient-limited conditions (211). These represent typical dryland environmental conditions, which suggests that in such environments, nitrifier denitrification participates in the release of N_2O (184, 211). It is noticeable that with the increasing temperatures linked to global climate change (59), ammonia-oxidizing archaeal abundances, along with their contribution to N_2O emissions, are expected to increase (184). However, to the best of our knowledge, the rate of N_2O emissions related to this specific process has never been investigated in drylands.

Nitrifying bacteria, such as *Nitrosomonas* spp., *Nitrosolobus* spp., *Nitrospira* spp., *Nitrosococcus* spp., and *Nitrosovibrio* spp., and nitrate oxidizers (e.g., *Nitrobacter* spp.) are capable of producing NO and N_2O during the oxidation of ammonium (207–209, 310–312). While their presence has been established in various niches of many drylands/deserts (Table 2) and supports the view that nitrification participates in dryland N loss, the overall low carbon content and water availability in drylands make it most certainly marginal during prolonged dry periods (205, 210). However, following precipitation events, drylands represent NO emission "hot spots," and nitrification is considered to dominate NO emissions under aerobic conditions (195). This has been linked particularly to the accumulation of N during the dry season, as plant uptake is negligible, and to decoupling it from the N biogeochemical cycling in soils (224). With the prolongation of drought periods, and therefore N accumulation, in drylands in relation to global climate change (1), NO and N_2O emissions via nitrification N loss may increase after each (rare) precipitation event, creating in the process a positive-feedback loop exacerbating climate change.

CONCLUSIONS AND PERSPECTIVES IN A WARMING WORLD

This review clearly shows that a myriad of specialized fungal and prokaryotic taxa participate in dryland N biogeochemical cycling (Fig. 1 and 2; Tables 1 to 4). Nevertheless, N-cycling microbial community and process data from major arid environments are missing (e.g., the Sahara Desert and southern African drylands) (Fig. 1). Similarly, the roles of some potentially important microbial groups and processes (e.g., nitrifier denitrification and nitrification in N_2O emissions) have yet to be studied in any detail at all. For example, the role of viruses and viral lysis in the release of nutrients and in organic matter turnover in desert soils is completely unknown (313). Also, the global contributions of microeukaryotes and macroinvertebrates in desert ecosystems to nitrogen budgets are largely unknown, despite clear evidence that these taxa actively participate in nitrogen cycling and food web dynamics in some deserts (314, 315). We expect that the ongoing development of high-throughput meta-omics technologies (124, 125, 316, 317) will help to fill in these knowledge gaps and also allow the detection of microbial N metabolisms particularly adapted to the oligotrophy and

dryness of desert ecosystems, as recently shown for carbon and energy acquisition processes of hyperarid Namib Desert and Antarctic Dry Valley soils (124, 318).

The effect of global climate change on arid ecosystem nitrogen cycling requires particular attention, especially since microbially mediated N turnover data are lacking in climate change models and the surface of hot drylands is expanding (1, 319–322). This is particularly relevant, as many microbial pathways can lead to the emissions of the potent greenhouse gas nitrous oxide (N_2O) (Fig. 2) (139). We note that the effects of climate change are geographically variable and therefore intimately dependent on the initial state of the ecosystem or region (139). The impacts of climate change on N-cycling microbial communities and processes should therefore be dryland dependent and evaluated as such. This is particularly noticeable since warming temperatures will have contrasting effects on hot and polar deserts, as the former will become hotter and drier while the latter will become hotter and more humid (319).

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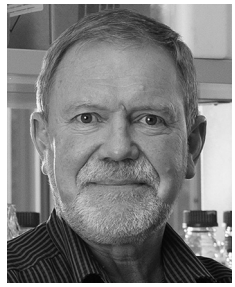

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