Microbial biogeochemical cycling of nitrogen in arid ecosystems

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SYNOPSIS

- Drylands are the most dominant terrestrial biome and Nitrogen [N] is their second most limiting factor after water.
- Human activities have increased global N atmospheric concentrations which has led to increasing atmospheric N deposition rates. This is modifying dryland ecosystems functioning and their N biogeochemical cycling.
- The biogeochemical cycling of N is largely microbially-mediated. This review describes the diversity, assembly, and abundances of the different microbial N-cycling guilds, as well as their process rates in the many dryland niches (e.g., open soils, biological soil crusts, hypoliths, endoliths and plant-influenced niches).
- The effect of global Climate Change on arid ecosystem nitrogen cycling requires particular attention, especially as various microbial N-cycling guilds can produce (nitrifiers and denitrifiers) or consume (denitrifiers and nitrifier denitrification) nitrous oxide [N_2O], a potent greenhouse gas.

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SUMMARY

Arid ecosystems cover ~40% of the Earth's terrestrial surface and store a high proportion of the global fixed N pool. They are low productivity, low biomass and polyextreme ecosystems, i.e., with (hyper)arid and (hyper)oligotrophic conditions and with high surface UV irradiation and evapotranspiration. These polyextreme conditions severely limit the presence of macro-fauna 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), nutrient biogeochemical cycling, and particularly N-cycling, in these ecosystems is 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-mineralisation, assimilatory and dissimilatory nitrate reduction and nitrification N-input processes and the denitrification and anaerobic ammonium oxidation (anammox) N-loss processes. We note that the application of modern meta-omics and related methods has generated comprehensive datasets 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 quantitate 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) over 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 (Figure 1). Drylands with an AI < 0.65 encompass various ecosystems such as scrublands, shrublands, grasslands, savannas, semi-deserts, 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 semi-arid to hyper-arid 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 poly-extreme conditions, microbial communities are most prevalent in islands of fertility ; i.e., in specialised shielded niches such as biological soil crusts (BSC), 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 (Teragram, 1×10^{9} kg) of N; 94% as bio-unavailable 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 five-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., is the most limiting nutrient (18, 19, 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) and nitrate (NO_3^-). These include biological N fixation [BNF] and nitrification, which are processes by which N is added to the environment (Figure 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) (Figure 2). Global annual terrestrial microbial production of N_2O has been estimated to amount to 7.2 – 13.2 Tg N $year^{-1}$; of which drylands contribute to 3 – 7 10^{-10} Tg N ha^{-1} $year^{-1}$ (21). Drylands covering ~6 billion hectares globally (22), this represents 1.8 - 4.2 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 availability is the dominant driver of NPP (18-20). In natural ecosystems, as opposed to engineered/man-made ecosystems like waste-water treatment plants or fertilized fields, three processes are responsible for *de novo* nitrogen inputs: (i) atmospheric wet (precipitation) as well as dry gaseous (NOx, HNO_3, and NH_3) and dust sources, (ii) lightning, and (iii) biological nitrogen fixation (BNF) (Figure 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 - 10.8 kg N ha^{-1} $year^{-1}$ and 9.4 - 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 – 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 drylands ecosystems, BNF is favoured 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 (Figure 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 (NOx, 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 (NOx), 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 up-taken 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 vary between ~0.5 to ~7.5 kg N ha^{-1} $year^{-1}$ in most drylands (46). However, it is desert/dryland dependant. In the Chihuahan Desert (USA), between 1989 and 2004, atmospheric ammonium and nitrate deposition was 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). Altogether, 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 17.8-27.8 mg L^{-1} and 36.2-71.2 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, 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 1.1-2.1 kg ha^{-1} $year^{-1}$ to 66.6-131.0 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 (±0.4) and 6.1 (±0.3) kg N ha^{-1} $year^{-1}$, respectively, over a 9-year period (2006-2015). 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 favour non-native 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 (north-western China), surface soil enzyme activities also varied after N addition (63). Altogether, this clearly shows that increasing atmospheric N deposition will modify dryland ecosystems functioning and their N biogeochemical cycling.

Biological Nitrogen Fixation (BNF)

Prokaryotic N-fixers in drylands

The phylogenetic affiliations and abundances of environmental diazotrophic taxa are generally evaluated using the nitrogenase *nifH* gene (Figures 1 & 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 community (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 these phyla have been detected in hot and cold deserts edaphic and cryptic niche communities (Figure 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 genera have already been described (89). The heterocystous cyanobacteria *Nostoc* spp. have been detected in desert niches globally (Figure 3C; Table 1). Non-heterocystous 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, which are obligate symbioses between cyanobacteria and fungi, and chlorolichens, symbiotic associations between green algae and fungi (94-98; Table 1).

BNF in the different dryland niches

Biological Soil Crusts

Biological Soil Crusts [BSCs] are complex microbial assemblages that can cover up to 70% of cold and hot deserts soil surfaces (4, 99, 100). Diazotrophic communities associated with BSCs in desert ecosystems have been well characterized (Table 1). BSCs are typically cyanobacteria-dominated, 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., *G. desertorum*), filamentous heterocystous (e.g., *Anabaena* spp., *Nostoc* spp., *Scytonema* spp.) and non-heterocystous (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 hyper-arid desert regions, which are characterised 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 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, estimates of the annual N-fixation flux contribution for each lichen-dominated BSCs species in the Colorado Plateau was 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).

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 α-, β-, and γ-proteobacterial 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 δ-, ε-, γ-Proteobacteria, Chlorobiota, Chloroflexota, Spirochaetota, Bacillota, Verrumicrobiota and Nitrospirota (78, 83; Table 1). Interestingly, metatranscriptomics data from Namib Desert hypoliths, analysed using co-occurrence networks, demonstrated that low abundance α-Proteobacterial 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 (Figure 3), these cryptic refuge lithic niches are widely assumed to act as productivity hotspots 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 hyper-arid 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 (0.02-0.174

nmol N g^{-1} h^{-1}) (65) and endoliths (0.097-2.95 mol C_2H_4 produced µg 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 hyper-arid 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 section 2.4.) and/or from atmospheric wet deposition (i.e., fog).

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., 121, 122) and their detection in meta-transcriptomes and –proteomes from hyper-arid 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 hyper-oligotrophy 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 specialised structures coating the roots of xerophytic grasses from the Poaceae and Haemodoraceae families (Figure 3D) (6, 127). Several N fixers have been isolated from rhizosheaths, including *Bacillus* spp., *Enterobacter* spp., *Serratia* spp., *Pseudomonas* spp., *Klebsiella* spp., *Agrobacteria radiobacter* and *Gluconacetobacter diazotrophicus* (128). An in-depth analysis of rhizosheath microbial communities associated with three Namib Desert dune grass species (*Stipagrostis sabulicola*, *S. seelyae* and *Cladoraphis spinosa*) showed that a sequence variant (SV) affiliated to the N-fixing *Microvarga* genus was abundant and was identified as a keystone taxon in the co-occurrence 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.

Factors controlling BNF in dryland ecosystems

Both the duration and the rate of nitrogenase activity in desert soil communities is largely controlled by the availability of water (91, 129-131). Under hyper-arid 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 solubilised 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 to 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 favoured during daylight hours, although it has been shown in BSCs to persist for 4-6h in the dark if sufficient C is available (91). The temperature dependence of BNF in the hottest hyper-arid desert soils is largely unknown. Given that surface soils in hot hyper-arid deserts (such as the Namib Desert) exceed 50^{o}C on a daily basis for much of each year (Bosch et al, submitted for publication) 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 (138). 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 mineralisation

Nitrogen mineralisation encompasses all the processes converting organic nitrogen to assimilable inorganic nitrogen (N-org → NH_4^+, NO_3^-; Figure 2). It therefore comprises

ammonification which only leads to the formation of ammonium (N-org → NH_4^+; Figure 2). This process is carried out by a cohort of heterotrophic prokaryotes and microeukaryotes (78, 83, 139) 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 mineralisation was positively correlated with soil moisture (primary factor) and negatively with soil C:N ratio (secondary factor; 140). The overall lack of water therefore explained why drylands displayed the lowest N mineralisation rates (140).

Soil leucine aminopeptidase (LAP, which degrades peptides) and β-N-acetylglucosaminidase (NAG, which degrades chitin) activities have been used as proxies for soil N-mineralisation capacity in various desert soils (141-145). Soil N-mineralisation in Antarctic Dry Valley soils was found either undetectable (when measuring NAG activity as a proxy for N mineralisation) or strongly influenced by temperatures (when measuring LAP activity), ranging from 0-15 nmol h^{-1} g^{-1} at 0°C to 15-50 nmol h^{-1} g^{-1} at 15°C (145). Hot desert microbial ammonification varied according to soil type (142), vegetation cover (143) and precipitation (144). 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 mineralisation in Namib Desert hypolithic communities involved only Actinobacteria and δ-Proteobacteria, 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 *vs* polar desert).

Assimilatory and Dissimilatory Nitrate Reduction

Assimilatory and dissimilatory nitrate reduction 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) (Figure 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 (Figure 2) (78, 83, 125). DNRA is mainly controlled by the C/N and NO_2^-/NO_3^- ratios (146), i.e., is favoured 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 (147). 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 (140). This strongly suggests that DNRA is generally an overlooked terrestrial process when studying the fate of environmental N.

In Antarctica, DNRA and ANR communities have been ubiquitously detected; i.e., observed in edaphic, hypolithic, chasmo- and crypotendolic niches (78) and 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, β- and δ-Proteobacteria 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 when compared to edaphic samples. The Antarctic DNRA community was also found to be niche-dependent as soil communities were richer in Actinobacteria, α-Proteobacteria and Deferribacterota and hypolithic communities in Bacteroidota, δ-Proteobacteria and Bacillota (83).

The detection of *nrfA* genes in shotgun metagenomes from Namib, Mojave 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 (140). 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 δ-Proteobacteria (*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 Anammox reaction (Figure 2). Similarly, reads assigned to the *nrfA* genes of the euryarchaeote Candidatus *Methanoperedens nitroreducens*, which is capable of the denitrifying anaerobic methane oxidation process (148), were detected in soils from the Gobi, Mojave and Australian deserts (Figure 1) (125). Altogether, 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 (Figure 2; $NH_3/NH_4^+ \rightarrow NO_3^-$) is the principal process determining the fate of biologically fixed N in the environment (149). While both NH_3 and NH_4^+ can be oxidized to nitrate, NH_4^+ predominates inorganic forms of N in soil and is rapidly converted to NO_3^- (150, 151). Also, NH_4^+ exists as exchangeable and soluble cations and don't easily leach from soil (150). In contrast, NH_3 exists in gas form that can easily escape from soil surfaces to the air, especially at higher pH range (150). The effect of substrate availability supply on nitrification can be found elsewhere (151, 152).

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) (153, 154). Despite being a critical component of N biogeochemical cycling (153), to the best of the authors' 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, 155) suggests that this guild may compete with chemoautotrophic nitrifiers and therefore may influence the fate of N in desert ecosystems (153).

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 (156), and (iii) nitrite oxidation (Figure 2). All ammonia oxidizers can oxidize ammonia to hydroxylamine and most can continue the process to form nitrite (154). Hydroxylamine oxidation to nitrite ($NH_2OH \rightarrow NO_2^-$) is catalysed by hydroxylamine dehydrogenase, encoded by the *haoA* gene. However, to the authors' 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). AOBs belong to the β- and γ-Proteobacteria classes (particularly the *Nitrosospira* genus, in arid environments) (157-159) and AOAs to the Nitrososphaerotaphylum (e.g., *Nitrososphaera* sp.; Table 2) (154, 160). The *amoA* gene, which encodes ammonia monooxygenase, is commonly used to study the abundance and diversity of ammonia oxidizers in the environment (Figures 1 & 2) (160) and both AOAs and AOBs have been frequently detected in hot and cold desert soils, BSCs and lithic habitats (e.g., 71, 78, 83, 158, 159, 161-167; Table 2).

Ammonia oxidizing communities in soils are globally dominated by AOAs over AOBs (168) and this has also been observed in most desert soil studies (163, 165, 169-171; Table 2). The high AOA/AOB ratio observed in desert ecosystems is thought to be related to the higher resilience of AOAs in more extreme environmental conditions (e.g., higher temperature and aridity) (163, 169, 172). Exceptions to this trend, where AOBs dominated, include Great Basin BSCs and Negev Desert arid and semiarid soils, semi-arid Australian surface soils and some (but not all) hyper-arid Antarctic Dry Valley soils (Figure 1; Table 2) (159, 164, 169, 173). The observation that the edaphic AOB/AOA ratios varied in different Antarctic soils was interpreted as the influence of micro-environmental conditions in structuring the ammonia oxidizing community (164). This was supported by observations that the AOB/AOA ratio in soils varied across an aridity gradient (174), where AOA abundances increased with increasing aridity, independently of the edaphic micro-environment, 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 filtering also participates in the structuring of the ammonia oxidizing community (Figure 1; Table 2).

The relative abundances of AOBs and/or AOAs in a given system does not, however, necessarily reflect their respective contributions to the nitrification process (159, 165). In Negev Desert soils, ammonia oxidation rates were positively correlated with AOB abundances (159), while a similar correlation was observed for AOA in Sonoran and Inner Mongolian desert soils (165, 171; Table 2). In semi-arid 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 AOBs regulate nitrification in semi-arid lands (173, 175).

Ammonia oxidation processes in arid soils are controlled by water availability/aridity, temperature, oxygen supply and substrate concentrations (131, 159, 165, 175-177). 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 (Figure 2) processes 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 (178-181). For example, increasing nitrification (and incomplete denitrification) will enhance N_2O emissions where nitrification will dominate over denitrification under aerobic conditions in dry soils (181). Also, evidence suggest that the distribution patterns of AOA are more responsive to elevated temperatures than AOB communities in dryland soils (182, 183). 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 (179, 180, 182, 184, 185), 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 GHG (Figure 2) (186).

This process is performed by phylogenetically diverse taxa, collectively termed nitrite oxidizing bacteria (NOB), catalysed by nitrite oxidoreductase and encoded by the *nxrAB*

genes (Figure 2) (186, 187) and remains an understudied step of the nitrogen cycle in desert soil environments.

The dominant NOB in desert soil environments belong to the *Nitrobacter* (α-Proteobacteria) and *Nitrospira* (Nitrospirota) genera (Table 2). *Nitrospira* has been frequently detected in Antarctic soils and lithic niches, both by gene-specific PCR (188) and GeoChip-based studies (78, 83). However, recent data suggest that desert soils harbour 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 (189). A survey comparing the functional diversities of Gobi, Namib, Australian and Mojave Desert soil microbiomes also showed a high diversity of *nxrA* gene harbouring 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 ($NH_3/NH_4^+ \rightarrow NO_3^-$; Figure 2) (190-192). *AmoA* gene phylogeny has shown that ~90% of the complete nitrifiers from dryland soils belonged to clade A.2. and ~5% to the clades A.1 and B (192). 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 (192). This observation may be linked to a high affinity for ammonia uptake and growth yields per mol of oxidised NH_4^+ when compared to incomplete ammonia oxidizers, making comammox bacteria particularly well adapted to oligotrophic environments such as desert soils (193). Furthermore, it may also explain why in some arid lands - and against global reported trends - the AOB/AOA ratio is high (Figure 1; Table 2) (159, 163-165, 169-171, 173). However, the extent to which comammox bacteria actively participate in desert soil N-cycling remains unknown, despite their apparent dominance in these habitats (192; Table 2). Comparing quantitatively the comammox and the various microbially-mediated nitrification processes (Figure 2) would notably enable to assess if comammox bacteria in drylands outcompetes 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 (Figure 2, 194)

while comammox bacteria NOx (i.e., nitrous acid [HONO], nitric oxide [NO] and nitrogen dioxide [NO_2]) only at very low yields (195).

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 (Figure 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 (196). Furthermore, while a cross biome analysis has shown that desert (including polar deserts) and semi-desert 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 vs 7.4 Tg N $year^{-1}$, respectively; 197). Altogether, 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 (138), 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, 198-203, 204, 183). 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 (205).

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 ($NH_4^+ \rightarrow NO/N_2O$) (206-208, 209-212, 183, 213) (Figure 2). Denitrifying anaerobic methane oxidation will not be discussed in this review as, to the best of the authors' knowledge, it has never been studied in desert environments. Furthermore, the fact that it has not been detected in some less extreme soils (214) 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 (215, 216), in hot deserts – particularly in summer – abiotic processes seem to dominate (200). Indeed, despite the fact that *active* denitrifiers have been detected in desert soils even during dry periods (e.g., 124), the intensification of N emissions – particularly nitrous oxide species – at temperatures >50°C favours the hypothesis that abiotic photodegradation and/or photochemical processes, driven by solar radiation, are responsible for hot desert NOx gas pulses (200, 212). This is further supported by the observation that Arctic and Antarctic snow cover also produces nitrogen oxide gases by photochemical (abiotic) processes (217).

Desert dust-derived N loss has been estimated to range between 4.8 and 84.6 Tg N $year^{-1}$ (196). Desert dust N emissions are particularly important for the surrounding (recipient) environments by acting as a natural fertilizer (e.g., 218, 219). It has been estimated that total N dust deposition from deserts amounts to ~0.2 Tg N $year^{-1}$ in the Mediterranean Sea (220).

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 ($Fe^{2+} + NO_3^-/NO_2^- + H_2O \rightarrow Fe_3O_4 + N_2O$) (221). 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); Figure 2) is an important source of NO and N_2O emissions in drylands and deserts (222-224), especially upon rewetting of dry soils (223, 224). When dry soils are rewetted, accumulated NO_2^- are rapidly converted to NO and N_2O (203, 223-225). Edaphic factors, such as pH and SOM, may influence chemodenitrification where acidic conditions and SOM-rich soils with high concentration of reduced metals favour nitrite reduction (226, 227). However, research suggest that neutral pH soils can also stimulate chemodenitrification as the latter is a surface-driven process (223, 226). Nitrite accumulates on mineral surfaces and favours nitrite reduction across a wide pH range (225). Conclusively, research to date have 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 (223, 228, 229).

Photodegradation is the process by which solar irradiance (UV and short wavelength visible light) directly breaks down organic material (OM), example lignin (230, 231) and

hemicellulose (232, 233), to release gaseous photoproducts (e.g., CO_2, CO, CH_4, H_2 and N_2O) through either photochemical mineralization (i.e., abiotic) or via microbial facilitation (i.e., biotic) (230, 231, 234-237). 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 (211, 238). This could be especially important in bare soils and senesced plant litter that are completely sun-exposed (211, 239, 240, 241), although UV-A and visible light can also contribute to litter decay and gas losses (211, 234, 242). However, some dryland field and laboratory studies have found contradictory results where mass loss was either not affected or negatively affected by UV-B radiation (243-245). Moreover, abiotic photodegradation has emerged as a primary factor of CO_2 emissions and C loss in drylands, contributing to 1-4 g C m^{-2} $year^{-1}$ (211, 234, 246). It is important to note that litter degradation also releases nitrogen and direct sunlight may cause the loss of gaseous N (e.g., NOx and NH_3) from soils (200). Conceptual models and field studies suggest that a combination of abiotic and biotic photodegradation contribute to litter degradation and mass loss in drylands (240, 247), where abiotic processes dominate during daytime and higher rates of microbial degradation occurs at night (247). 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, (240, 247). 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 (212, 248). 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 (249).

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, neighbouring 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*) (Figures 1 & 2) (203, 250-252). Of these N gases, NO and N_2O have a large impact on atmospheric chemical composition and, thus, on climate (253). 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 (NOx in Figure 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 (254). Nitrous oxide (N_2O) is a potent greenhouse gas that promotes stratospheric ozone (ozone in the second-lowest layer of Earth's atmosphere) depletion (253, 255).

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, 162, 256-259; Table 3). It has been shown that fungi dominate denitrification processes during the dry seasons in arid and semi-arid ecosystems, contributing to >50% of the total soil N_2O emissions (183, 260-263). 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 (264). 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 (265). A summary of N_2O producing fungi and associated N_2O production processes can be found elsewhere (264). 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 (266-268). This is particularly relevant to Arctic desert soils which have pH values ranging from ~4.4 to ~8 (269, 270). As AOA usually outnumber AOB in N-depleted soils and oligotrophic environments, it is reasonable to suggest that AOA is an important N_2O source (268). 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 $year^{-1}$ (251) to ~200 Tg N $year^{-1}$ (271). In terms of deserts, estimates of denitrification rates are highly variable, ranging from 0.4–10 kg N ha^{-1} $year^{-1}$ in hot deserts and BSC's (e.g., Chihuahuan, Sonoran and Negev Deserts) (198, 272) to 19 kg N ha^{-1} $year^{-1}$ in cold deserts (Colorado Plateau) (162, 273, 274). Denitrification genes also show highly variable abundances in hot and cold desert soils and BSCs (Figure 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 (Figure 1). Although denitrification estimates are available for a number of deserts, it remains an understudied process in extreme environments as compared 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* (Figure 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 (275).

Desert soil N emissions were found to be independent of microbial community composition (203), while those of BSCs were influenced by crust type (e.g., light, dark, chlorolichen and moss biocrust) (276; 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, 252, 277-280). Denitrifying enzymes in hot desert soils show optimal activities between 30°C and 40°C (281, 282). 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 (280, 283-285). This clearly demonstrates a niche adaptation of the desert denitrifying guilds (286, 287).

NO and N_2O emissions in drylands are usually highest following precipitation and/or irrigation events (201, 205, 223, 228, 288). Wetting typically causes high soil respiration pulses (289-291), together with the release of intracellular solutes from microbial cells undergoing osmotic stress, resulting in a high flux of nutrients into soils (288, 292). 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 (183, 288). 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 (183).

Several studies suggest that high levels of labile C and inorganic N promote denitrification in soils (10, 278, 279, 293, 294). 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; and (ii) enhancing microbial growth and metabolism (associated with high O_2 consumption), thereby forcing heterotrophs to switch from oxic to anoxic metabolism (295-297). Similarly, increased soil NO_3^- concentrations can result in higher denitrification rates and N_2O emissions (293, 296). However, this is subjected to certain conditions such as O_2 tension and sufficient C availability (296). 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 compared to soils from interspaces (293, 298). 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 (299-302). Generally, denitrification rates increase with increasing pH and organic C content (to an optimum pH of ~7-8), 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) (300).

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 (286, 303). 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)

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 (Figure 2). This process is performed by members of only six known bacterial genera from the Candidate Brocadiales order (Planctomycetota), but which are commonly found in many natural and engineered ecosystems (304). Anammox can be quantified with ^{15}N incorporation assays and qualitatively assessed using the phylogenetic diversity and abundances of the *hzsA/B*

(Hydrazine synthase subunits A/B) genes (e.g., 305). Globally, the abundance and diversity of anammox bacteria have been shown to be environment-specific (i.e., niche-partitioned) (304). 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 (214, 306). 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 (Figure 2; 307), and also water, the main limiting factor (before N) in dryland productivity. Consequently, and while 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, 308; Table 4).

Nitrifier denitrification and nitrification

Nitrifier denitrification and nitrification are microbial processes contributing to the release of gaseous N from ammonium (Figure 2). Despite the existence of isotopic methods enabling the tracing of N_2O emissions (210), segregating the respective contributions of nitrification or nitrifier denitrification in the release of gaseous N remains difficult (210, 223).

Nitrifier denitrification is essentially performed by ammonia oxidizing bacteria under water- and nutrient-limited conditions (210). These represent typical dryland environmental conditions which suggests that, in such environments, nitrifier denitrification participates in the release of N_2O (183, 210). It is noticeable that with the increasing temperatures linked to global climate change (59), ammonia oxidizing archaea abundances, alongside with their contribution to N_2O emissions, are expected to increase (183). 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 (206-208, 309, 310, 311). 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 (204, 209). However, following precipitation events, drylands represent NO emission “hotspots” and nitrification is considered to dominate NO emissions under

aerobic conditions (194). This has particularly been linked to the accumulation of N during the dry season as plant uptake is negligeable and decoupling it from the N biogeochemical cycling in soils (223). With the prolongation of drought periods – and therefore N accumulation - in drylands in relation with 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 specialised fungal and prokaryotic taxa participates in dryland N biogeochemical cycling (Figures 1 and 2; Tables 1-4). Nevertheless, N-cycling microbial communities and processes data from major arid environments are missing (e.g., the Sahara Desert and southern African drylands; Figure 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 (312). Also, the global contributions of microeukaryotes and macroinvertebrates in desert ecosystem to nitrogen budgets are largely unknown, despite clear evidence that these taxa actively participate in nitrogen cycling and food web dynamics in some deserts (313, 314). We expect that the ongoing development of high-throughput meta-omics technologies (124, 125, 315, 316) will enable 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 (e.g., 124, 317).

Effect of global Climate Change on arid ecosystem nitrogen cycling requires particular attention, especially as microbially-mediated N-turnover data are lacking in Climate Change models and that the surface of hot drylands is expanding (1, 318, 319-321). This is particularly relevant as many microbial pathways can lead to the emissions of the potent greenhouse gas nitrous oxide [N_2O] (Figure 2) (138). We note that the effects of Climate Change are geographically variable, and therefore intimately dependent on the initial state of the ecosystem or region (138). 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 as warming temperatures will have contrasted effect on hot or

polar deserts as the former will become hotter and drier while the latter will become hotter and more humid (318).

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FIGURE LEGENDS

Figure 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 minutes; https://data.apps.fao.org/map/catalog/srv/eng/catalog.search#/home) and visually represented with ArcGIS Pro. The AI classification is available in the figure legend. Hot, cold and polar deserts where quantification of microbial cycling genes has been performed are indicated by numbers. Quantitative expression (qPCR) 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 barplots present different scales. Genes detected by metagenomic and/or metatranscriptomic data without available quantitative expressions levels are indicated by "D". D: Detected. N.E: Not Evaluated. BSC: Biological Soil Crusts. References in Tables 1, 2 and 3.

Figure 2. The biogeochemical cycle of Nitrogen. Denitrification encompasses the nitrate, nitrite, nitric oxide and nitrous oxide reduction reactions and nitrification the aerobic ammonia, the 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 AMMmonia 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 volatilisation have notably been positively correlated to soil pH, $CaCO_3$ and salt contents and negatively to soil cation exchange capacity, organic matter and clay contents (364).

Figure 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 run-off pan with extensive *Nostoc* spp. growth. **D.** Rhizosheath-root structure of *Stipagrostis ciliata* (Namib Desert) **E.** Namib Desert stratified salt pan microbial

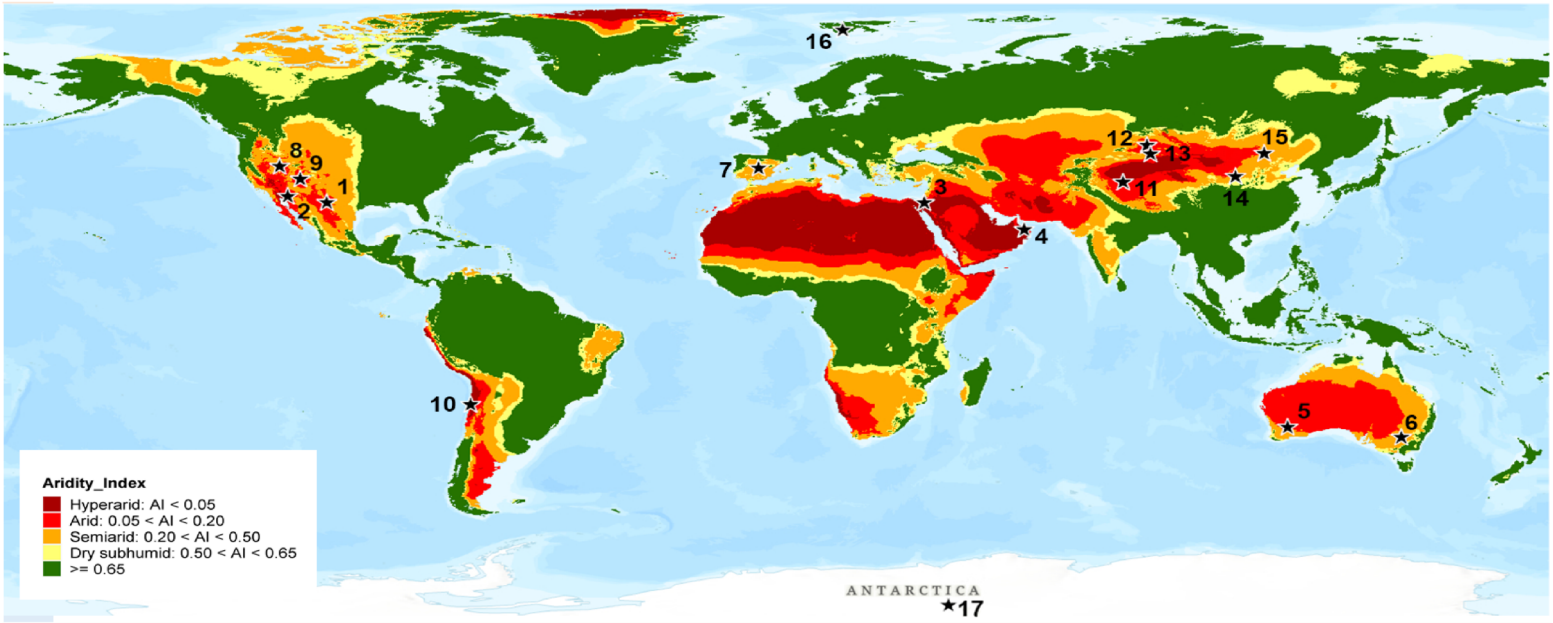
mat. The black bar represents 3 cm and the black arrows indicate the productive and N-fixing zone.

Educated in France, Jean-Baptiste Ramond completed his PhD in Microbiology/Microbial Ecology in 2008. He then moved to South Africa for a postdoctoral research fellowship (2009-2012) at the University of the Western Cape (Cape Town) and a research fellowship at the Centre for Microbial Ecology and Genomics (CMEG) of the University of Pretoria (2012-2019). In 2019, he was appointed Assistant professor at the Pontificia Universidad Católica de Chile and in parallel is an Extraordinary Lecturer of the Department of Biochemistry, Genetics & Microbiology of the University of Pretoria (NRF C2-rated since 2021) and a Visiting Academic in the Faculty of Humanities and Social Sciences of Oxford Brookes University (UK). Using *omics* technologies, his research mainly aims at better understanding the adaptation of environmental microbial communities to extreme environmental conditions and climate change, particularly in deserts.

Karen Jordaan received her Masters and Ph.D. degrees in Environmental Sciences from the North-West University, South Africa. She is currently a Fondecyt-CONICYT Postdoctoral Fellow associated with the Faculty of Biological Sciences based at Pontificia Universidad Católica de Chile, Santiago, Chile. Her main research interest focuses on understanding the impacts of extreme environments, mainly drylands, on microbial community composition, diversity, function, and interactions/co-occurrences between microorganisms.

Beatriz Díez. Dr. in Biology from the Autónoma Universidad de Barcelona (UAB) - Institute of Marine Sciences (CMIMA-CSIC) in Spain in 2001. During her PhD, she revealed the identity, diversity, and distribution of completely new picoeukaryotes in marine environments using for the first-time molecular methods. Postdoctoral fellow at the Department of Botany, Stockholm University (Sweden), studying the phylogeny, activity, and ecological importance of nitrogen-fixing cyanobacteria in marine systems; and at CMIMA-CSIC Barcelona (Spain), studying microbial ecology of marine systems. In 2010, Assistant Professor at the Department of Molecular Genetics and Microbiology of the P. Universidad Católica de Chile, where since 2016 she is Associate Professor at BDíez-Lab (bdiezlab.com) studying the ecological role of microbes and viruses, their impact on biogeochemical cycles, as well as their responses to environmental changes and perturbations, and adaptations (metabolic and genetic) combining quantitative molecular, genomic, metaomic and biogeochemical approaches.

Don Cowan was educated at the University of Waikato (New Zealand) and completed a 4-year period of postdoctoral research before moving to a Lectureship at University College London (UK) in 1985. After 16 years in London he moved to University of the Western Cape (RSA), where he established the Institute for Microbial Ecology and Metagenomics. He moved to the University of Pretoria in May 2012 in the dual role as Director of both the University of Pretoria Institutional Research Theme in Genomics and his research group, the Centre for Microbial Ecology and Genomics. He is an NRF A1-rated researcher. Don Cowan's research activities in microbial ecology are mostly linked by the theme of ‘environmental extremes’. For the past two decades he has worked on the microbial ecology of Namib Desert soils and at the lower end of the biotic temperature scale, studying the microbiology of the Dry Valleys of Eastern Antarctica in collaboration with researchers from all over the world.


Aridity_Index
Hyperarid: AI < 0.05
Arid: 0.05 < AI < 0.20
Semiarid: 0.20 < AI < 0.50
Dry subhumid: 0.50 < AI < 0.65
>= 0.65
ANTARCTICA
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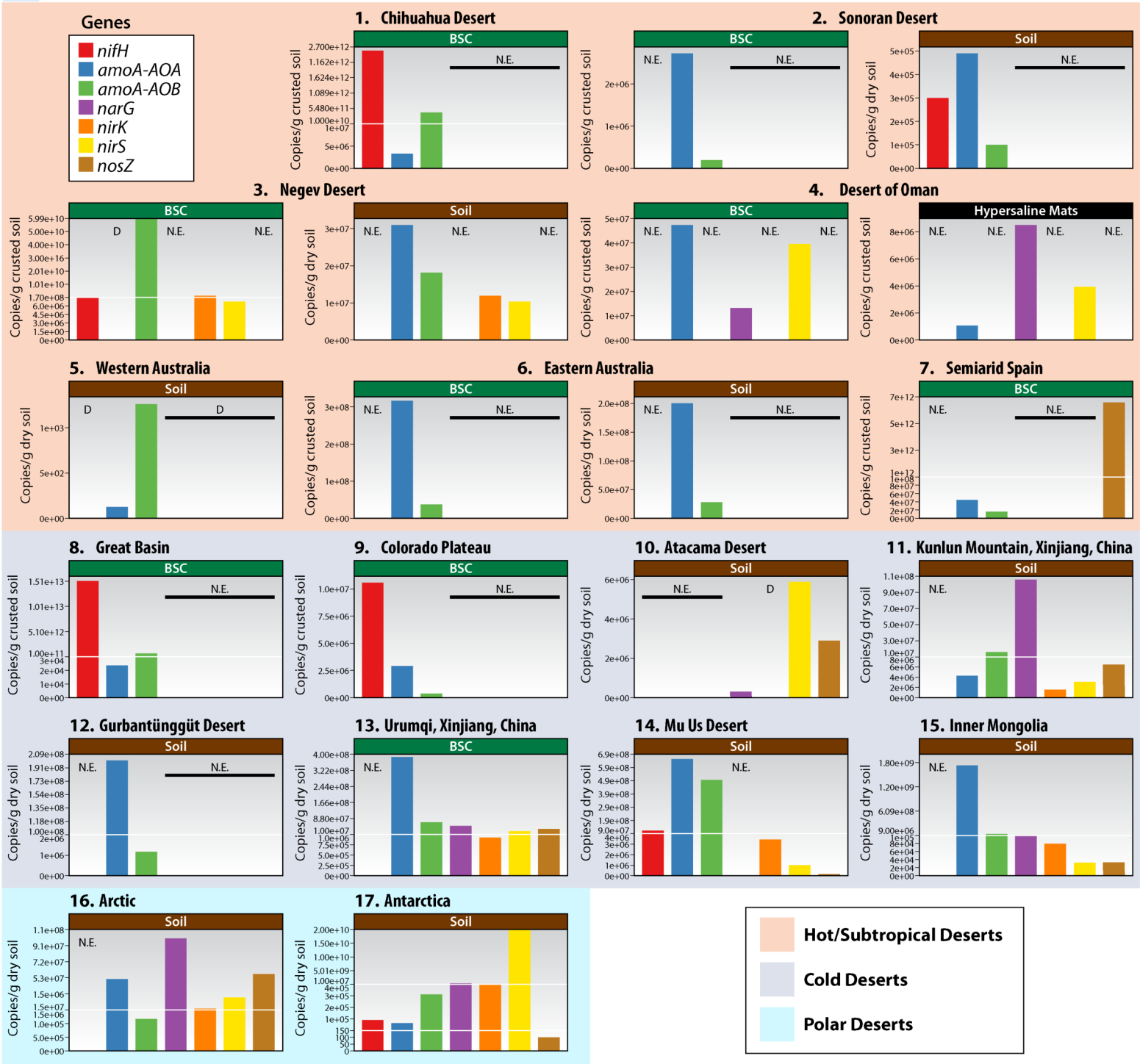
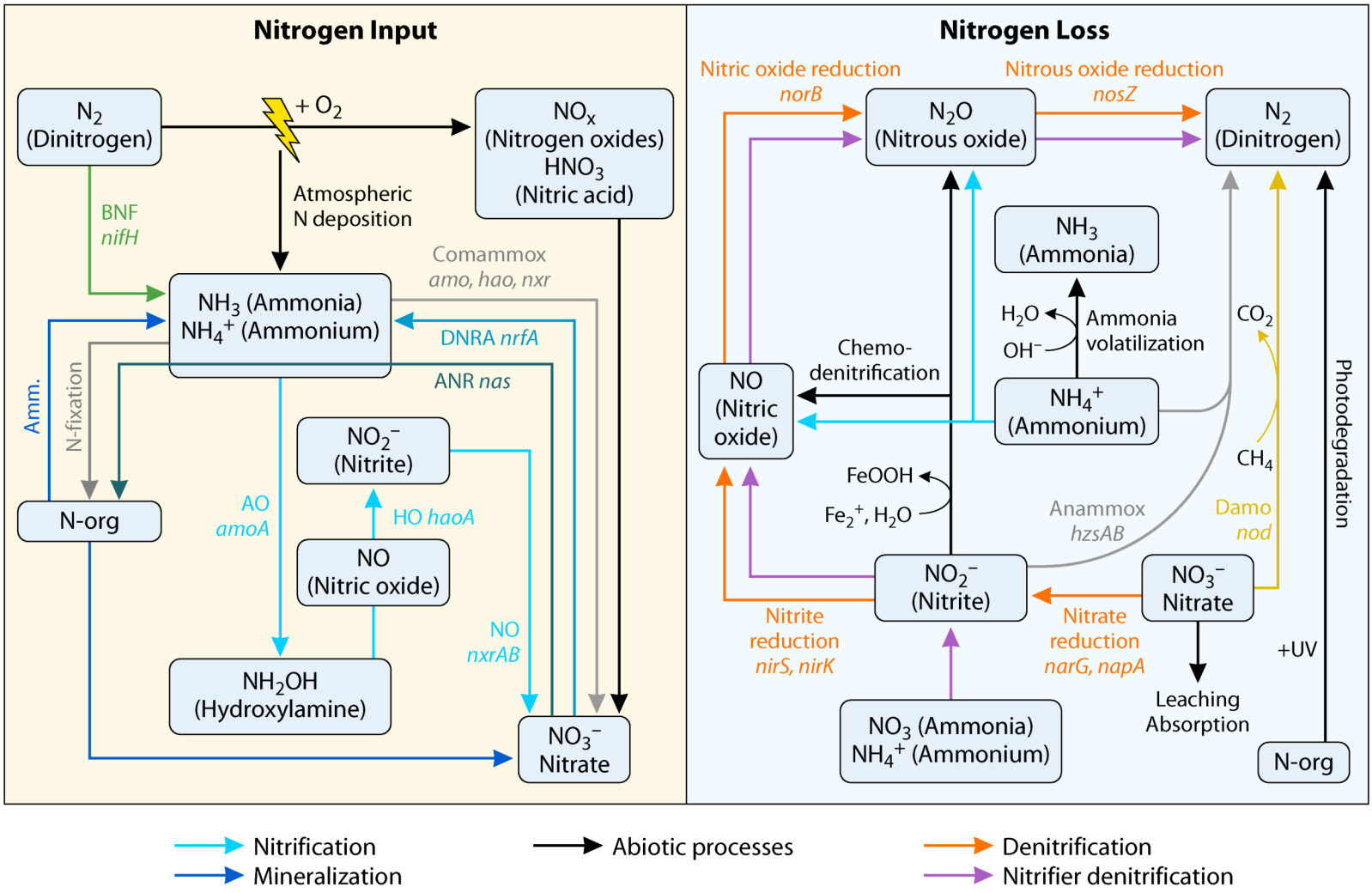
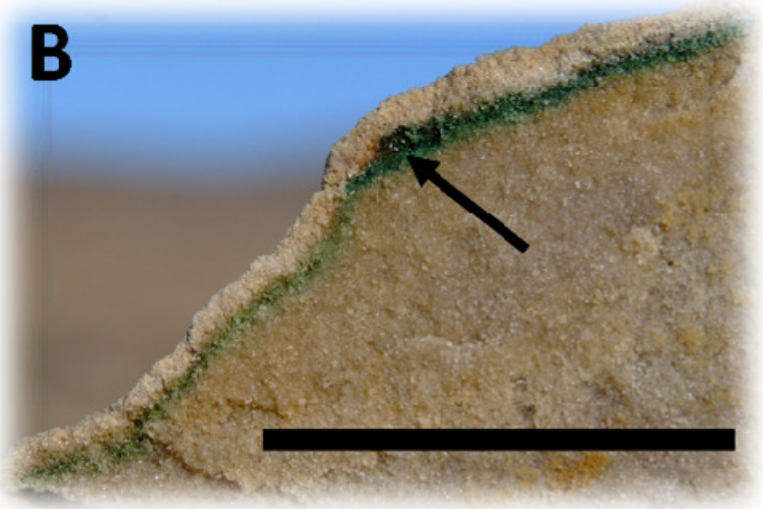

Genes
nifH
amoA-AOA
amoA-AOB
narG
nirK
nirS
nosZ
1. Chihuahua Desert
2. Sonoran Desert
3. Negev Desert
4. Desert of Oman
5. Western Australia
6. Eastern Australia
7. Semiarid Spain
8. Great Basin
9. Colorado Plateau
10. Atacama Desert
11. Kunlun Mountain, Xinjiang, China
12. Gurbantünggüt Desert
13. Urumqi, Xinjiang, China
14. Mu Us Desert
15. Inner Mongolia
16. Arctic
17. Antarctica
BSC
Soil
Hypersaline Mats
Copies/g crusted soil
Copies/g dry soil
N.E.
D
Hot/Subtropical Deserts
Cold Deserts
Polar Deserts

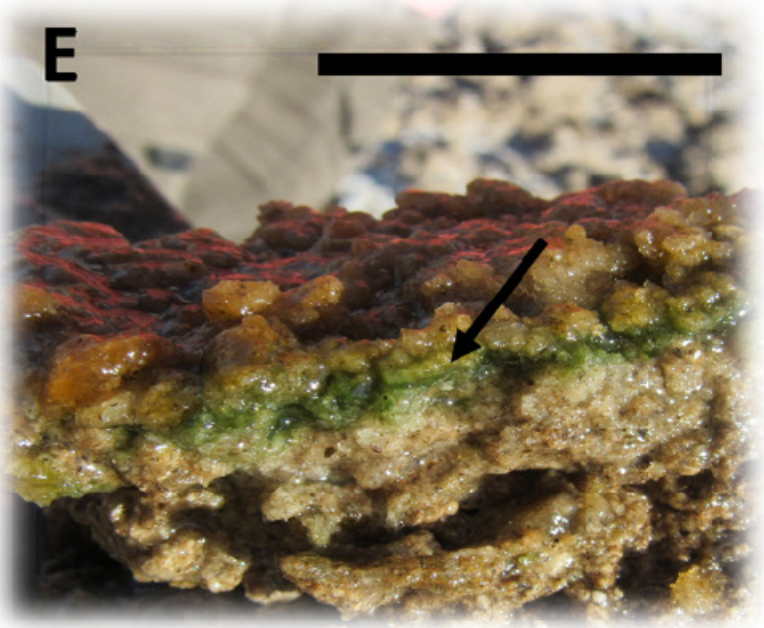

Nitrogen Input
N_2 (Dinitrogen)
+ O_2
NO_x (Nitrogen oxides) HNO_3 (Nitric acid)
BNF *nifH*
Atmospheric N deposition
Comammox *amo, hao, nxr*
NH_3 (Ammonia) NH_4^+ (Ammonium)
DNRA *nrfA*
ANR *nas*
Amm.
N-fixation
NO_2^- (Nitrite)
AO *amoA*
HO *haoA*
N-org
NO (Nitric oxide)
NO *nxrAB*
NH_2OH (Hydroxylamine)
NO_3^- Nitrate
Nitrogen Loss
Nitric oxide reduction *norB*
Nitrous oxide reduction *nosZ*
N_2O (Nitrous oxide)
N_2 (Dinitrogen)
NH_3 (Ammonia)
H_2O
OH^-
Ammonia volatilization
CO_2
Chemo-denitrification
NO (Nitric oxide)
NH_4^+ (Ammonium)
CH_4
FeOOH
Fe_2^+, H_2O
Anammox *hzsAB*
Damo *nod*
NO_2^- (Nitrite)
NO_3^- Nitrate
Photodegradation
Nitrite reduction *nirS, nirK*
Nitrate reduction *narG, napA*
+UV
Leaching Absorption
NO_3 (Ammonia) NH_4^+ (Ammonium)
N-org
Nitrification
Mineralization
Abiotic processes
Denitrification
Nitrifier denitrification


A


B


C


D


E

Habitat type	Desert	Acetylene reduction Assay rates	*nifH* detection and/or abundances	Diversity of diazotrophs	References
Biological Soil Crust	Canyonlands, Utah	Light crust: 0.13 ± 0.05 µmol m^{-2} h^{-1} Dark crust: 0.86 ± 0.26 µmol m^{-2} h^{-1}	N.E.	N.E.	279
	Chihuahuan Desert	~40 - 100 µmol m^{-2} h^{-1}	N.E.	*Scytonema* sp.*, Microcoleus steenstrupii, Microcoleus vaginatus, Pseudanabaena* sp.	308
		Early successional crust: ~3 - 20 µmol C_2H_4 m^{-2} d^{-1} Late successional crust: ~10 - 100 µmol C_2H_4 m^{-2} d^{-1}	N.E.	N.E.	322
		0,04-12,69 nmol C_2H_4 m^{-2} h^{-1} 20 nmol C_2H_4 cm^{-2} h^{-1}	N.E.	N.E.	130
		Lichen crust: ~0 - 100 µmol N m^{-2} h^{-1}	5.13 x10^{12} copies g^{-1}	*Nostoc* spp.*, Tolypothrix* spp., *Scytonema* spp.	131
		Light crust: ~0 - 50 µmol N m^{-2} h^{-1}	2.52 x10^{12} copies g^{-1}		
		Poorly developped crust *(Microcoleus* spp.-dominated): ~5 µmol m^{-2} h^{-1}	1.8 x10^{6} copies g^{-1} soil	*Microcoleus steenstrupii*, *Microcoleus vaginatus*	106
		Mature crust (mixed cyanobacteria, lichen and moss): ~12 µmol m^{-2} h^{-1}	3.4 x10^{7} copies g^{-1} soil	*Microcoleus steenstrupii, Chrococcidiopsis* sp., *Scytonema* sp.	
		N.E.	(+)	*nifH* clusters S1 (29/121; *Scytonema* sp.), S2 (7/121; *Scytonema hyalinum*), T2 (4/121; *Tolypothrix* sp.), U1 (13/121), U2 (52/121), other cyanobacterial *nifH* sequences (8/121), other bacterial *nifH* sequences (8/121)	103
		Lichen crust: ~0 - 100 µmol N m^{-2} h^{-1} Light crust: ~0 - 60 µmol N m^{-2} h^{-1}	5.13 x10^{12} copies g^{-1} 2.52 x10^{12} copies g^{-1}	*Nostoc* spp.*, Tolypothrix* spp., *Scytonema* spp.	131
	Colorado Plateau	~30 - 50 µmol m^{-2} h^{-1}	N.E.	*Scytonema* sp.*, Microcoleus steenstrupii, Microcoleus vaginatus, Pseudanabaena* sp.	308
		Early successional crust: ~3 - 76 µmol C_2H_4 m^{-2} d^{-1} Late successional crust: ~18 - 107 µmol C_2H_4 m^{-2} d^{-1}	N.E.	N.E.	322
		Lichen crust: 11.0 ± 5.7 - 57.9 nmol C_2H_4 cm^{-2} h^{-1}	N.E.	N.E.	323
		Cyanobacteria dominated crust: ~15 - 30 nmol C_2H_4 m^{-2} h^{-1} Lichen crust: ~10 - 90 nmol C_2H_4 m^{-2} h^{-1}	N.E.	*Microcoleus vaginatus, Scytonema myochrous* *Collema tenax (Nostoc* sp. as N-fixing phycobiont)	324

	Light cyabnobacteria crust: 0 - 0.80 nmol cm^{-2} h^{-1} Dark cyanobacteria crust: 0 - 5 nmol cm^{-2} h^{-1} *Colema*-crust: 0 - 13 nmol cm^{-2} h^{-1}	N.E.	*Microcoleus vaginatus* *Nostoc commune, Scytonema myochrous,* *Colema* sp	91
	N.E.	(+)	*nifH* clusters S1 (69/473; *Scytonema* sp.), S2 (62/473; *Scytonema hyalinum*), N1 (134/473; *Nostoc* sp), N2 (28/473; *Nostoc commune*), T1 (128/473; *Spirirestis* sp.), other cyanobacterial *nifH* sequences (17/473), other bacterial *nifH* sequences (83/473)	103
	Poorly developed crust *(Microcoleus* spp.-dominated): ~2.5 µmol m^{-2} h^{-1} Mature crust (mixed cyanobacteria, lichen and moss): ~20 µmol m^{-2} h^{-1}	1.1 $x10^{6}$ copies g^{-1} soil 2.0 $x10^{7}$ copies g^{-1} soil	*Microcoleus steenstrupii, Phormidium murrayii, Phormodium* sp., *Microcoleus vaginatus* *Microcoleus steenstrupii, Microcoleus sociatus, Phormidium* spp*, Scytonema* sp,	106
	Dark crust: 48.00 ± 9.31 µmol C_2H_2 reduced m^{-2} h^{-1} Light crust: 6.53 ± 1.87 µmol C_2H_4 $m^{-2}h^{-1}$	N.E.	N.E.	177
	Collema-dominated biocrusts: 1.6 nmol C_2H_2 cm^{-2} h^{-1} *Squamarina lentigera*-dominated biocrust: 0.2 nmol C_2H_2 cm^{-2} h^{-1} *Gyalolechia desertorum*-dominated biocrust: 0.4 nmol C_2H_2 cm^{-2} h^{-1}	N.E.	*Collema* spp. *Squamarina lentigera* *Gyalolechia desertorum*	98
Great Basin Desert	~15 - 90 nmol C_2H_4 cm^{-2} h^{-1}	N.E.	N.E.	324
	Ungrazed: 0.37 - 2.54 g N ha^{-1} h^{-1}	N.E.	N.E.	325
	4.3 - 72.2 nmol C_2H_4 m^{-2} s^{-1}	N.E.	N.E.	132
	10.5 - 84.0 nmol C_2H_4 m^{-2} s^{-1}	N.E.	N.E.	326
	Light crust: ~0 - 200 µmol N m^{-2} h^{-1} Dark crust: ~0 - 370 µmol N m^{-2} h^{-1}	3.94 $x10^{12}$ copies g^{-1} 2.63 $x10^{13}$ copies g^{-1}	*Nostoc* spp., *Tolypothrix* spp., *Scytonema* spp.	131
Gurbantunggut Desert	Cyanobacterial crust: 2.26 - 9.81 $x10^{3}$ nmol C_2H_4 m^{-2} h^{-1} Lichen crust: 6.54 $x10^{2}$ - 9.06 $x10^{3}$ nmol C_2H_4 m^{-2} h^{-1} Moss crust: 6.38 $x10^{2}$ - 2.03 $x10^{3}$ nmol C_2H_4 m^{-2} h^{-1}	N.E.	N.E.	110
Kalahari Desert	0.6 - 6.8 nmol C_2H_4 nmol m^{-2} h^{-1}	N.E.	N.E.	327

Mojave Desert	~30 - 200 µmol m^{-2} h^{-1}	N.E.	*Scytonema* sp., *Microcoleus steenstrupii, Microcoleus vaginatus, Pseudanabaena* sp.	308
	Lichen crust: 11.3 ± 7.7 - 25.2 ± 11.7 µmol C_2H_4 m^{-2} h^{-1} Non-lichen crust: 0 - 27.0 ± 26.3 µmol C_2H_4 m^{-2} h^{-1}	N.E.	N.E.	135
Negev Desert	34 nmol C_2H_4 cm^{-2} h^{-1}	N.E.	N.E.	328
	Cyanobacterial crust: 1.0 - 1.2 g N m^{-2} $year^{-1}$	N.E.	N.E.	329
	Cyanobacterial crust (n=4): N.E.	$6.7x10^7$- $3.4 x10^8$ copies cm^{-2}	*Microcoleus vaginatus (4/4)*, *Scytonema* sp. (3/4), *Phormidium* sp. (1/4), *Nostoc* sp. (1/4)	330
	Moss crust (n=1): N.E.	$1.6 x10^8$ copies cm^{-2}	*Microcoleus vaginatus, Nostoc* sp.	
Omani Desert	58.5 ±2.6 mmol C_2H_4 reduced m^{-2} h^{-1} (or 183–258 mg N m^{-2} h^{-1})	N.E.	*Microcoleus vaginatus, Nostoc* sp, *Scytonema* sp, *Brasilonema* sp, *Petalonema* sp	104
Sahel Desert	0.001 - 4.2 nmol C_2H_4 cm^{-2} h^{-1}	N.E.	*Nostoc* sp., *Scytonema javancum*	133
Sonoran Desert	~50 - 100 µmol m^{-2} h^{-1}	N.E.	*Scytonema sp., Microcoleus steenstrupii, Microcoleus vaginatus, Pseudanabaena sp.*	308
	78 nmol C_2H_4 cm^{-2} h^{-1}	N.E.	N.E.	331
	N.E.	N.E.	*Synechococcus* sp., *Microcoleus vaginatus, Microcoleus steenstrupi, Chroococcidiopsis* sp., *Cylindrospermum* sp., *Scytonema hyalinum*	107
Tengger Desert	Cyanobacterial-algal crust: 16.6 mmol C_2H_4 m^{-2} h^{-1} Lichen crust: 6.9 mmol C_2H_4 m^{-2} h^{-1} Moss crust: 2.6 mmol C_2H_4 m^{-2} h^{-1}	N.E.	N.E.	111
	Moss and bacterial BSC: N.E.	Moss (mean relative abundance ± SD, n=6): 0.0021 ± 0.0007 Bacterial (mean relative abundance ± SD, n=6): 0.0060 ± 0.0031	N.E.	332

Soil	Roxby Downs, Australia	N.E.	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.); α-Proteobacteria (*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.); β-Proteobacteria (*Derxia* sp., *Dechloromonas* sp., *Rubrivivax* sp., *Herbaspirillum* spp.), γ-Proteobacteria (Alteromonadales, *Beggiatoa* sp., *Neiella* sp., *Halorhodospira* sp., *Methylovulum* sp., *Agarivorans* sp., *Pseudomonas* sp., *Solimonas* sp.); δ-Proteobacteria (*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.)	125
	Gobi Desert	N.E.	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.); α-Proteobacteria (*Rhodoblastus* sp., *Cohaesibacter* sp.), β-Proteobacteria (*Rhodocyclales* spp.); γ-Proteobacteria (*Succinivibrio* sp., Candidatus *Contendobacter* sp., *Ectothiorhodospira* sp., *Halorhodospira* sp.)	
	Mojave Desert	N.E.	2.4% total predicted genes	Bacillota (*Sporobacer* sp., *Clostridum* spp., *Eubacterium* sp., *Marvinbryantia* sp., *Lachnoclostridium* spp.); Planctomycetota (*Blastopirellula* sp.); γ-Proteobacteria (*Allochromatium* sp., *Ectothiorhodospira* sp., *Halorhodospira* sp.)	

North-eastern desert region of Egypt	N.E.	2.51 x10^4 copies g^{-1} soil	α-Proteobacteria *(Rhizobium* sp., *Bradyrhizobium* sp.), Betaproteobacteria *(Ideonella* sp., *Derxia* sp., *Dechloromonas* sp., *Zoogloea* sp.), γ-Proteobacteria *(Azomonas* sp.), Bacilli *(Paenibacillus* sp.)	333
Gurbantunggut Desert	N.E.	N.E.	*Microcoleus* sp., *Chroococcidiopsis* sp., *Phormidium* sp., *Nostoc* spp.	170
Namib Desert	N.E.	(+)	Pseudomonadota	79
	N.E.	N.E.	Nostocales	123
	N.E.	(+)	N.E.	124
	N.E.	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.); α-Proteobacteria (*Sphingomonas* sp.); β-Proteobacteria (*Rhodocyclales* spp.), γ-Proteobacteria (*Marichromatium* sp., *Nitrincola* sp., *Agarivorans* sp., *Thiorhodospira* sp.); Cyanobacteria (*Trichormus* sp.)	125
Mu Us Desert	N.E.	1.3 x10^7 - 2.0 x10^8 copies g^{-1} soil	N.E.	334
Sonoran Desert	Undisturbed site: 2.4 ± 0.05 nmol C_2H_4 soil g^{-1} day^{-1}	3.02 x10^5 copies g^{-1} soil	*Azospirillum* sp., *Rhizobium* sp., *Pseudomonas* sp.	335
Tengger Desert	Control site: 0.025 ± 0.008 mmol C_2H_4 m^{-2} h^{-1}	N.E.	α-Proteobacteria (*Mesorhizobium* sp.), ε-Proteobacteria (*Arcobacter* sp.), Cyanobacteria (*Plectonema* sp.), Verrucomicrobiota, Bacillota	67
King Sejong Station & Cape Burk area (Antarctica)	N.E.	4.0 x10^4 - 1.4 x10^5 copies g-1 soil	N.E.	256
Miers Valley (Antarctica)	N.D. (0/14)	N.E.	N.E.	65
	N.E.	(+)	Archaea, Actinomycetota, α-β-δ-γ-ε-Proteobacteria, Chlorobiota, Chloroflexota, Cyanobacteria, Bacillota, Spirochaetota, Bacteroidota, Fusobacteriota	83
Anchorage Islands (Antarctica)	N.E.	D	N.E.	103
Anvers Island (Antarctica)	12.31 - 59.32 μmol N m^{-2} h^{-1}	N.E.	N.E.	336

	McKelvey Valley (Antarctica)	N.E.	(+)	Archaea, Actinomycetota, Cyanobacteria, Bacillota, Nitrospirota, α-β-δ-γ-ε-Proteobacteria, Spirochaetota	78
	18 Antarctica soils	N.E.	6 *nif* hits in 3/18 shotgun metagenomes	Cyanobacteria	120
Hypolith	Namib Desert	N.E.	(+)	Cyanobacteria, α-Proteobacteria	71
	Qaidam Basin	N.E.	N.D.	*Chroococcidiopsis* sp., *Phormidium* sp., *Micrococcus* sp.	114
	Taklimakan Desert	N.E.	N.D.	*Chroococcidiopsis* sp., *Phormidium* sp	
		N.E.	(+)	*nifH:* α-Proteobacteria (Rhodospirillales, Rhizobiales), γ-Proteobacteria (Pseudomonadales) / 16S rRNA: 14,6% of the sequences, including *Chroococcidopsis* sp. and *Phormidium* sp.	68
	Tibetan Plateau	N.E.	(+)	*nifH*: α-Proteobacteria (Rhodospirillales, Rhizobiales), β-Proteobacteria (Burkholderiales) / 16S rRNA: 18,4% of the sequences, including *Chroococcidopsis* sp. and *Phormidium* sp.	
	Turpan Depression	N.E.		*Chroococcidiopsis* sp.	114
	McKelvey Valley (Antarctica)	N.E.	(+)	Archaea, Actinomycetota, Cyanobacteria, Bacillota, Nitrospirota, α-β-δ-γ-ε-Proteobacteria, Spirochaetota	78
	Miers Dry Valley (Antarctica)	0.02–0.174 nmol N g^{-1} h^{-1} (6/12)	(+)	Cyanobacteria, Pseudomonadota	65
		N.E.	(+)	Archaea, Actinomycetota, α-β-δ-γ-ε-Proteobacteria, Chlorobiota, Chloroflexota, Cyanobacteria, Bacillota, Spirochaetota, Verrucomicrobiota	83
	McMurdo Dry Valleys (Antarctica)	N.E.	(+)	*nifH:* α-Proteobacteria (Rhizobiales), β-Proteobacteria (Burkholderiales) / 16S rRNA: 5,3% of the sequences, including *Phormidium* sp.	68
	Arctic	N.E.	N.D.	16S rRNA: 13,8% of the sequences, including Chroococcidopsis sp. and *Phormidium* sp.	
Endolith	7 hot and 41 cold deserts	Detected (1 Antarctic/48)	N.E.	N.E.	112
	Al-Jafr Basin Desert	N.E.	N.E.	*Chroococcidiopsis* sp.	113
	Mojave Desert	N.E.	N.E.	*Chroococcidiopsis* sp.	
	Atacama Desert	N.E.	N.E.	*Chroococcidiopsis* sp.	
				N.D.	70
			N.D.	N.E.	119

		N.E.	*Chroococcidiopsis* sp.	337
McKelvey Valley	N.E.	(+)	Archaea, Actinomycetota, Cyanobacteria, Bacillota, Nitrospirota, α-β-δ-γ-ε-Proteobacteria, Spirochaetota	78
McMurdo Dry Valleys	Aerobic 20°C: 0.095 - 1.2 mol C_2H_4 µg $Chla^{-1}$ g $rock^{-1}$ h^{-1}	N.E.	*Chroococcidiopsis sp.*	88
	Aerobic 5°C: 0.099 - 2.1 mol C_2H_4 µg $Chla^{-1}$ g $rock^{-1}$ h^{-1}			
	Anaerobic 20°C: 1.07 - 2.24 mol C_2H_4 µg $Chla^{-1}$ g $rock^{-1}$ $h^{-}1$			
	Anaerobic 5°C: 1.5-2.95 mol C_2H_4 µg $Chla^{-1}$ g $rock^{-1}$ h^{-1}			

Table 1. Microbial Nitrogen fixation in hot and cold dryland/desert habitats. D: Detected; N.D.: Not Detected; N.E.: Not Evaluated

Habitat type	Desert	Potential ammonia oxidation rates	*amoA* detection and/or abundances	Diversity of ammonia oxidizers and/or nitrifiers	References
Biological Soil Crust	Arid & Semiarid Eastearn Australia	N.E.	*amoA*-AOB: ~3.72 x10^{7} copies g^{-1} soil *amoA*-AOA: ~3.16 x10^{8} copies g^{-1} soil	N.E.	174
	Chihuahuan Desert	Lichen crust: ~0 - 500 µmol N m^{-2} h^{-1} Light crust: ~0 - 210 µmol N m^{-2} h^{-1}	*amoA*-AOB: 9.80 x10^{11} copies g^{-1} *amoA*-AOB: 5.92 x10^{11} copies g^{-1}	N.E.	131
		N.E.	*amoA*-AOA: 1.5 × 10^{3} – 6.7 × 10^{6} copies gram of crusted $soil^{-1}$ *amoA*-AOB: 8.7 × 10^{4} – 5.0 × 10^{5} copies g crusted $soil^{-1}$	*Nitrososphaera* sp.	169
		~20 - 100 µmol m^{-2} h^{-1}	N.E.	N.E.	308
	Colorado Plateau	N.E.	*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.	169
		~40 - 50 µmol m^{-2} h^{-1}	N.E.	N.E.	308
		Dark crust: 41.98 ± 21.08 µmol m^{-2} h^{-1}	7.93 ± 5.65 x10^{3} AOB cells g^{-1} *	N.E.	177
		Light crust: 53.38 ± 28.08 µmol m^{-2} h^{-1}	6.69 ± 6.20 x10^{3} AOB cells g^{-1} *	N.E.	
	Great Basin	N.E.	*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.	169
		Dark crust: ~0 - 400 µmol N m^{-2} h^{-1} Light crust: ~0 - 840 µmol N m^{-2} h^{-1}	*amoA*-AOB: 1.99 x10^{12} copies g^{-1} *amoA*-AOB: 7.43 x10^{11} copies g^{-1}	N.E.	131
	Mojave Desert	~40 - 260 µmol m^{-2} h^{-1}	N.E.	N.E.	308
	Negev Desert	Cyanobacterial crust: N.E.	*amoA*-AOB: ~3.16 x10^{10} - 6.31 x10^{10} copies cm^{-2} *amoA*-AOA: ~1 x10^{3} - 1.58 x10^{3} copies cm^{-2} *Nitrobacter* sp: ~7.94 x10^{3} - 2 x10^{4} copies cm^{-2}	*Nitrosospira* sp. Distantly related to *Nitrososphaera* sp. *Nitrobacter* sp.	330
		Moss crust: N.E.	*amoA*-AOB: ~7.95 x10^{10} copies cm^{-2}	*Nitrosospira* sp.	

			amoA-AOA: ~2 x10^4 copies cm^{-2}	Distantly related to *Nitrososphaera* sp.	
			Nitrobacter sp.: 2.51 x10^5 copies cm^{-2}	*Nitrobacter* sp.	
	Omani Desert	Cyanobacterial crust : 15 ± 2 µmol N m^{-2} h^{-1}	β-Proteobacteria: 1.3±0.1 x10^6 copy nb g^{-1} crust	N.E.	162
			γ-Proteobacteria: 2.9 ±0.1 x10^7 copy nb g^{-1} crust	N.E.	
			amoA-AOA: 9.3 ±13.1 x10^7 copy nb g^{-1} crust	N.E.	
		Lichen crust : 11 ±5 µmol N m^{-2} h^{-1}	β-Proteobacteria: 1.6±0.1 x10^7 copy nb g^{-1} crust	N.E.	
			γ-Proteobacteria: 2.0±1.4 x10^8 copy nb g^{-1} crust	N.E.	
			amoA-AOA: 2.6 ±2.6 x10^6 copy nb g^{-1} crust	N.E.	
	Semiarid Spain (Aranjuez Experimental Station)	N.E.	Low biocrust cover*: amoA*-AOB: ~1.9 x10^7, 1.7 x10^7, 1.75 x10^7, 1.5 x10^7; *amoA*-AOA: ~1.4 x10^8, 1.7 x10^7, 1.2 x10^7, 1.6 x10^6 copies g^{-1} soil High biocrust cover: *amoA*-AOB: ~1.85 x10^7, 1.7 x10^7, 1.8 x10^7, 1.7 x10^7; *amoA*-AOA: ~1.5 x10^8, 1.9 x10^7, 1.4 x10^7, 1.2 x10^7 copies g^{-1} soil	N.E.	179
	Sonoran Desert	~50 - 100 µmol m^{-2} h^{-1}	N.E.	N.E.	308
		N.E.	*amoA*-AOA: 2.8 × 10^3 – 5.5 × 10^6 copies gram of crusted $soil^{-1}$ *amoA*-AOB: 3.9 × 10^3 – 3.7 × 10^5 copies gram of crusted $soil^{-1}$	*Nitrososphaera* sp.	169
	Tengger Desert	Moss and bacterial BSC: N.E. Moss and bacterial BSC: N.E.	<u>Moss</u> (mean relative abundance ± SD, n=6): 0.0034 ± 0.0010 <u>Bacterial</u> (mean relative abundance ± SD, n=6): 0.0066 ± 0.0022	N.E.	332
Soil	Arid region, Xinjiang, China	Nitrifying enzyme activity (NEA): ~0.4 - 0.58 µg NO_3-N+NO_2-N g^{-1} h^{-1}	*amoA*-AOA: ~12 x10^7, 32 x10^7, 50 x10^7, 60 x10^7 copies g^{-1} soil *amoA*-AOB: ~4 x10^7, 5 x10^7, 11 x10^7 copies g^{-1} soil	N.E.	338
	Arid-semiarid region (Kunlun Mountain), Xinjiang, China	NEA: ~0.06 - 0.1 µg NO_3-N+NO_2-N g^{-1} h^{-1}	*amoA*-AOA: ~1.7 x10^6, 2.5 x10^6, 2.5 x10^6, 5.2 x10^6, 6.2 x10^6, 8.4 x10^6 copies g^{-1} soil *amoA*-AOB: ~1 x10^6, 20 x10^6, 40 x10^6, 9 x10^6, 13 x10^6, 9 x10^6 copies g^{-1} soil	N.E.	339
	Atacama desert	N.E.	N.E.	*Nitrosospira* sp.	158 161

Semiarid Western Australia	N.E.	*amoA*-AOB: ~1.26 x10^3 copies g^{-1} soil *amoA*-AOA: ~1.26 x10^2 copies g^{-1} soil	N.E.	340
Arid & Semiarid Eastearn Australia	N.E.	*amoA*-AOB: ~2.63 x10^7 - copies g^{-1} soil *amoA*-AOA: ~2.00 x10^8 copies g^{-1} soil	N.E.	174
Australian Desert	N.E.	1.8 (±0.4) % total predicted gene 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.	125
Gobi	N.E.	0.7 % total predicted genes (AOA)	*Nitrososphaera* sp., Candidatus *Nitrosocosmicus* sp.	
Gurbantunggut Desert	N.E.	*amoA*-AOB: 1.17 ×10^4 - 2.36 x10^6 copies g^{-1} soil *amoA*-AOA: 3.55 ×10^5 - 4.02 ×10^8 copies g^{-1} soil	*Nitrososphaera* sp.	170
Inner Mongolia Desert	~1.8 mg NO_2-N kg^{-1} dry soil d^{-1}	*amoA*-AOB: 1.6 x10^7 - 1.6 x 10^8 copies g^{-1} dry soil	*Nitrosospira* sp.	175
		amoA-AOA: 9 x10^9 - 1 x10^{10} copies g^{-1} dry soil	*Nitrosospharea* sp.	
	~0,36 µg NO_2-N g^{-1} h^{-1}	*amoA*-AOA: 2.5 x10^5 copies g^{-1} soil	N.E.	171
		amoA-AOB: 0.2 x10^5 copies g^{-1} soil	N.E.	
	0-2cm depth: 1.2 ± 0.64 mg N kg^{-1} dry soil d^{-1} 2-5cm depth: ~2.8 mg N kg^{-1} dry soil d^{-1} 5-10cm depth: ~2.8 mg N kg^{-1} dry soil d^{-1}	*amoA*-AOB: ~1.78 x10^6 copies g-1 soil; *amoA*-AOA: ~3.16 x10^7 copies g^{-1} soil *amoA*-AOB: ~1.00 x10^6 copies g-1 soil; *amoA*-AOA: ~5.0 x10^7 copies g^{-1} soil N.E.	*Nitrospira* sp., *Nitrosomonas* sp., *Nitrosovibrio* sp., *Nitrososphaera* sp.	341
	N.E.	*amoA*-AOA: ~4.9 x10^7, 7 x10^7, 3.9 x10^7, 2.0 x10^7, 1.5 x10^7, 1.5 x10^7 copies g^{-1} soil *amoA*-AOB: ~8.5 x10^5, 6.0 x10^5, 1.0 x10^5, 3.5 x10^5, 2.5 x10^5, 3.0 x10^5 copies g^{-1} soil	N.E.	342
Mojave Desert	N.E.	2.4% total predicted genes (AOA)	*Nitrososphaera* sp., Candidatus *Nitrosocosmicus* sp.	125
Mu Us Desert	N.E.	*amoA*-AOA: 3.6 x10^6 - 1.3 x10^9 copies g^{-1} soil *amoA*-AOB: 5.2 x10^6 - 9.8 x 10^8 copies g^{-1} soil	N.E.	334
Namib Desert	N.E.	N.E.	*Nitrososphaera* sp.	167
		1.4% total predicted genes (AOA)	*Nitrososphaera* sp., Candidatus *Nitrosocosmicus* sp.	125

Negev Desert	0 - 20 µM NO_2-N	N.E.	*Nitrosospira* sp., *Nitrosomonas* sp.	157
	Dry: 86 ± 17 - 120 ±24 µg-N kg^{-1} soil h^{-1}	Dry: *amoA*-AOB: ~3.16 $x10^5$ - 1.58 $x10^7$ copies g^{-1} soil; Wet: ~1.00 $x10^5$ - 6.31 $x10^5$ copies g^{-1} soil	N.E.	163
	Wet: 102 ±24 - 140 ±31 µg-N kg^{-1} soil h^{-1}	Dry: *amoA*-AOA: ~1.26 $x10^5$ - 2.51 $x10^6$ copies g^{-1} soil; Wet: 5.01 $x10^5$ - 2.51 $x10^6$ copies g^{-1} soil		
	N.E.	*amoA*-AOB: 6.25 $x10^6$, 2.47 $x10^7$ copies g^{-1} soil *amoA*-AOA: 1.37 $x10^8$, 1.36 $x10^7$ copies g^{-1} soil	N.E.	343
	83 (±10) - 115 (±20) µg-N kg^{-1} soil h^{-1}	Arid, Winter: *amoA*-AOB: ~2.51 $x10^7$, 3.98 $x10^7$, 5.01 $x10^7$ copies g^{-1} soil Semiarid, Winter: *amoA*-AOB: ~2.51 $x10^7$, 3.16 $x10^7$, 3.16 $x10^7$ copies g^{-1} soil Arid, Summer: *amoA*-AOB: ~7.94 $x10^6$, 2.00 $x10^7$, 2.82 $x10^7$ copies g^{-1} soil Semiarid, Summer: *amoA*-AOB: ~8.91 $x10^6$, 1.58 $x10^7$, 2.00 $x10^7$ copies g^{-1} soil Arid, Winter: *amoA*-AOA: ~6.31 $x10^6$, 1 $x10^7$, 1.26 $x10^7$ copies g^{-1} soil Semiarid, Winter: *amoA*-AOA: ~1.26 $x10^7$, 1.58 $x10^7$, 2.00 $x10^7$ copies g^{-1} soil Arid, Summer: *amoA*-AOA: ~8.91 $x10^7$, 1 $x10^8$, 1.26 $x10^8$ copies g^{-1} soil Semiarid, Summer: *amoA*-AOA: ~3.98 $x10^7$, 5.62 $x10^7$, 6.31 $x10^7$ copies g^{-1} soil	*Nitrosospira* sp., *Nitrosophaera* sp.	159
	N.E.	Sand: *amoA*-AOA: ~3.98 $x10^5$ copies g^{-1} soil; *amoA*-AOB: ~8.91 $x10^4$ copies g^{-1} soil Loess: *amoA*-AOA: ~4.47 $x10^5$ copies g^{-1} soil; *amoA*-AOB: ~4.41 $x10^6$ copies g^{-1} soil	N.E.	344
Sonoran Desert	0.3 - 3 µg NO_2-N g^{-1} h^{-1}	*amoA*-AOB: ~1 $x10^5$ copies g^{-1} soil *amoA*-AOA: ~4.4 $x10^5$ - 5.4 $x10^5$ copies g^{-1} soil	*Nitrosopharea* sp., *Nitrosomonas* sp., *Nitrosospira* sp.	165
King Sejong Station & Cape Burk area (Antarctica)	N.E.	*amoA*-AOB: 1.9 $x10^4$ - 2.5 $x10^4$ copies g^{-1} soil *amoA*-AOA: 2.9 $x10^{-2}$, 2.1 $x10^{-3}$, 1.0 $x10^{-4}$ copies g^{-1} soil	N.E.	256
Anvers Island (Antarctica)	AAO: 0.11 - 2.47 µmol N m^{-2} h^{-1}	N.E.	N.E.	336
McMurdo Dry Valleys (Antarctica)	N.E.	N.E.	*Nitrospira* sp.	188

	Upper Wright Valley in McMurdo Dry Valleys (Antarctica)	N.E.	*amoA*-AOB: ~2.8 x10^3 copies g^{-1} soil *amoA*-AOA: ~5.0 x10^4 copies g^{-1} soil	AOAs distantly related to *Nitrosphaera* sp. and AOBs distantly-related to *Nitrosomonas* sp. and *Nitrosospira* sp.	164
	Beacon Valley in McMurdo Dry Valleys (Antarctica)	N.E.	*amoA*-AOB: ~6.0 x10^3 copies g^{-1} soil *amoA*-AOA: ~1.0 x10^5 copies g^{-1} soil		
	Battleship Promontory Valley in McMurdo Dry Valleys (Antarctica)	N.E.	*amoA*-AOB: ~2.3 x10^5 copies g^{-1} soil *amoA*-AOA: ~1.0 x10^5 copies g^{-1} soil		
	Miers Valley in McMurdo Dry Valleys (Antarctica)	N.E.	*amoA*-AOB: ~1.38 x10^6 copies g^{-1} soil *amoA*-AOA: ~4.0 x10^5 copies g^{-1} soil		
		N.E.	D	*Nitrososphaera* sp., *Nitrospira* sp.	172
	Taylor Valley (Antarctica)	N.E.	*amoA*-AOB detected	*Nitrosospira* sp.	145
	18 Antarctica soils	N.E.	16 hits in 10/18 shotgun metagenomes	Bacteroidota, Cyanobacteria, Pseudomonadota	120
	Signy Island (Antarctica)	N.E.	Vegetated: *amoA*-AOA: 0.9 ± 1.6 x10^3 copies g^{-1} soil; *amoA*-AOB: 0.4 ± 0.3 x10^5 copies g^{-1} soil Fell-Field: *amoA*-AOA: 15.3 ± 8.7 x10^3 copies g^{-1} soil; *amoA*-AOB: 3.6 ± 6.5 x10^5 copies g^{-1} soil	N.E.	345
	Anchorage Island (Antarctica)	N.E.	Vegetated: *amoA*-AOA: 0.3 ± 0.5 x10^3 copies g^{-1} soil; *amoA*-AOB: 3.5 ± 1.2 x10^5 copies g^{-1} soil Fell-Field: *amoA*-AOA: 14.4 ± 11.0 x10^3 copies g^{-1} soil; *amoA*-AOB: 7.8 ± 3.1 x10^5 copies g^{-1} soil		
	Svalbard, Greenland, Siberia (Arctic)	*In situ:* ~0.4 - 50 µg N g^{-1} dw soil d^{-1}	*amoA*-AOA: 2 x10^6 ± 3 x10^5 - 2 x10^8 ± 2 x10^7 copies g^{-1} soil *amoA*-AOB: 4 x10^5 ± 6 x10^4 - 2 x10^6 ± 3 x10^5 copies g^{-1} soil	*Nitrososphaera* sp.,	346
	Canadian High Arctic	N.E.	*amoA*-AOA: ~0.7 x10^5 - 1.4 x10^6 copies g^{-1} soil	N.E.	258
Hypolith	Namib Desert	N.E.	N.D.	*Nitrosomonas* sp., *Nitrobacter* sp., *Nitrospira* sp.	71
	Antarctica	N.E.	N.E.	Archaea and Bacteria	78, 83
Endolith	Antarctica	N.E.	N.E.	Archaea and Bacteria	78, 83

Hypersaline Mat	Omani Desert	0.8 ±0.4 nmol N g^{-1} h^{-1}	β- Proteobacteria: 6.7 ± 1.72 x10^{6} copy g^{-1} mat γ-Protebacteria: 7.2 ± 2.23 x10^{7} copy g^{-1} mat *amoA*-AOA: 0.1 ± 0.10 x10^{7} copy g^{-1} mat	N.E.	347

Table 2. Microbial Nitrification in hot and cold dryland/desert habitats. *: culturable based; D: Detected; N.D.: Not Detected; N.E.: Not Evaluated; AOA: Ammonia

Habitat type	Desert	Denitrification rates	Denitrification gene detection and/or abundances	Diversity of denitrifiers	References
Biological Soil Crust	Chihuahan Desert	~1 µmol m^{-2} h^{-1}	N.E.	N.E.	308
	Mojave Desert	~0.7 - 1 µmol m^{-2} h^{-1}			
	Sonoran Desert	~1 µmol m^{-2} h^{-1}			
	Colorado Plateau	~1 µmol m^{-2} h^{-1}			
		38 ng N m^{-2} s^{-1}; 0.7 kg N ha^{-1} $year^{-1}$	N.E.	N.E.	274
	Canyonlands, Utah	Light crust: 48 µg N m^{-2} day^{-1} Dark crust: 418 µg N m^{-2} day^{-1}	N.E.	N.E.	279
	Negev Desert	0.01 N_2O-N kg $soil^{-1}$ h^{-1}	N.E.	N.E.	288
		Cyanobacterial crust: 0.8 - 1.3 N_2O mg m^{-2} d^{-1}	*nirK:* 2 - 8 x10^8 copies cm^{-2} *nirS:* ~5.01 - 7.94 x10^6 copies cm^{-2}	N.E.	330
		Moss crust: 1.4 - 2.4 N_2O mg m^{-2} d^{-1}	*nirK*: 20 x10^8 copies cm^{-2} *nirS:* ~7.94 x10^6 copies cm^{-2}	N.E.	
	Omani Desert	Lichen crust: 58 ± 20 µmol N m^{-2} h^{-1} (total denitrification; N_2O + N_2)	Nitrate reducers (*narG*): 2.2 ± 0.9 x10^7 copy nb g^{-1} crust Nitrate reducers (*napA*): 9.6 ± 4.1 x10^7 copy nb g^{-1} crust Nitrite reducers (*nirS*): 2.0 ± 0.1 x10^7 copy nb g^{-1} crust	*nirS*: *Paracoccus denitrificans*	162
		Cyanobacterial crust: 584 ± 101 µmol N m^{-2} h^{-1} (total denitrification; N_2O + N_2)	Nitrate reducers (*narG*): 4.5 ± 2.2 x10^6 copy nb g^{-1} crust Nitrate reducers (*napA*): 8.9 ± 1.7 x10^6 copy nb g^{-1} crust Nitrite reducers (*nirS*): 6 ± 1.4 x10^7 copies g^{-1} crust	*nirS*: Cyanobacteria; *Paracoccus denitrificans; Azospirillum* sp.	
	Semiarid Spain (Aranjuez Experimental Station)	Control Low biocrust cover: ~10 µg N_2O m^{-2} d^{-1} Control High biocrust cover: ~20 µg N_2O m^{-2} d^{-1}	Control Low biocrust cover: *nosZ:* ~3.16 x10^{12} copies g^{-1} soil Control High biocrust cover: *nosZ:* ~1 x10^{13} copies g^{-1} soil	N.E.	180
	Soebatsfontein, Succulent Karoo	Cyanobacterial crust: 208 ± 15 ng NO-N m^{-2} s^{-1} Lichen crust: 94.85 ng NO-N m^{-2} s^{-1}	N.E.	N.E.	348

		Moss crust: 47.61 ng NO-N m^{-2} s^{-1}			
	Tengger Desert	Moss and bacterial BSC: N.E.	Moss (mean relative abundance ± SD): *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	N.E.	332
		Moss and bacterial BSC: N.E.	Bacterial (mean relative abundance ± SD): *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		
Soil	Arid region, Xinjiang, China	Control: -0.3 - 4.5 g N ha^{-1} d^{-1}	N.E.	N.E.	349
		Control: 4.30 ± 0.59 g N_2O-N ha^{-1} d^{-1}	*narG:* ~30 x10^6, 70 x10^6 copies g^{-1} soil *nirS:* ~10 x10^6, 18 x10^6, 30 x10^6, 52 x10^6 copies g^{-1} soil *nirK:* ~7.5 x10^5, 8 x10^5, 22 x10^5 copies g^{-1} soil *nosZ:* ~10 x10^6, 26 x10^6, 43 x10^6, 81 x10^6 copies g^{-1} soil	N.E.	338
		Control: 45.6 - 235 µg N_2O-N m^{-2} h^{-1}	*nirS:* ~1.8 x10^4 copies g^{-1} soil *nirK:* ~1.3 x10^4 copies g^{-1} soil *nosZ:* ~4.1 x10^3 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: Nitrospirillum* sp., *Pseudomonas* sp., *Sinorhizobium* sp., *Shinella* sp., *Aeromonas* sp., *Adicovorax* sp., *Comamonas* sp., *Maritimibacter* sp., *Thioalkalivibrio* sp., *Sulfitobacter* sp., *Bordetella* sp., *Azospirillum* sp.	350
	Arid-semiarid region (Kunlun Mountain), Xinjiang, China	Control: 244 ± 20 g N_2O-N ha^{-1}	*narG:* ~13 x10^6, 60 x10^6, 65 x10^6, 210 x10^6, 65 x10^6, 225 x10^6 copies g^{-1} soil *nirK:* ~0.7 x10^6, 0.7 x10^6, 2.3 x10^6, 1.7 x10^6, 2.2 x10^6, 2.5 x10^6 copies g^{-1} soil	N.E.	339

		nirS: ~4.5 x10^6, 1.5 x10^6, 2.5 x10^6, 2.5 x10^6, 4.0 x10^6, 4.1 x10^6 copies g^{-1} soil *nosZ:* ~6.0 x10^6, 7.0 x10^6, 15.0 x10^6, 2.75 x10^6, 1.8 x10^6, 7.0 x10^6 copies g^{-1} soil		
Atacama Desert	Semi-arid soil: 1.81 ± 0.41 ng N_2O g^{-1} h^{-1}	*nirK:* 31 clones (semi-arid 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* *nirS: Corynebacterium* sp., *Pseudomonas* sp., *Alcaligenes* sp., *Azoarcus* sp., *Dechloromonas* sp., *Paracoccus* sp., *Azospirillum brasilense*, *Simplicispira psychrophila*	257
	Arid soil: non-detectable	*nirS:* 40 clones (semi-arid soils)		
	N.E.	A1042: *napA:* ~2.51 x10^5; *narG:* ~7.94 x10^4; *nirS:* ~6.31 x10^6; *cnorB:* ~1.58 x10^6; *qnorB:* ~7.94 x10^5; *nosZ:* ~3.98 x10^6 copies g-1 soil A1243: *napA:* ~6.31 x10^5; *narG:* ~6.31 x10^5; *nirS:* ~5.01 x10^6; *cnorB:* ~1 x10^6; *qnorB:* ~6.31 x10^6; *nosZ:* ~1.26 x10^6 copies g-1 soil A1700: *napA:* ~5.01 x10^5; *narG:* ~7.94 x10^4; *nirS:* ~3.98 x10^6; *cnorB:* ~1.26 x10^6; *qnorB:* ~1.58 x10^6; *nosZ:* ~1.58 x10^6 copies g-1 soil A2029: *napA:* ~1.58 x10^6; *narG:* ~5.01 x10^5; *nirS:* ~1 x10^7; *cnorB:* ~2.51 x10^6; *qnorB:* ~4.47 x10^6; *nosZ:* ~5.01 x10^6 copies g-1 soil A2116: *napA:* ~5.62 x10^5; *narG:* ~6.31 x10^4; *nirS:* ~3.98 x10^6; *cnorB:* ~2.51 x10^6; *qnorB:* ~2.24 x10^6; *nosZ:* ~2.51 x10^6 copies g-1 soil		351
Roxby Downs, Australia	N.E.	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	125
Chihuahuan Desert	Bajadas: 9 ng N g^{-1} h^{-1} Playas: 192 ng N g^{-1} h^{-1}	N.E.	N.E.	281

	Dry soil: <0.1 ng NO-N cm^{-2} h^{-1}	N.E.	N.E.	129
Colorado Plateau	Dry soil: 0.8 ng NO_x-N m^{-2} s^{-1} and 1.0 ng N_2O-N m^{-2} s^{-1}	N.E.	N.E.	203
Gobi	N.E.	*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	125
Great Basin Desert	19 kg N ha^{-1} $year^{-1}$	N.E.	N.E.	273
	Bajadas: 43 ng N g^{-1} h^{-1} Playas: 163 ng N g^{-1} h^{-1}	N.E.	N.E.	281
Gurbantunggut Desert	Control: 1.49 ± 0.61 µg N m^{-2} h^{-1}	N.E.	N.E.	205
Inner Mongolia Desert	Denitrification rates: 0.48 - 7.64 g N_2O-N ha^{-1} d^{-1} N_2O production rates: 0.59 - 16.02 g N ha^{-1} d^{-1}	N.E.	N.E.	352
	Nitrate Reduction: 0.34 µg g^{-1} h^{-1}	*nirK*: ~0,8 x10^5 copies g^{-1} soil *nirS*: ~3,3 x10^4 copies g^{-1} soil *nosZ*: 3,4 x10^4 copies g^{-1} soil	N.E.	171
	Controls: 0.016 ± 0.007 kg N_2O m^{-2} h^{-1}	N.E.	N.E.	353
	0.01 - 0.10 µg N_2O-N g^{-1} soil h^{-1}	*narG:* ~9.5 x10^6, 12 x10^6, 17.5 x10^6, 3.5 x10^6, 2.0 x10^6, 3.0 x10^6 copies g^{-1} soil	N.E.	342
Namib Desert	N.E.	*nar & nir* genes detected	*nar:*Nitrospiracea / *nir*: Rubrobaceraceae, Geodermatophilaceae, Frankiaceae, Micrococcaceae, Mycobaceriaceae, Streptomycetaceae) genes	124
	N.E.	*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	125
Mojave Desert	Bajadas: 13 ng N g^{-1} h^{-1} Playas: 237 ng N g^{-1} h^{-1}	N.E.	N.E.	281
	Denitrification: 161 ± 96 µg N m^{-2} d^{-1}	N.E.	N.E.	354

	N_2O fluxes: 30 ± 20 µg N m^{-2} d^{-1} Potential DEA: 146 ± 8 mg N m^{-2} d^{-1}			
	N_2O fluxes (incubations, control soils): 17.5 ± 1.5 mg N_2O-N m^{-2} DEA interspace: 0.11 ± 0.08 µg N_2O-N m^{-2} s^{-1} DEA under *Larrea tridentata*: 1.10 ± 0.26 µg N_2O-N m^{-2} s^{-1} DEA under *Lycium* spp.: 0.76 ± 0.26 µg N_2O-N m^{-2} s^{-1} DEA under *Pleuraphis rigida*: 0.43 ± 0.19 µg N_2O-N m^{-2} s^{-1}	N.E.	N.E.	293
	DEA controls: 1.23 ± 0.25 µg N_2O-N g^{-1} min^{-1}	N.E.	N.E.	298
	Bare soil & soil under grass: 0.6 - 3.1 ng N g^{-1} soil d^{-1} Ant nest soil: 1.6 - 2.0 ng N g^{-1} soil d^{-1}	N.E.	N.E.	278
	Soil under *Larrea tridentata*: 2.39 ± 1.28 ng N_2O-N m^{-2} h^{-1} Interspaces: 2.74 ± 1.11 ng N_2O-N m^{-2} h^{-1}	N.E.	N.E.	355
	N.E.	*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	125
Mu Us Desert	N.E.	*nirS:* ~1 x10^6 copies g^{-1} soil *nirK:* ~3.5 x10^6 copies g^{-1} soil *nosZ:* ~1 x10^5 copies g^{-1} soil	N.E.	334
Negev Desert	~25 µg N kg^{-1} h^{-1}	N.E.	N.E.	314
	0.04 N_2O-N kg $soil^{-1}$ h^{-1}	N.E.	N.E.	288
	Sand: ~0.1 - 4.5 mg N_2O m^{-2} d^{-1} Loess: ~0.1 - 6.0 mg N_2O m^{-2} d^{-1}	Sand: *nirS:* ~3.98 x10^6 copies g^{-1} soil; *nirK:* ~5.62 x10^5 copies g^{-1} soil Loess: *nirS:* ~1.58 x10^7 copies g^{-1} soil; *nirK:* ~5.62 x10^6 copies g^{-1} soil	N.E.	344
Sonoran Desert	Wetted soil under *Prosopis* shrubs: 11.6 g N ha^{-1} h^{-1} Wetted soil at interspaces: 0.2 g N ha^{-1} h^{-1}	N.E.	N.E.	272

	2.4 ± 2.2 ng N_2O-N m^{-2} s^{-1}	N.E.	N.E.	356
	Desert site: 3.7 - 14 µg N_2O-N m^{-2} h^{-1} and 5 - 16 µg NO-N m^{-2} h^{-1}	N.E.	N.E.	201
Soebatsfontein, Succulent Karoo	9 ± 3 ng NO-N m^{-2} s^{-1}	N.E.	N.E.	348
18 Antarctica soils	N.E.	*nap*: 2 hits in 1/18 shotgun metagenomes *nar*: 5 hits in 4/18 shotgun metagenomes *nor*: 86 hits in 14/18 shotgun metagenomes *noz*: 32 hits in 8/18 shotgun metagenomes	Bacteroidota Actinomycetota, Pseudomonadota Acidobacteria, Bacteroidota, Chlofoflexi, Cyanobacteria, Pseudomonadota Actinomycetota, Verrucomicrobiota, Archaea	120
University Valley, McMurdo Dry Valleys (Antarctica)	N.E.	*narG, nasA, napA:* 62 reads of metagenome *nirK, nirS, nirA, nirB, nrfA:* 56 reads of metagenome	N.E.	357
Anchorage Island (Antarctica)	N.E.	*nir*, *nar*, *nas*, *nos*	N.E.	103
King Sejong Station & Cape Burk area (Antarctica)	N.E.	*narG:* ~1 10^8 copy g^{-1} dry soil *nirS:* ~1 10^{11} copy g^{-1} dry soil *nirK:* ~1 10^5 copy g^{-1} dry soil *norB:* ~1 10^3 copy g^{-1} dry soil *nosZ:* ~1 10^2 copy g^{-1} dry soil	N.E.	256
Anvers Island (Antarctica)	0.15 - 2.38 µmol N m^{-2} h^{-1}	N.E.	N.E.	336
Signy Island (Antarctica)	N.E.	Vegetated: *nirK:* 0.1 ± 0.1x10^7 copies g^{-1} soil; *nirS:* 1.1 ± 0.7x10^7 copies g^{-1} soil Fell-Field: *nirK:* 5.6 ± 8.5 x10^7 copies g^{-1} soil; *nirS:* 8.6 ± 9.8 x10^7 copies g^{-1} soil	N.E.	345
Anchorage Island (Antarctica)	N.E.	Vegetated: *nirK:* 0.1 ± 0.0 x10^7 copies g^{-1} soil; *nirS:* 1.4 ± 1.2 x10^7 copies g^{-1} soil	N.E.	

		Fell-Field: *nirK:* NA; *nirS:* 11.6 ± 11.0x10^7 copies g^{-1} soil		
Rotmoosferner glacier, Ötz Valley (Arctic)	N.E.	*narG:* 1.6 x10^8, 1.7 x10^8, 1.4 x10^8, 7.7 x10^7, 1.1 x10^8, 1.9 x10^8, 1.9 x10^8, 1.2 x10^8, 1.2 x10^8, 1.1 x10^8 copies g^{-1} soil *nirS:* 1.9 x10^7, 2.2 x10^7, 1.1 x10^8, 4.9 x10^6, 3.1 x10^7, 5.6 x10^7, 2.4 x10^7, 3.8 x10^7, 1.8 x10^7, 7.6 x10^7 copies g^{-1} soil *nirK:* 7.7 x10^6, 1.1 x10^7, 2.2 x10^7, 2.9 x10^7, 5.7 x10^7, 8.9 x10^6, 1.0 x10^7, 1.4 x10^7, 2.4 x10^7, 3.2 x10^7 copies g^{-1} soil *nosZ:* 1.3 x10^7, 3.7 x10^7, 5.1 x10^7, 1.2 x10^8, 2.8 x10^8, 1.4 x10^7, 5.3 x10^7, 2.3 x10^7, 7.1 x10^7, 1.3 x10^8 copies g^{-1} soil	N.E.	358
Zackenberg lowlands, Greenland (High Arctic)	Active layer (top soil): 0.01 - 1.37 µg N_2O-N kg^{-1} h^{-1}	N.E.	N.E.	359
Russian discontinuous permafrost tundra (Arctic)	Cryoturbated: 1.2 - 1.8 µmol N_2O g^{-1} DW Unturbated: NA	Cryoturbated *narG:* 6.5 ± 2.0x10^4 copies ng^{-1} DNA *nirK:* 5.1 ± 2.1 x10^0 copies ng^{-1} DNA *nirS:* 4.6 ± 1.0 x10^3 copies ng^{-1} DNA *nosZ:* 1.2 ± 0.2 x10^1 copies ng^{-1} DNA Unturbated *narG:* 6.5 ± 2.5x10^2 copies ng^{-1} DNA *nirK:* 3.5 ± 1.1x10^1 copies ng^{-1} DNA *nirS:* 7.2 ± 0.9x10^3 copies ng^{-1} DNA *nosZ:* 2.7 ± 1.2x10^0 copies ng^{-1} DNA	narG: Actinomycetota *nirK:* α-Proteobacteria *nirS:* α-Proteobacteria, β-Proteobacteria *nosZ:* α-Proteobacteria	360
Palsa peat Skalluvaara, northwestern Finnish Lapland (Arctic)	Vegetated unfertilized palsa peat soil (*in situ*): 0.01 - 0.02 µmol N_2O m^{-2} h^{-1} Unsupplemented palsa peat soil microcosms, 0-20cm: 0.4 nmol N_2O g^{-1} DW Unsupplemented palsa peat soil microcosms, >20cm: 1 nmol N_2O g^{-1} DW	Unsupplemented palsa peat soil microcosms, 0-20cm *narG:* 1.5 ± 0.1x10^4 copies ng^{-1} DNA *nirK:* 1.4 ± 0.3x10^0 copies ng^{-1} DNA *nirS:* 2.5 ± 0.3x10^2 copies ng^{-1} DNA *nosZ:* 4.3 ± 0.8x10^1 copies ng^{-1} DNA Unsupplemented palsa peat soil microcosms,	*narG: Actinomycetota,* α-Proteobacteria *nirK:* α-Proteobacteria *nirS:* α-Proteobacteria, β-Proteobacteria *nosZ:* α-Proteobacteria, β-Proteobacteria	361

			>20cm *narG:* 5.1 ± 0.2x10^4 copies ng^{-1} DNA *nirK:* 8.6 ± 2.3x10^{-1} copies ng^{-1} DNA *nirS:* 3.7 ± 0.7x10^1 copies ng^{-1} DNA *nosZ:* 8.8 ± 0.8x10^1 copies ng^{-1} DNA		
	Daring Lake, Northwest Territories, (Canadian low Arctic)	0.16 nmol N_2O m^{-2} s^{-1}	N.E.	N.E.	362
	McGill Arctic Research Station (MARS) (Canadian high Arctic)	Trough soils: 0.291 ± 0.086 mg N_2O m^{-2} day^{-1} Raised polygon soils: 0.121 ± 0.16 mg N_2O m^{-2} day^{-1}	Trough soils (25cm): *nirS:* -3 log copies Raised polygon soils (5 cm): *nirS:* -1.1 log2 copies Raised polygon soils (25 cm): *nirS:* -5 log2 copies	*nirS*: Nitrosomonadales; Acidiferrobacterales; Rhodocyclales; Xanthomonadales; Pseudomonadales; Rhodobacterales; Burkholderiales *nirS*: Xanthomonadales; Pseudomonadales; Acidiferrobacterales; Burkholderiales	285
Cryptoendolith	University Valley, McMurdo Dry Valleys (Antarctica)	N.E.	*narG, nasA, napA:* 66 reads of metagenome *nirK, nirS, nirA, nirB, nrfA:* 62 reads of metagenome	N.E.	357
Hypolith	Namib Desert	N.E.	*nar*, *nor*, *nap*	Actinomycetota	71
Hypersaline Mat	Omani desert	2.0 ± 1.0 nmol N g^{-1} h^{-1}	*narG*: 8.5 ± 0.7 10^6 copy g^{-1} mat *nirS*: 3.9 ± 1.5 10^6 copy g^{-1} mat *napA*: 9.3 ±0.7 10^7 copy g^{-1} mat	*nosZ* (*Halmonas koreensis*, *Rhodanobacter* sp., *Pseudomonas* sp., *Marinobacter* sp.), *nirK* (Rhizobiales)	347
Microbial Mats	Fildes Peninsula (Maritime Antarctica)	N.E.	*nirK:* 57 phylotypes *nirS:* 29 phylotypes *nosZ:* 79 phylotypes	*nirK: Octadecabacter antarcticus* *nirS: Rubrivivax gelatinosus*, *Paracoccus denitrificans* *nosZ: Rhodopseudomonas palustris*, *Azospirillum lipoferum*, *Pseudomonas*	363

sp., *Rhodoferax ferrireducens*

Table 3. Microbial Denitrification in hot and cold dryland/desert habitats. D: Detected; N.D.: Not Detected; N.E.: Not Evaluated

Habitat type	Desert	ANAMMOX rates	Annamox genes	Anaerobic Ammonia Oxidizers	References
Biological Soil Crust	Omani Desert	Lichen crust: N.D.	N.E.	N.E.	162
		Cyanobacterial crust: N.D.	N.E.	N.E.	
	Mojave Desert	D.	N.E.	N.E.	308
	Chihuahan Desert	D.	N.E.	N.E.	
	Sonoran Desert	D.	N.E.	N.E.	
	Colorado Plateau	D.	N.E.	N.E.	
Soil	Australia	N.E.	N.D.	Candidatus *Brocadia* sp., Candidatus *Brocadia* sp.	125
	Mojave Desert	N.E.	N.D.	N.D.	
	Gobi	N.E.	N.D.	N.D.	
	Namib Desert	N.E.	N.D.	N.D.	
Hypolith	Namib Desert	N.E.	N.D.	N.D.	71
Hypersaline Mat	Omani Desert	N.D.	N.E.	N.E.	347

Table 4. Microbial Anaerobic Ammonium Oxidation (Anammox) in hot and cold dryland/desert habitats. D: Detected; N.D.: Not Detected; N.E.: Not Evaluated