INTRODUCTION

The soil N cycle consists of several N pools and inter-connected transformations (Figure 1). Microbial biomass is central to the processes involved in producing and immobilizing inorganic N. Furthermore, microbial biomass contributes directly to the pool of soil organic N through its death and turnover. The placement of soil microbial diversity and dynamics into context with biological functions associated with the N cycle still remains a grand challenge (Myrold and Bottomley, 2008; Strickland et al., 2009; McGuire and Treseder, 2010). Conservation of soil N depends on the maintenance of a balance between the rate of depolymerization of organic N, the portion of it that is mineralized to NH₄⁺, and the rate of NH₄⁺ consumption by three different sinks: (a) plant growth, (b) heterotrophic microbial assimilation, and (c) NH₄⁺-oxidizing bacteria (AOB) and archaea (AOA). Simplicistically speaking, when sink (c) is larger than (a) plus (b), NH₄⁺ accumulates and becomes vulnerable to leaching and/or denitrification from the ecosystem. It is the microbiology underpinning these alternate fates of NH₄⁺ that is the framework of this review.

HOW DOES GROSS MINERALIZATION OF N (N_{min}) AND GROSS IMMOBILIZATION OF N (N_{imm}) OCCUR IN THE SAME SOIL VOLUME?

For >50 year soil scientists have measured fluxes of NH₄⁺ production and consumption in soils using the ¹⁵N isotope pool dilution approach (Kirdman and Bartholomew, 1954; Davidson et al., 1991; Hart et al., 1994; Murphy et al., 2003). Gross rates of N mineralization in soil are positively correlated with total soil C and N contents and the size of the microbial biomass pool (Booth et al., 2005). Furthermore, gross rates of microbial NH₄⁺ and NO₃⁻ assimilation are positively and linearly related to gross N mineralization rates. The fact that heterotrophic NH₄⁺ assimilation (N_{imm}) can be a sink of substantial magnitude in the same soil volume where NH₄⁺ is also being produced by mineralization (N_{min}) has prompted a variety of explanations over the years. Clearly, the balance between N_{min} and N_{imm} will be influenced by the extent that microbial growth (N_{imm}) is coupled to N_{min} (Figure 1). For example, it has been proposed that N_{imm} and N_{min} processes are carried out concurrently by physically separated microbial populations growing on different C sources of different C:N ratios (Schimel and Bennett, 2004; Schimel and Hattenschwiler, 2007;
Manzoni et al., 2008). Co-existing metabolisms of different microbial groups, such as fungi and bacteria, with different C and N spectra usage and growth efficiencies might also influence the balance between $N_{\text{min}}$ and $N_{\text{assim}}$ in the same soil volume (Boyle et al., 2008; Rinnan and Baath, 2009). Figure 2 represents an attempt to illustrate how physiological heterogeneity among soil microbial subpopulations caused by varying degrees of starvation/dormancy might influence their relative demands for C and N (Schimel et al., 2007; Allison et al., 2010; Dworkin and Shah, 2010; Lennon and Jones, 2011), as might antagonistic competition between bacteria and fungi for growth resources (Rousk et al., 2008, 2010b). Finally, the relative portions of dissolved organic nitrogen (DON) ammonified/assimilated will depend upon the relative needs of the microbial populations for C and N. For example, it has been shown that soil proteolytic activity can be increased by N limitation and decreased by increased $NH_4^+$ availability illustrating the well accepted role of soil proteins as N sources (Sims and Wander, 2002; Allison and Vitousek, 2005). Yet, proteolytic activity can also be repressed by addition of glucose (Geisseler and Horwath, 2008) suggesting a role for DON as a C source.

**SUBSTRATE-RESPONSIVE POPULATION: GROWTH READY OR NOT?**

Whereas it is well accepted that the vast majority (>80%) of soil microbes probably reside in some state of dormancy, several studies have shown that at least one-half of soil microbial populations are respiratorily active (Jones and Lennon, 2010; Lennon and Jones, 2011; Hobbie and Hobbie, 2012). Furthermore, it is well known that soil respiration responds rapidly (within 1–3 h) to the addition of exogenous C substrates, including amino acids (Jones and Murphy, 2007; Jones et al., 2009). This response is the basis of the well-established substrate-induced respiration (SIR) assay used to measure soil microbial biomass (Anderson and Domsch, 1978). In SIR the rule-of-thumb is that 40 $\mu$g of respiratorily active soil biomass C generates a respiratory response of $\sim$0.48 $\mu$g CO$_2$-C/h. With this relationship in mind, a recent series of papers by Rousk et al. (2008, 2009, 2010b) focused on factors influencing the relative contributions of fungi and bacteria to soil activities. They determined that substrate-induced soil microbial biomass ranged between 100 and 200 $\mu$g microbial biomass C/g soil which would support a substrate-induced rate of respiration of $\sim$1.3–2.6 $\mu$g CO$_2$-C/g soil/h or $\sim$30–60 $\mu$g CO$_2$-C/g soil/day. The bacterial and fungal growth potentials of the same soils were measured by following $^3$H-leucine incorporation into hot trichloroacetic acid (TCA) precipitable material (presumed to be protein), and $^{14}$C acetate incorporation into ergosterol, respectively. The rates of leucine assimilation ranged between 10 and 100 pmol/g soil. We have attempted to extrapolate from these data to obtain a rate
FIGURE 2 | Conceptual diagram to illustrate how the fate of soil N pools might be controlled by the growth-active fraction (GAF) of the substrate-responsive population (SRP) of microorganisms. The heights of the individual vertical columns represent the SRP of different taxa and their widths represent the relative sizes of each taxon as part of the whole microbial community. The shaded portion of each column represents the GAF of each SRP taxon. The left side depicts that low molecular weight (LMW) dissolved organic N (DON) is taken up and metabolized by the SRP but N is only assimilated by the GAF. The balance between NH$_4^+$ mineralized versus N immobilized will be influenced by the relative amounts of GAF versus SRP and determine the net NH$_4^+$ mineralized. The right panel depicts that growth-active heterotrophs and NH$_3$-oxidizing archaea (AOA) and bacteria (AOB) will compete for NH$_4^+$ with the outcome being affected by the GAF/SRP ratio of the NH$_4^+$ assimilating heterotrophs (assuming that AOA and AOB only assimilate a small fraction of NH$_4^+$ consumed) and by the relative sizes of and kinetic properties of the SRP populations of AOA and AOB. A similar panel could be drawn to show the assimilation of NO$_3^-$ by the GAF of heterotrophic microorganisms.

of N assimilation into protein. We used the following correction factors/assumptions, that ~50% of assimilated leucine is incorporated into protein, and that only 10% of the total soil bacterial population is extracted and represented in the soil slurrying assay (Baath, 1994, 1998; Roux, personal communication). We further assumed that leucine incorporation into protein tracks total protein synthesis, that leucine represents ~8–10% of microbial cell protein (Kirchman et al., 1985; Neidhardt et al., 1990), and that the average N content of protein is 16%. These rates of leucine incorporation extrapolate to ~0.28–2.8 μg N assimilated/g soil/day. In the case of fungal growth potential, the rates of acetate incorporation into ergosterol (C$_{28}$H$_{44}$O, mw = 396) ranged between 10 and 80 pmol acetate incorporated/g soil/h, equivalent to ~0.7–5.7 pmol ergosterol synthesized/g soil/day (assuming a minimum of 14 acetate molecules required per molecule of ergosterol), and ~6.8–54.4 ng ergosterol synthesized/g soil/day. Using the authors’ biomass conversion factor (5 ng ergosterol/1 μg fungal biomass), the ergosterol synthesis rate extrapolates to 3.3–10.9 μg fungal biomass formed/g soil/day. Assuming that fungal biomass is 45% C and has a C:N of 10:1 this growth rate is equivalent to ~0.86–4.8 μg N immobilized/g soil/day. From the sum of the leucine/ergosterol assays the rate of N assimilation ranges from ~0.34 to 3.4 μg N/g/day. These values fall within the range of NH$_4^+$ assimilation rates that have been measured in whole soils by $^{15}$N isotope pool dilution (0.1–10 μg NH$_4^+$/N/g/day; Booth et al., 2005). Another approach to this issue is to consider that the substrate-responsive biomass of 100–200 μg C/g soil has the potential to respire exogenous C at a rate of 30–60 μg CO$_2$/C/g/day. If this rate of respiration is coupled to C assimilation at a yield efficiency of 50%, then 30–60 μg C are assimilated/g/day. If bacteria were solely responsible for the C assimilation with a C:N of 5:1, this extrapolates to 6–12 μg N assimilated/g/day. Alternatively, if fungi were solely responsible with a C:N 10:1, the rate equals 3–6 μg N assimilated/g/day. This range of potential N assimilatory values (3–12 μg N/g/day) falls within the range of NH$_4^+$ assimilation rates mentioned above; it is somewhat higher than the range of N assimilation estimated from the leucine incorporation and ergosterol synthesis data.

Important unanswered questions are: (1) to what extent does the dormant, substrate-responsive microbial population actually process DON and contribute to Nmin? (2) How quickly does a substrate-responsive population transition into a N assimilatory sink and shift the Nmin:Nassim balance? (3) How well does the leucine plus acetate assimilatory subpopulations of bacteria and fungi detected in the Roux et al. (2008, 2009, 2010b)
studies represent the NH₄⁺ sink routinely detected in ¹⁵N isotope pool dilution whole soil studies (4) Or, does the leucine incorporating bacterial population represent a DON assimilating subpopulation that might be different from the NH₄⁺ assimilating subpopulation?

WHAT CONTROLS THE OUTCOME OF COMPETITION FOR NH₃/NH₄⁺ BETWEEN HETEROTROPHS AND NH₃ OXIDIZERS, AND AMONG DIFFERENT NH₃ OXIDIZERS?

It has been shown that the extent of NO₃⁻ leaching from arable and grassland soils correlates well with the ratio of the rate of N nitrification/rate of N immobilized (NH₄⁺; Stockdale et al., 2002). Yet, the factors underpinning the relative rates of N and I and the range of magnitude of NO₃ ratio are not well understood. For example, gross nitrification rates can consume the majority of NH₄⁺ mineralized at low N mineralization rates (<2 µg N/g soil/day). However, as the rate of N mineralization increases and both NH₄⁺ assimilation and nitrification increase, the latter consumes a disproportionately lower percentage of NH₄⁺ than the former (Booth et al., 2005). A combination of increased C availability and a higher affinity for NH₄⁺/NH₃ has been proposed to play a role in the relative success of heterotrophic microorganisms over AOB (Kleiner, 1981; Chen and Stark, 2000). Heterotrophic bacteria have an affinity for NH₄⁺ that ranges between 3.7 and 13.2 µM (Ray et al., 1999). In contrast, the affinity for NH₃⁺ by strains of Nitrosospira, the dominant genus of soil AOB, ranges from 78 to 590 µM NH₄⁺ (Jiang and Bakken, 1999; Bollmann et al., 2005; Taylor and Bottonley, 2006) implying that AOB might compete poorly with heterotrophs for NH₃⁺ under soil conditions with adequate labile C. On the other hand, it has been observed that heterotrophic assimilation of NH₄⁺ was less than NO₃⁻ assimilation, suggesting that NH₃ oxides can compete successfully with heterotrophs for NH₄⁺ (Burger and Jackson, 2003). To add more complexity to this topic, evidence was recently obtained that the thaumarchaeal community of an acidic peat soil (pH range 3.8–4.7) preferentially oxidized NH₄⁺/NH₃ generated from organic N sources over excessogenous NH₃ (Levicnik-Hofferle et al., 2012). One interpretation of these results is that AOA are involved in the direct uptake of DON, and that oxidation of NH₃ occurs after assimilation of 16S rRNA gene sequences recovered from the active T-RFs in the summer samples did not overlap with the growth-active organisms were minor components of the community. Although there were more T-RF overlaps between the active and total communities of the summer shrub soil samples, many “active” T-RFs in the summer samples did not overlap with the total summer community. Because the balance between N cycling activities of tundra soils shifts between winter (net N immobilization dominant) and summer (net N immobilization dominant), this study serves to illustrate the importance of determining the amounts of growth that occur in the growth-active subpopulations during the winter and summer periods. This will impact the amount of N immobilized and the overall balance of the N cycle.

IDENTIFICATION OF “PO ssibly GRO WTH-ACTIVE” SUBPOPULATIONS BY TARGETING NUCLEIC ACID SYNTHESIS

We have raised the issue of why it might be important to delineate between substrate-responsive and growth-active subpopulations and hypothesized that the latter are most likely candidates for N immobilizing activity (see How Does Gross Mineralization of N (Nimm) and Gross Immobilization of N (Nimm) Occur in the Same Soil Volume?, Substrate-Responsive Population: Growth Ready or Not?, and What Controls the Outcome of Competition for NH₄⁺/NH₃ Between Heterotrophs and NH₃ Oxidizers, and Among Different NH₃ Oxidizers). We have selected three papers from recent literature where nucleic acid analytical approaches were used to identify potentially growth-active subpopulations in soil communities.

BoxU-LABELED DNA

McMullan et al. (2011) used the thymidine analog, 5-bromo-3-deoxyuridine (BoxU), to identify the growth responsive subpopulation in Arctic tundra shrub and tussock associated soils at different times of the year. BoxU was added to soil along with a small quantity of various monomeric substrates (100 µg C/g soil of either glucose, glutamate, or vanillin) sufficient to “act as a tracer of extant microbial activity” and yet insufficient to stimulate overall CO₂ production. Winter and summer soils were incubated at −2°C for 28 days, and at 4°C for 2 days, respectively. After incubation DNA was extracted, BoxU-labeled DNA recovered by immunocapture, and 16S rRNA genes PCR amplified and analyzed with the T-RFLP approach. None of the BoxU-labeled terminal restriction fragments (T-RFs) recovered from winter samples of shrub soil matched up with the T-RFs representing the total winter community suggesting that “winter growth-active” organisms were minor components of the community. Although there were more T-RF overlaps between the active and total communities of the summer shrub soil samples, many “active” T-RFs in the summer samples did not overlap with the total summer community. Because the balance between N cycling activities of tundra soils shifts between winter (net N immobilization dominant) and summer (net N immobilization dominant), this study serves to illustrate the importance of determining the amounts of growth that occur in the growth-active subpopulations during the winter and summer periods. This will impact the amount of N immobilized and the overall balance of the N cycle.

³⁵S-LABELLED DNA

Aanderud and Lennon (2011) targeted the growth-active members of a soil population carrying out DNA synthesis after rewetting a soil with ³⁵Ο-labeled H₂O. Labeled H₂O was added to field dry soil to raise water content from 0.05 to 0.25 g H₂O/g. Samples were incubated for 72 h, DNA was extracted, and “heavy” DNA separated from “light” DNA by gradient density centrifugation. Pyrosequencing was used to compare the composition of 16S rRNA gene sequences recovered from the light DNA at time zero with that of heavy DNA extracted after 72 h of incubation. The contributions of some phyla to the heavy DNA fraction increased by about 10% (Alpha-, Beta-,
and Gamma-proteobacteria), whereas the contribution of other taxa declined (Chloroflexi, Delta-proteobacteria) implying that selective growth had occurred. Because Alpha-proteobacteria are generally more abundant than Gamma-proteobacteria in bulk soils (Lauber et al., 2009; Rousk et al., 2010a) the relative similar population increases during the rewet, implies that the amount of biomass increased and N-immobilized by Alpha-proteobacteria might be greater than by Gamma-proteobacteria.

RELATIVE QUANTITIES OF rRNA VERSUS rDNA GENE SEQUENCES Baldrian et al. (2011) extracted DNA and RNA from both the litter and humus layers of a spruce forest and used a pyrosequencing approach to compare the relative amounts of 16S rRNA and 16S rDNA gene sequences of bacteria, and compared the relative amounts of RNA and DNA sequences of the TFSI–5.8S–ITS2 region of fungi. Whereas several abundant fungal OTUs identified from DNA sequences were also highly enriched in RNA sequences, a substantial percentage of fungal OTUs (18%) were only found in the RNA community, implying that less abundant fungi might be potentially growth-active. This idea was further supported by the most abundant “cellobiohydrolase” (cbh) transcripts originating from less abundant fungi.

IDENTIFYING THE RELATIVE CONTRIBUTIONS OF DIFFERENT MICROBIAL GROUPS TO N CYCLE ACTIVITIES USING SELECTIVE PROTEIN SYNTHESIS INHIBITORS Several studies have attempted to tease apart the relative contributions of different groups of soil microorganisms to N cycling activities by targeting protein synthesis (Castaldi and Smith, 1998; Laughlin and Stevens, 2002; Tungaraza et al., 2003; Castaldi, 2005; Myrold and Posavetz, 2007; Boyle et al., 2008; Rousk et al., 2008, 2009, 2010b). In this section, we highlight two published papers where protein synthesis inhibitory antibiotics were used to differentiate (a) the contributions of bacteria and fungi to NH₄⁺ uptake and N mineralization, and (b) the relative contributions of AOA and AOB to soil NH₃ oxidizing potential.

FUNGAL AND BACTERIAL CONTRIBUTIONS TO N CYCLING BASED UPON USE OF ANTIBIOTICS AND ¹⁵N ISOTOPE POOL DILUTION MEASUREMENTS Boyle et al. (2008) compared the effects of the bacterial and fungal protein synthesis inhibitors, bronopol and cycloheximide on gross rates of N cycling in forest soils using the ¹⁵N isotope pool dilution method. Bronopol temporarily suppressed NH₄⁺ consumption in high N soils implying that bacteria dominated NH₄⁺ consumption uptake, and that fungi were not involved in NH₄⁺ consumption even when bacterial growth was inhibited. In contrast, bronopol had no effect on NH₄⁺ consumption in a low N soil under the conifer Douglas-fir implying that bacteria were not involved in NH₄⁺ consumption, or, if they were, bacterial consumption could be interchangeably replaced by fungal consumption. Soil ammonification was increased by bronopol at the high N site, implying that when bacterial-dependent NH₄⁺ consumption was stopped, organic N mineralization continued and NH₄⁺ accumulated. Cycloheximide consistently increased both ammonification and NH₄⁺ consumption, implying that when fungal protein synthesis was stopped more NH₄⁺ was made available for bacterial consumption. These data point to fungi likely consuming organic N for protein synthesis. Clearly much remains to be learned about the factors influencing the relative contributions of bacteria and fungi to processing organic and inorganic N sources, and what factors influence the extent the two types of microorganisms operate independently or compete for N resources.

THE RELATIVE CONTRIBUTIONS OF AMMONIA-OXIDIZING ARCHAEA AND BACTERIA TO SOIL NITRIFICATION POTENTIALS Although the ability of AOA to oxidize NH₃ and grow autotrophically in soil has been well established (Offre et al., 2009; Zhang et al., 2010; Verhamme et al., 2011), and that AOA dominate NH₃/NH₄⁺ oxidation under strongly acidic soil conditions (Stoppek et al., 2010; Lehtovirta-Morley et al., 2011), little is known about what influences the relative contributions of AOA and AOB to soil nitrification under most other soil conditions. Taylor et al. (2010) developed a short-term assay based upon selective inactivation of ammonia monooxygenase (AMO) by acetylene. After removal of acetylene the recovery of the nitrification potential (RNP) was followed in the presence and absence of protein synthesis inhibitors/antibiotics and/or fungicides. The success of the assay is based upon determining the fraction of the RNP that occurs within 24–36 h post acetylene removal in the presence of protein synthesis inhibitors and which is assumed to be due to AOA (Taylor et al., 2010). This study showed that in recently N fertilized cropped soils with high NP, the majority of RNP activity is due to AOB, and that in pasture and grassland soils with lower NP activity, RNP is due primarily to AOA or to a mixture of AOA and AOB. A subsequent study has shown that the factors controlling the relative contributions are complex with cropping treatment, soil conditions, and NH₄⁺ availability influencing their relative contributions in the field (Taylor et al., 2012). Further studies are required that combine measurements of the relative contributions of AOA and AOB to nitrification with those of N immobilization to determine if AOA/AOB contributions affect the N/I ratio.

CONCLUDING REMARKS Over the past 25 years considerable effort has been spent refining our understanding of how the physical and chemical properties of the soil environment interact with microbial communities to maintain an overall balance between the mineralization and immobilization of soil N. During the past 10 years considerable information has been generated on the overall diversity and composition of soil microbial communities. In this review, we have selected a few recent publications that are focused upon the activities of subpopulations of soil microbes and discussed how the implications of this work may lead to a better understanding of N cycling. Clearly, this mini-review is not meant to be all inclusive, but we hope that the readers’ attention has been drawn to “soil phenomena” into which they might “dig” and “unearth” an increased level of understanding about the physiology and growth response behaviors of soil subpopulations and how they influence the balance between mineralization, nitrification, and immobilization of soil N.
ACKNOWLEDGMENTS

The concepts and ideas presented in this mini-review are based upon published work of our own laboratory, of our professional colleagues, and by the thoughts of two anonymous reviewers. Our own research was funded by grants from NSF IGERT, USDA CSREES, USDA NIFA, and USDA.

REFERENCES

Aanderud, Z. T., and Lennon, J. T. (2011). Validation of heavy-water stable isotope probing for the characterization of rapidly responding soil bacterial communities. Appl. Environ. Microbiol. 77, 4969–4976.

Allison, S. D., and Vitousek, P. M. (2005). Responses of extracellular enzymes to simple and complex nutrient inputs. Soil Biol. Biochem. 37, 955–964.

Allison, S. D., Wallenstein, M. D., and Bradford, M. A. (2010). Soil carbon response to warming dependent on microbial physiology. Nat. Geosci. 3, 336–340.

Andersson, J. P. E., and Dorned, K. H. (1979). Physiological method for quantitative measurement of microbial biomass in soils. Soil Biol. Biochem. 10, 215–221.

Barth, E. (1994). Measurement of protein synthesis by soil bacterial assemblies with the leucine incorporation technique. Soil Biol. Biochem. 26, 151–162.

Barth, E. (1998). Growth rates of bacterial communities in soils at varying pH a comparison of the thymidine and leucine incorporation techniques. Microb. Ecol. 36, 318–327.

Bakardjieva, L., Kukic, M., Ignaceva, J., Vukovic, V., Vetrovsky, E., et al. (2011). Active and total microbial communities in forest soils are largely different and highly stratified by decomposition. ISME J. 6, 248–258.

Bellmann, A., Schmidt, J. A., Saunders, A. M., and Nicolaisen, M. H. (2005). Influence of starvation on potential ammonia-oxidizing activity and amoA mRNA levels of Nitrospirae bacteria. Appl. Environ. Microbiol. 71, 1276–1282.

Booth, M. S., Stark, J. M., and Rastetter, E. B. (2005). Control on nitrogen cycling in terrestrial ecosystems: a review of empirical and modeling data. Ecol. Model. 75, 139–157.

Borgo, S. A., Torell, R., Bottomley, P. J., and Myrold, D. D. (2008). Bacterial and fungal contributions to nitrogen cycling under Douglas fir and red alder at two sites in Oregon. Soil Biol. Biochem. 40, 445–451.

Burger, M., and Jackson, I. L. (2010). Chemical immobilization of ammonium and nitrate in relation to ammonification and nitritation rates in organic and conventional cropping systems. Soil Biol. Biochem. 42, 29–36.

Caralp, S. (2005). Cyclodextrin inhibits of protein-protein nitrate production across a soil moisture gradient. Biol. Fertil. Soils 41, 296–298.

Castaldi, S., and Smith, K. A. (1998). Effect of cyclodextrin on the NO3 and NO2 production in a forest and an agricultural soil. Biol. Fertil. Soils 27, 107–110.

Chen, J., and Stark, J. M. (2000). Plant species effects on carbon and nitrogen cycling in a upland-cedared wheatgrass soil. Nat. Geosci. 2, 47–57.

Davidson, E. A., Hart, S. C., Shaman, C. A., and Finster, M. K. (1991). Measuring gross nitrogen mineralization, immobilization, and nitrification with N-15 isotope addition in intact soil cores. J. Soc. 42, 335–349.

Dowling, J., and Shah, I. M. (2010). Exit from dormancy in microbial organisms. Nat. Rev. Microbiol. 8, 800–816.

Gutzler, D., and Horwath, W. R. (2008). Regulation of extracellular protease activity in soil in response to different sources and concentrations of nitrogen and carbon. Soil Biol. Biochem. 40, 2940–2958.

Hart, S. C., Nason, G. E., Myrold, D. D., and Perry, D. A. (1994). Dynamics of gross nitrogen transformations in an old-growth forest the carbon connection. Ecology 75, 480–491.

Hobbie, J. E. (2012). Exit from dormancy. Ecol. Monogr. 82, 533–552.

Jones, D. L., and Murphy, D. V. (2007). Controls on nitrogen mineralization, “in situ” versus tracer data. Proc. Natl. Acad. Sci. U.S.A. 104, 18–23.

Jones, J. T., and Jones, S. E. (2011). Evidence for fungal dominance of denitrification and co-denitrification in a grassland soil. Soil Sci. Soc. Am. J. 76, 1540–1544.

Laughlin, R. J., and Stevens, R. J. (2002). Microbial community structure at varying pH: a comparison of the varying pH: a comparison of the maintenance of microbial diversity. Soil Biol. Biochem. 34, 1589–1597.

Kirkham, D., and Bartholomew, W. V. (1954). Equations for following nutrient transformations in soil, utilizing tracer data. Proc. Soil Sci. Soc. U.S.A. 18, 33–34.

Koschke, D. (1981). The transport of NH3 and NH4 across biological membranes. Biochim. Biophys. Acta 659, 41–52.

Lauber, C. L., Hamady, M., Knight, R., and Fierer, N. (2009). Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Appl. Environ. Microbiol. 75, 3111–3118.

Lehtovirta-Morley, L. E., Stoecker, K., Vilcinskas, A., Prosser, J. I., and Nicol, G. W. (2011). Cultivation of an obligate aerobic ammonia oxidizer from a nitriﬁxing acid soil. Proc. Natl. Acad. Sci. U.S.A. 108, 15992–15997.

Lennon, J. T., and Jones, S. E. (2011). Microbial seed banks: the ecologi- cal and evolutionary implications of dormancy. Nat. Rev. Microbiol. 9, 119–128.

Levins-Rzadowski, S., Nicol, G. W., Ameen, L., Mandel-Meicle, J., and Prosser, J. I. (2012). Stimulation of thiaminase-mediated ammonia oxidation by ammonia derived from organic nitrogen but not added inorganic nitrogen. FEMS Microbiol. Ecol. 80, 116–123.

Levinson, S., Proctor, A., and Schmed, J. P. (2008). Soil hetero- geneity in lumped mineralization–immobilization models. Soil Biol. Biochem. 40, 1147–1150.

Lennon, J. T., and Jones, S. E. (2011). Microbial seed banks: the ecologi- cal and evolutionary implications of dormancy. Nat. Rev. Microbiol. 9, 119–128.

Lindow, D. S., Nielbo, D. B., Prudil, D., and Ellis-Bram, J. (1999). Temp- erature dependence of inorganic nitrogen uptake: reduced affinity for nitrate at suboptimal temperatures in both algae and bacteria. Appl. Environ. Microbiol. 65, 2577–2584.

Rusak, J., Brook, P. C., Barth, E. (2010). Improving the mech- anisms for the opposing pH rela- tionships of fungal and bacterial growth in soil. Soil Biol. Biochem. 42, 926–948.

Rusak, J., Brooks, P. C., and Barth, E. (2008). Contrasting the soil pH effects on fungal and bacterial growth support functional redundancy in carbon mineralization. Appl. Environ. Microbiol. 75, 1599–1599.

McMullen, S. K., Wallenstein, M. D., and Schmed, J. P. (2011). A cross- seasonal comparison of active and total bacterial community compos- ition in Arctic tundra soil using hemo- deoxyuridine labeling. Soil Biol. Biochem. 43, 285–295.

Murphy, D. V., Buxton, S., Stockdale, E. A., Fillery, L. P. J., Lennon, J. T., Hatch, D. J., et al. (2005). Gross nitrogen ﬂuxes in soil: theory, measurement and application of 15N pool dilution labeling. Adv. Agron. 80, 69–118.

Myrold, D. D., and Bottomley, P. J. (2008). “Nitrogen mineralization and immobilization,” in Nitrogen in Agricultu- ral Systems, eds J. S. Schopfer and W. R. Rast (Madison, WI: ASA- CSSA-SSSA), 153–168.

Nicol, G. W. (2007). Potential importance of bact-eria and fungi in nitrate assimila- tion in soil. Soil Biol. Biochem. 39, 1735–1745.

Ochman, E. C., Ingraham, J. L., and Schloss, M. (1990). Physiology of the Bacterial Cell. A Molecular Approach. Sunderland, MA: Sinauer Associates, Inc.

Page Bottomley et al.

Microbial subpopulations and the N cycle

Frontiers in Microbiology | Territorial Microbiology

October 2012 | Volume 3 | Article 379 | 6
Rousk, J., Baiyai, T. A., and Reath, E. (2008). Examining the fungal and bacterial niche overlap using selective inhibitors in soil. *FEMS Microbiol. Ecol. 63*, 356–358.

Schimel, J., Bahri, T. C., and Widdows, M. (2007). Microbial stress response physiology and its implications for ecosystem function. *Ecology 88*, 1386–1390.

Schimel, J. P., and Bennett, J. (2004). Nitrogen mineralization: challenges of a changing paradigm. *Ecology 85*, 591–602.

Schimel, J. P., and Hattenschwiler, S. (2007). Nitrogen transfer between decomposing leaves of different N status. *Soil Biol. Biochem. 39*, 1424–1436.

Sims, G. K., and Wander, M. M. (2002). Proteolytic activity under nitrogen or sulfur limitation. *Appl. Soil Ecol. 19*, 217–222.

Stockdale, E. A., Hatch, D. J., Murphy, D. V., LeGrand, S. F., and Watson, C. J. (2002). Verifying the nitrification to immobilization ratio (N/I) as a key determinant of potential nitrate loss in grassland and arable soils. *Agron. Res. 22*, 831–838.

Stopnisek, N., Gubry-Rangin, C., Hofferle, S., Nicol, G. W., Mandic-Mulec, I., and Prosser, J. I. (2010). Thaumarchaeal ammonia oxidation in an acidic forest peat soil is not influenced by ammonium amendment. *Appl. Environ. Microbiol. 76*, 7626–7634.

Taylor, A. E., Zaglin, L., Watson, T. A., Myrold, D. D., and Bottomley, P. J. (2012). Dynamics of ammonia-oxidizing archaea and bacteria populations and contributions to soil nitrification potentials. *ISME J. doi: 10.1038/ismej.2012.51 [Epub ahead of print].

Taylor, A. E., Zaglin, L. H., Dooley, S., Myrold, D. D., and Bottomley, P. J. (2010). Evidence for different contributions of archaea and bacteria to the ammonia-oxidizing potential of diverse Oregon soils. *Appl. Environ. Microbiol. 76*, 7691–7698.

Touma, M., Singla-Pstein, S., Parlar, K., Komeke, M., Schmidhofer, A., Urich, T., et al. (2011). Nitrosophaera viennensis, an ammonia oxidizing archaeon from soil. *Proc. Natl. Acad. Sci. U.S.A. 108*, 8420–8423.

Tinganira, C., Bron, N., Rousseau, V., Bayrens, W., and Coenye, L. (2003). Influence of bacterial activity on nitrogen uptake rates determined by the application of antibiotics. *Oecologia 45*, 475–489.

Verhamme, D. T., Prosser, J. I., and Nicol, G. W. (2011). Ammonia concentration determines differential growth of ammonia-oxidizing archaea and bacteria in soil microcosms. *ISME J. 5*, 1067–1071.

Zhang, L. M., Offre, P. R., He, J. Z., Verhamme, D. T., Nicol, G. W., and Prosser, J. I. (2010). Autotrophic ammonia oxidation by soil thaumarchaeota. *Proc. Natl. Acad. Sci. U.S.A. 107*, 17240–17245.

Conflict of Interest Statement: The authors declare that the findings cited from their own research in this miniature review was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.