Effects of nitrogen deposition and fertilization on N transformations in forest soils: a review

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Received: 31 October 2014 / Accepted: 8 January 2015 / Published online: 29 January 2015
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Abstract

Purpose Understanding how process-specific nitrogen (N) transformations in natural forest soils are modified by N deposition and fertilization is critically important to gain mechanistic insights on the links between global N deposition and N enrichment and loss in forest soils.

Materials and methods Here we identify the general characteristics and the main mechanisms of N deposition- and fertilization-induced modifications in multiple N transformations, including N immobilization, N mineralization, nitrification (autotrophic nitrification and heterotrophic nitrification), and denitrification, in forest soils by literature survey.

Results and discussion Overall, N status, soil C/N ratios, C availability, and soil pH are key factors separately and/or interactively affecting the effects of N deposition and fertilization on forest soil N transformations. In the N-limited stage, N deposition and fertilization can act as a stimulator of N mineralization by removing microbial N limitation and reducing the C/N ratios of the substrate being decomposed. In the N-unlimited stage, N added to forest ecosystems can retard N mineralization, which may primarily be a result of decreased microbial activity due to soil acidification and low C availability. The changes in N mineralization may drive a corresponding change in N immobilization, autotrophic nitrification, and denitrification. Despite the fact that ammonia-oxidizing archaea (AOA) has a higher affinity than ammonia-oxidizers (AOB) for low-concentration ammonia (NH_3), low NH_3

availability may still limit the rate of ammonia oxidation (autotrophic nitrification) in acidic forest soils even in the case of high NH_4^+ input. Heterotrophic nitrification, however, may be favored if soil C/N ratios and pH decrease with N deposition and fertilization. The responses of denitrification and N_2O emission to N deposition and fertilization in forests may be nonlinear, with a trend of stimulation in the short term but a decline over time, partly because soil pH has a contrast effect on denitrification capacity and N_2O emission.

Conclusions There are various effects of N deposition and fertilization on forest soil N transformations; thus, their responses to N deposition are still not well characterized and understood. N deposition- and fertilization-induced modifications in soil N transformations have important implications for N enrichment, N loss, and soil acidification in forest ecosystems. In the future, more research is required to investigate on dissimilatory nitrate reduction to ammonium (DNRA) process and link microbial community characteristics and functions of microbial extracellular enzymes with these rate processes in forest soils to narrow the uncertainty in evaluating and predicting ecosystem responses to global N deposition.

Keywords DNRA · N_2O emission · N deposition · N transformations · Soil acidification

Responsible editor: Zhihong Xu

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1 Introduction

Atmospheric deposition of reactive nitrogen (N), resulting mainly from combustion of fossil fuels and artificial fertilizer application, has increased at local, regional, and global scales (Galloway et al. 2003, 2008). It is predicted that in the coming decades, global atmospheric deposition rates of reactive N over land may increase by a factor of 2.5 (Lamarque et al. 2005). Continual reactive N deposition has induced many

negative effects, such as N saturation, eutrophication, and acidification, posing a threat to terrestrial and aquatic ecosystems (Aber et al. 1989; Goulding et al. 1998). Among various types of ecosystems, forest ecosystems have received much more attention. In general, low N availability limits many aboveground and belowground properties of forest ecosystems, such as tree growth, productivity, biodiversity, and C sequestration (Levy-Booth et al. 2014). However, N enrichment due to reactive N deposition and fertilization in forest ecosystems has many unexpectedly negative effects: biodiversity loss (Lu et al. 2010), productivity reduction (Aber et al. 1989), and increased greenhouse gas emissions (Liu and Greaver 2009).

There has been particular interest in the effects of N deposition and fertilization on key N transformations in the soil such as N mineralization (net and gross N mineralization), nitrification (net and gross nitrification, autotrophic nitrification, and heterotrophic nitrification), denitrification, and immobilization (gross N immobilization, NH_4^+ immobilization, and NO_3^- immobilization) (Aber et al. 1998; Brenner et al. 2005; Corre et al. 2007; Gundersen et al. 1998; Jordan et al. 2005; Schmidt et al. 2007; Tietema 1998), mainly because they could provide important information on N enrichment and loss in forest ecosystems (Templer et al. 2008; Vitousek et al. 1979; Zhang et al. 2013a). For example, exogenous N input from N deposition and fertilization to forest ecosystems may disturb the balance between microbial N mineralization and immobilization that determines how much mineral N is released into soils (Hodge et al. 2000; Kaye and Hart 1997), and contributes to rate processes such as nitrification and denitrification (Corre et al. 2007), N_2O emission (Butterbach-Bahl et al. 1998; Hall and Matson 1999; Jassal et al. 2011; Zhang et al. 2008), and soil acidification (Liu et al. 2010; Zhao et al. 2007).

However, due to the fact that N transformations in forest soils occur simultaneously and are highly correlated (Fig. 1), there are interactions between transformations in response to N deposition and fertilization. In addition, besides the amounts and forms of N deposition and fertilization, soil N transformations could be greatly affected by many factors and processes as shown in Fig. 1 (Aber et al. 1998; Bengtsson and Bergwall 2000; Corre et al. 2007; Xu et al. 2013; Zhang et al. 2009), making it difficult to identify the main controls, pathways, and mechanisms affecting process-specific transformations and isolate the effects of N deposition and fertilization, and thus resulting in a lack of mechanistic understanding of the links between N cycling and increased N_2O emission and soil acidification in response to N deposition and fertilization (Templer et al. 2008; Zhao et al. 2007).

In this paper, we briefly review the effects of N deposition and fertilization on rate processes (e.g., N immobilization, N mineralization, nitrification, and denitrification) that govern the fate of N in natural forest soils. We focus on (1) the general characteristics of N deposition- and fertilization-induced modifications in these rate processes and (2) the main mechanisms and factors influencing the effects of N deposition and fertilization on these rate processes with the purpose to narrow the uncertainty in evaluating and predicting ecosystem responses, such as forest soil N enrichment, loss, retention and acidification, to global N deposition.

2 General characteristics of exogenous N-addition-induced modifications in N transformations

Due to the fact that the differences in ecosystem type, the level of N loading, the dose, and species of N application and experimental conditions, there may be various effects of N

Fig. 1 The nitrogen (N) transformations and their controllers in forest soils. *Nmin* N mineralization, *Nim* N immobilization, *DNRA* dissimilatory nitrate reduction to ammonium, NH_4^+ ammonium N, NO_3^- nitrate N, *SON* soil organic N, *DON* dissolved organic N, *Cm* microbial biomass,

ORP redox potential, *OXC* oxidation capacity, *AOA* ammonia-oxidizing archaea, *AOB* ammonia-oxidizers. This figure is a modification from Levy-Booth et al. (2014)

Table 1 General characteristics and mechanisms of fertilization-induced modifications in forest soil N transformations

Authors	Forest	N treatment duration	N application rate (R^a)	Methods	Response	Explanation proposed by the authors
Priha and Smolander (1995)	Norway spruce forest	About 30 years	Close to 1	Laboratory incubation of humus layer samples (fumigation extraction)	Decreased microbial biomass N (17 %) and increased net N mineralization (>25 %)	None
Aber et al. (1998)	Red pine plantation and native mixed hardwoods and a mature, healthy spruce-fir system	>8 years	Low N, close to 2; high N, >4	Laboratory incubation of forest-floor samples	Measured maximum rates of net N mineralization under high N conditions were 1.2 to 2.4 times the control (or low N conditions) values, which dropped near or below control values in the late stage (a N-limited site hardwood stand excluded); increased net nitrification in most sites (hardwood stand excluded)	The alternation in net N mineralization was related to C supply, C/N ratios of soil organic matter and the production of humus-degrading enzymes. N retention efficiency, mycorrhizal function, and N status affected the response of net nitrification
Gundersen et al. (1998)	5 coniferous forest stands at the NITREX sites (3 low N deposition sites and 2 high N deposition sites)	Low N deposition sites, 4 to 5 years of N addition; high N deposition sites, 6 years of N removal (roofs)	Low N deposition sites, 0.7 to 2; high N deposition sites, -1	Field and laboratory incubation of forest-floor samples	Increased trend of net (increased by a factor of 0.3 to 1.6) N mineralization in N-unsaturated forest sites	N status
Bengtsson and Bergwall (2000)	Norway spruce forest	>30 years	1 to 6 ^b	Laboratory incubation of O horizon samples using $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ labeling	Absence of enhanced transformation rates of NH_4^+ and NO_3^- ; denitrification was negatively correlated with the amount of fertilization	No obvious changes in the number of soil bacteria; lower accessibility of NO_3^- ions to denitrifiers on soil particles, low soil pH depresses denitrification and too low NO_3^- to exert influence on denitrification
Corre et al. (2003)	Acidic beech forest	At least 10 years	Close to 5	Laboratory incubation of organic and 0–5 cm soil using ^{15}N dilution techniques and chloroform fumigation	Reduced NH_4^+ and NO_3^- immobilization rates; an uncoupled microbial N cycling	Decreased microbial biomass due to decreased supply of labile C
Brenner et al. (2005)	Deciduous (balsam poplar) and coniferous (white spruce) forest stands	3.5 years	500	Field incubation of intact core consisting of both organic and mineral soil at a depth of 0–20 cm	Fertilization increased net nitrification (285 %) but tended to reduce net ammonification (27 %) in the balsam poplar site; in the white spruce site, it stimulated net ammonification (44 %) but showed no effects on net nitrification in the white spruce site	Tree species
Perakis et al. (2005)	Unpolluted old-growth temperate forest	1 year (N added as $^{15}\text{NH}_4^+$, $^{15}\text{NO}_3^-$)	0.1, 4, 8, 16, 32, 64, 128, 256, and 500	Field and laboratory incubation of surface soil (0–10 cm) using ^{15}N pool dilution and acetylene inhibition	Absence of stimulated effects on gross N cycling and potential nitrification	Ammonium-oxidizer populations were not stimulated, nonlinear responses of N retention and loss to excessive N supply

Table 1 (continued)

Authors	Forest	N treatment duration	N application rate (R^a)	Methods	Response	Explanation proposed by the authors
Wertz et al. (2012)	Lodgepole pine and spruce stands	6 years	200 kg N ha ⁻¹ year ^{-1c}	Laboratory incubation of organic and mineral soil using a soil-slurry method combined with acetylene inhibition	Nitrification was dominated by autotrophic nitrification (54.6 to 96.9 %)	Abundances of AOB and <i>Nitrobacter</i> -like NOB, rather than AOA and <i>Nitrospira</i> -like NOB abundances increased under fertilization

^a N application rate (R) was calculated as the ratio of N application rates to background rates of atmospheric N deposition in the study sites

^b Background rates of atmospheric N deposition in the study site were referred to the data of Flückiger and Braun (1998)

^c No background rates of atmospheric N deposition were available to calculate R

deposition and fertilization on forest soil N transformations. The general characteristics and mechanisms of N deposition-induced modifications in N transformations are summarized in Tables 1 and 2 based on available literature and information. Additionally, estimated N losses as N₂O and NO in N-deposited and N-fertilized forest sites from the published reports are presented in Table 3.

2.1 N immobilization

N immobilization by microbes or uptake by plants could have large influences on soil N transformations and the fate of N imported to forest ecosystems. There are multiple lines of evidence that the main fate for the deposited and added N to forest soils is microbial N immobilization, especially under N-limited conditions (Bengtsson and Bergwall 2000; Templer et al. 2005; Zogg et al. 2000). It is likely that N added to these soils may not promote the net release of NH₄⁺ and autotrophic nitrification until microbial N limitation is removed (Hodge et al. 2000; Schimel and Bennett 2004).

However, there is usually a reduction in the amounts and rates of microbial N immobilization in forest soils under high N deposition and fertilizer input conditions (Bengtsson and Bergwall 2000; Corre et al. 2003, 2007; Priha and Smolander 1995; Smolander et al. 1994). For instance, Bengtsson and Bergwall (2000) found that long-term fertilized (30 years) root-free Norway spruce forest soils (O horizon) immobilized less of ¹⁵N-labeled NH₄⁺ and NO₃⁻ relative to unfertilized control soils, confirming the results in Smolander et al. (1994) and Priha and Smolander (1995) that microbial N in the humus layer decreased by 17 % in N-fertilized plots relative to the controls. In the N-saturated plots (fertilization at a rate of 140 kg N ha⁻¹ year⁻¹ for at least 10 years) of an acidic beech forest, both NH₄⁺ immobilization rates (organic layer) and NO₃⁻ immobilization rates (organic and 0–5 cm soil) were found to reduce (Corre et al. 2003). Natural N deposition gradient experiments are also in support of such a trend (Corre et al. 2007). For example, investigation on the changes in microbial N cycling in organic and 0–5 cm mineral soils under spruce forests with similar stand, climatic, and soil characteristics along an ambient N enrichment gradient shows that the maximum microbial N immobilization occurs in intermediate ambient N (Corre et al. 2007). It should be noted that if soil microbial N cycling is characterized by low N immobilization that is uncomparable to gross N mineralization and nitrification in N-deposited and N-fertilized forest sites, it may be a sign of uncoupled soil N cycling (Corre et al. 2003; Tietema 1998). However, as shown in Tables 1 and 2, there is a lack of data or useful indexes (e.g., N application/deposited rates) to indicate how much N added or deposited to forest ecosystems will induce a shifted change in the amounts and rates of microbial N immobilization as well as a shifted response of other soil N processes.

Table 2 General characteristics of forest soil N transformations along natural N deposition gradient

Authors	Forest	N deposition	Methods	Explanation proposed by authors
Tietema (1998)	5 coniferous forest stands at the NITREX sites (3 low N-saturated sites and 2 N-limited sites)	N-limited sites: P^a close to 0; N-saturated sites: P in the range of 0.53 to 0.58	Laboratory incubation of forest-floor samples using ^{15}N dilution and numerical simulation model	N status
Lovett and Rueth (1999)	Northern hardwood forest in the USA	4.2 to 11.1 kg N ha ⁻¹ year ⁻¹	Laboratory incubation of organic, surface (0–10 cm), and subsurface soil (>10 cm)	Species-related effects
Jordan et al. (2005)	Mixed conifer forest	Heavy load of N deposition dominated by dry N deposition and acid deposition	Laboratory incubation of organic and 0–10 cm mineral soil using a soil-slurry method combined with acetylene inhibition	Particular species of autotrophic AOB were not activated by increased N availability; potential nitrification activity was not dominated by the activity of autotrophic AOB, but rather was a product of other microorganisms or processes thriving in the N-saturated soil
Corre et al. (2007)	Spruce forest stands across Germany	Low N: P^b falls into the values of 0.04–0.13; intermediate N enrichment: $P \leq 0.26$; highly N enriched: $P > 0.42$. P indicated by leaching/throughfall N ratios	Laboratory incubation of organic and 0–5 cm mineral soil using ^{15}N dilution technique and chloroform fumigation	Higher microbial decomposition, available C, and microbial biomass favored gross N mineralization; increased gross N mineralization, autotrophic nitrification and C availability, and stronger acid tolerance of autotrophic nitrifiers and heterotrophic fungal nitrifiers were conducive to gross nitrification; increased N mineralization and available C favored microbial NH_4^+ immobilization; higher NH_4^+ and C availability, lower pH, and greater diffusion rate of NO_3^- favored microbial NO_3^- immobilization, or vice versa
Fang et al. (2011)	14 forests along an urban-rural transect in southern China	11.7 to 65.1 kg N ha ⁻¹ year ⁻¹	Laboratory incubation of 0–10 mineral soil	High soil N availability

^a P was indicated by the ratios of output/input N^b P was estimated to be the ratios of leaching/throughfall N

Table 3 Estimated N losses as N₂O and NO in N-deposited and N-fertilized forest sites

Authors	Forest	N deposition and addition	Methods	Estimated N emissions as NO and N ₂ O	The ratio of N losses as N ₂ O and NO to N deposited and added ^a	Sources of N ₂ O and NO
Butterbach-Bahl et al. (2002)	Scots pine forest soils of the northeastern German lowlands	15 to 22 kg N ha ⁻¹ year ⁻¹	Field measurement using the chamber technique	NO, 3.1–39.1 µg N m ⁻² h ⁻¹ ; N ₂ O, 4.7–32.0 µg N m ⁻² h ⁻¹	NO, 2.7–34.5 %; N ₂ O, 4.1–28.0 %	–
Hall and Matson (1999)	Two tropical rainforests of Hawai'i	22 Tg N year ⁻¹	Dose-response experiment	–	NO, 2 %; N ₂ O, 4 %	–
Horváth et al. (2006)	Spruce forest (S) and oak forest (O)	1.42 (S) and 1.59 (O) g N m ⁻² year ⁻¹	Field measurement using chamber technique	S, 1.2 µg NO-N m ⁻² h ⁻¹ and 15 µg N ₂ O-N m ⁻² h ⁻¹ ; O, 2.1 µg NO-N m ⁻² h ⁻¹ and 20 µg N ₂ O-N m ⁻² h ⁻¹	NO, 0.74–1.16 %; N ₂ O, 9.25–11.02 %	–
Pilegaard et al. (2006)	European forests (7 coniferous sites (C) and 8 deciduous sites (D))	0.22 to 3.85 g N m ⁻² year ⁻¹	Field measurement using chamber technique	C, 0.006 to 81.7 µg NO-N m ⁻² h ⁻¹ and 0.3 to 14.8 µg N ₂ O-N m ⁻² h ⁻¹ ; D, 0.7 to 13.4 µg NO-N m ⁻² h ⁻¹ and 4.9 to 20.3 µg N ₂ O-N m ⁻² h ⁻¹	C, 0.03–24.53 % (NO) and 0.52–11.47 % (N ₂ O); D, 0.61–9.02 % (NO) and 2.28–19.27 % (N ₂ O)	NO and N ₂ O were produced mainly from nitrification and denitrification, respectively
Venterea et al. (2003)	Pine forest and mixed hardwood forest	50 (low N) and 100 (high N) kg N ha ⁻¹ year ⁻¹ above background (control) (8 kg N ha ⁻¹ year ⁻¹)	Field measurement using closed chamber and laboratory incubation (acetylene inhibition)	NO: In pine site, fertilization elevated NO fluxes of 100–200 µg NO-N m ⁻² h ⁻¹ relative to control; in hardwood site, only high N induced similar effects on NO fluxes: N ₂ O, <10 % of NO flux	NO, 3.0–3.7 % (high N plots) and 8.3 % (low N plots) in the pine site	Increased autotrophic nitrification may be responsible for elevated NO fluxes

^a The ratio of N losses as N₂O and NO (estimated emission rates of N₂O and NO) to N deposited and added (the rates of N deposition and fertilization application) was calculated based on the method used by Horváth et al. (2006)

2.2 N mineralization

In native forest systems, N mineralization contributes greatly to soil mineral N production, greatly affecting plant nutrient availability, microbial activity and diversity, carbon (C) sequestration, and soil rate processes.

Examination of the effects of N deposition and fertilization on N mineralization has been mostly focused on net N mineralization in forest ecosystems (Aber et al. 1998; Brenner et al. 2005; Gundersen et al. 1998; Lovett and Rueth 1999; Zak et al. 2006), with only few studies providing information on gross N mineralization by means of ^{15}N dilution and tracing techniques (Corre et al. 2003, 2007; Tietema 1998) (Tables 1 and 2), showing an inhibitory trend if forest ecosystems have approached a status of “N saturation.” For example, Aber et al. (1998) found measured maximum rates of net N mineralization in forest floor from various types of ecosystems in the USA under high N conditions were 1.2 to 2.4 times the control (or low N conditions) values, which dropped near or below control values in the late stage (a N-limited hardwood stand was excluded). By synthesizing data from European NITREX (NITrogen saturation Experiments) project, Gundersen et al. (1998) found that in N-limited forest ecosystems, N addition can increase net mineralization in forest floors by a factor of 0.3 to 1.6. Mechanistic insights on the effects of N deposition and fertilization on forest soil N production and consumption could be acquired from the measurement of gross rates (e.g., gross N mineralization, gross N immobilization, and gross nitrification). However, the response trends of gross N mineralization to N deposition and fertilization are not so well characterized as that of net N mineralization in forest ecosystems, which may differ between soil layers (organic and mineral layers) and physiological capacity of soil microbes in forest stands with different site characteristics (e.g., soil properties: soil texture, soil pH, contents of organic C, mineral N and base cations; forest stand structure: tree species and understory vegetation; environmental conditions: mean annual temperature, mean annual precipitation) (Bengtsson and Bergwall 2000; Corre et al. 2003, 2007; Perakis et al. 2005). Nevertheless, it is important to note that almost exactly the same results and tendencies of measured rates of net mineralization (forest floor) from five European coniferous forests and gross N mineralization (organic and 0–5 cm mineral soil) from Germany spruce forest ecosystems were obtained from natural N deposition gradient experiments, showing that the measured rates increased up to intermediate ambient N enrichment gradient but somewhat dropped at N-enriched conditions (Corre et al. 2007; Tietema 1998). However, as summarized in Tables 1 and 2, it is not difficult to find that studies on the effects of N deposition on forest soil N mineralization as well as other N transformation processes

have been conducted in temperate zones in developed North American and European countries, and most of the limited number of studies are from coniferous forest stands (Aber et al. 1998; Brenner et al. 2005; Corre et al. 2003, 2007; Gundersen et al. 1998; Tietema 1998), indicating a lack of study on subtropical, tropical, and boreal forest ecosystems.

2.3 Nitrification

Nitrification plays an important role in regulating N availability and NO_3^- leaching in forest ecosystems. Nitrification is generally divided into autotrophic nitrification and heterotrophic nitrification in soils, which are mainly carried out by chemoautotrophic ammonium-oxidizing bacteria (AOB, represented by the *Nitrosomonas* species) and nitrite-oxidizing bacteria (NOB, represented by the *Nitrobacter* species) and by certain heterotrophic bacteria and fungi possessing the potential to oxidize both organic and inorganic N compounds, respectively (De Boer and Kowalchuk 2001). Generally, autotrophic nitrification in soils is favored by increased availability of NH_3 , pH close to neutral, and good aeration (Barnard et al. 2005). In acidic soils, especially those with low C/N ratios, heterotrophic nitrification is favored (Barnard et al. 2005; De Boer and Kowalchuk 2001).

The effects of N deposition and fertilization on net and gross nitrification in forest soils show a large variability (Aber et al. 1998; Brenner et al. 2005; Corre et al. 2007; Gundersen et al. 1998; Perakis et al. 2005). For instance, Brenner et al. (2005) found that during the growing season, fertilization ($100 \text{ kg N ha}^{-1} \text{ year}^{-1}$) induced a large increase in annual net nitrification (285 %) in the balsam poplar site but showed only slight effects on net nitrification in white spruce site, suggesting that there existed tree species-related effects on the responses (Brenner et al. 2005; Lovett and Rueth 1999). However, it should be noted that nitrification (both net and gross nitrification) in forest soils usually follows the same change pattern of N mineralization in response to N deposition and fertilization (Aber et al. 1998; Corre et al. 2007). In addition, it is worthy of note that N deposition and fertilization could affect the pathways for forest soil NO_3^- production. For example, in two acidic forest soils that long suffered from a heavy load of N deposition dominated by dry N deposition and acid deposition, it was found that nitrification in organic and 0–10 cm mineral soils was dominated by heterotrophic nitrification (Jordan et al. 2005). However, Wertz et al. (2012) reported that autotrophic nitrification still contributed mostly (54.6 to 96.9 %) to nitrification in N-amended organic and mineral soils of lodgepole pine and spruce stands. However, to our knowledge, research on specific pathway-related processes such as autotrophic nitrification and heterotrophic nitrification in N-deposited and N-fertilized forest sites is still very lacking (Tables 1 and 2).

2.4 Denitrification and N₂O emission

Denitrification plays a critical role in greenhouse gas N₂O emission in forest ecosystems. Denitrification is generally favored by high availability of C and NO₃[−], poor aeration, and neutral pH (Booth et al. 2005; Xu et al. 2013). In terms of N loss in forest ecosystems, the influence of N deposition and fertilization on denitrification may be insignificant (Gundersen 1991). However, more and more attention is being paid to denitrification process in forests under increasing N deposition due to the high global warming potential of N₂O (Hall and Matson 1999; Levy-Booth et al. 2014). Although some studies have shown that N deposition and fertilization to forest ecosystems have minor effects on soil N₂O emission (Magill et al. 1997), there is mounting evidence that excessive N deposition to forest ecosystems, especially to N-unlimited forest ecosystems, has promoted soil N₂O emission (Butterbach-Bahl et al. 1998; Gundersen et al. 2012; Hall and Matson 1999; Jassal et al. 2011; Pilegaard et al. 2006; Zhang et al. 2008). For example, Hall and Matson (1999) found that N addition stimulated N₂O emissions in both phosphorus (P)-limited and N-limited tropical forest soils, with a greater stimulation in the P-limited forest. In the above studies, increased N₂O emission in most cases is attributed to increased denitrification. However, the linkage between denitrification and increased N₂O emission and how denitrification process and N₂O emission in forest soils are affected by increased N deposition and fertilization remain unclear (Aronson and Allison 2012; Bengtsson and Bergwall 2000; Levy-Booth et al. 2014). For example, Bengtsson and Bergwall (2000) found that long-term fertilization decreased the denitrification capacity of Norway spruce forest soils. Also, a meta-analysis of environmental impacts on nitrous oxide release in response to N amendment showed that increased reactive N entering natural systems, forest ecosystems included, may induce a short-term positive effect on soil N₂O emission; however, such an effect could diminish over time (Aronson and Allison 2012).

3 Mechanisms and factors for N-addition-induced modifications in N transformations

3.1 N immobilization

The rates and amounts of microbial N immobilization could be influenced by N mineralization, available C, NH₄⁺ availability, acidic conditions, the diffusion rate of NO₃[−], sources of fertilizer, microbial biomass, and N status (Bengtsson and Bergwall 2000; Corre et al. 2003, 2007; Tietema 1998). In general, increased N mineralization and available C will drive a corresponding increase in microbial NH₄⁺ immobilization in

forest soils (Corre et al. 2007). As for microbial NO₃[−] immobilization, it is generally favored by high NH₄⁺ and C availability, low soil pH, and greater diffusion rate of NO₃[−] (Corre et al. 2007). For example, the reduced rates of NH₄⁺ and NO₃[−] immobilization in the N-saturated plot of acidic beech forest soils are considered to be a result of decreased microbial biomass owing to decreased supply of labile C (Corre et al. 2003).

As reported, gross N mineralization, C availability, and microbial biomass can provide useful information on the changes in the rates and amounts of microbial N immobilization in forest soils in response to N deposition and fertilization. However, a question remains to be resolved about whether the change in microbial biomass in N-deposited and N-fertilized forest sites may primarily be a result of change in soil bacteria or fungi or both in forest soils of different pH values.

3.2 N mineralization

N mineralization is at least a two-step process: the depolymerization of N-containing polymers by microbial (including mycorrhizal) extracellular enzymes into organic N-containing monomers (amino acids, amino sugars, nucleic acids, etc.) and subsequent ammonification (Schimel and Bennett 2004). The first step is to regulate overall N cycling in soils (Schimel and Bennett 2004). As reported, N mineralization in forest soils may be affected separately and/or interactively by a range of factors and processes (Fig. 1), such as C/N ratios of soil organic matter (SOM) (Bengtsson et al. 2003; Hodge et al. 2000; Kaye and Hart 1997), soil pH (Fang et al. 2004), soil microbes (e.g., microbial biomass and activity) (Bengtsson et al. 2003; Tietema 1998), microbial extracellular enzymes (Enowashu et al. 2009), and quality and decomposition of litter (e.g., C/N ratios and N content of lignin) (Janssens et al. 2010).

At the ecosystem level, it may be useful to focus on soil C/N ratios, microbial activities (microbial biomass and respiration), and C availability as the key factors responsible for the effects of N deposition and fertilization on forest soil N mineralization (Aber et al. 1998; Booth et al. 2005; Corre et al. 2007; Tietema 1998; Zhu et al. 2013). For instance, data on soil characteristics and gross N transformation rates from across a wide range of ecosystems, forest ecosystems included, show that gross N mineralization rate is positively correlated with microbial biomass and C availability that are negatively correlated with soil C/N ratio (Booth et al. 2005). Also, Tietema (1998) found that gross N mineralization and immobilization rates from five European coniferous forest floors along a N deposition gradient were correlated with microbial respiration rates. These occur mainly due to two facts: (1) most N transformations in soils, with an exception of autotrophic nitrification, are carried out by heterotrophic bacteria and fungi that depend highly on labile C supply (Hodge et al.

2000); and (2) soil C/N ratio exerts great influences on the balance between N mineralization and immobilization. In theory, N is sequestered from soils by both fungi and bacteria if the C/N ratios of the substrate for decomposition are greater than about 30:1; N is released (N mineralization) by fungi but sequestered by bacteria if the C/N ratios are between 12.5:1 and 30:1; and N is released by both fungi and bacteria if the C/N ratios are less than about 12.5:1 (Hodge et al. 2000). For example, the direct N inputs from N deposition and fertilization to canopy leaves, litterfall, and soil have been reported to increase plant leaf N concentration (Fang et al. 2011; Hietz et al. 2011; Zak et al. 2008) and fine root N content (Magill et al. 2004), which has the potential to reduce the C/N ratios of the substrate being decomposed in forest ecosystems, and thus facilitating net microbial N mineralization greatly (Hodge et al. 2000; Kaye and Hart 1997).

However, N deposition and fertilization can also act as an inhibitor to forest soil N mineralization (Aber et al. 1998; Corre et al. 2007; Gundersen et al. 1998; Janssens et al. 2010). Firstly, the retardation of N mineralization is associated with the C/N ratio, N concentration, and lignin content of the substrate being decomposed (Fog 1988; Janssens et al. 2010).

Secondly, the decreased N mineralization may be a result of decreased microbial activities, which can be reflected from decreased microbial respiration and microbial biomass (Liu and Greaver 2010). For example, reduced microbial activity has been frequently reported from fertilized forest soils (Compton et al. 2004; Demoling et al. 2008; Frey et al. 2004; Wallenstein et al. 2006). Two meta-analysis papers also confirm such a trend, showing that N deposition tends to reduce microbial biomass in the N-poor boreal forest soils (Treseder 2008) and decrease heterotrophic respiration and microbial biomass in N-unlimited temperate forest soils (Janssens et al. 2010). As suggested by Wallenstein et al. (2006), the decreased microbial activity in these fertilized forest soils could be that soil bacteria are more likely limited by a lack of C. For example, Eisenlord et al. (2013) found that experimental N deposition significantly altered the compositions of functional genes derived from actinobacterial and fungal communities in a hardwood forest ecosystem. In addition, they found that the richness and diversity of genes involved in the decomposition of starch (~12 %), hemicellulose (~16 %), cellulose (~16 %), chitin (~15 %), and lignin (~16 %) were also significantly reduced by experimental N deposition. Lots of studies have proven that increased N deposition to forest ecosystems has led to soil acidification (Fluckiger and Braun 1998; Liu et al. 2010), which may also affect the activities of soil microbes and C availability (Bárta et al. 2010; Fang et al. 2004). For instance, in a highly acidic spruce forest soil, the amounts of dissolved organic C (DOC) and dissolved N were found to be very low (Bárta et al. 2010). It is well accepted that mycorrhizal fungi exert strong controls over belowground C allocation in forest ecosystems, greatly

affecting microbial turnover in the rhizosphere (Janssens et al. 2010; Kuzyakov and Xu 2013; Lilleskov et al. 2001, 2002; Tietema 1998; Treseder 2008). Here, we further conjecture that the change in mycorrhizal fungi, resulting from Al_3^+ release in the process of soil acidification, is likely to play a role in the decreased N mineralization.

Finally, changes in microbial extracellular enzymes involved in N transformations may provide mechanistic insights on the decreased N mineralization. Microbial extracellular enzymes play a pivotal role in catalyzing the litter loss, SOM decomposition, and nutrient transformations (Berg and Meentemeyer 2002; Nie et al. 2014). Although Treseder et al. (2001) proposed that N availability may be a limiting factor affecting the production of N-rich enzymes, high N availability has been proven to alter the activities of certain enzymes involved in SOM decomposition. Inhibitory effects on the decomposition of recalcitrant SOM under high N addition are generally attributed to the repression on extracellular enzyme activity and lignin degradation (Berg and Meentemeyer 2002; Carreiro et al. 2000; Hagedorn et al. 2003; Hodge et al. 2000; Sinsabaugh et al. 2002). For example, Carreiro et al. (2000) found chronic N addition increased cellulose activity in decaying leaf litter of flowering dogwood, red maple, and red oak, but substantially inhibited the activity of lignin-degrading phenol oxidase in high lignin oak litter. In agreement with Carreiro et al. (2000), Frey et al. (2004) also found that the activity of phenol oxidase, a lignin-degrading enzyme produced by white-rot fungi, decreased significantly with the decreased ratio of fungal to bacterial in pine and hardwood forest stands that were amended with chronic N deposition. Furthermore, the suppression in lignin-degrading enzyme may have offset the stimulation of N addition on cellulose-degrading enzymes (Frey et al. 2004). Specifically, two N cycling enzymes, β -N-acetyl-glucosaminidase and leucine aminopeptidase that are respectively involved in the degradation of chitin and the degradation of proteins and peptides, are mentioned mostly in available literature (DeForest et al. 2012; Enowashu et al. 2009). Sinsabaugh et al. (1993) assumed that low N availability could induce the activity of β -N-acetyl-glucosaminidase while high N availability may result in a noncompetitive inhibition. For example, Enowashu et al. (2009) reported that the activities of N cycling enzymes such as urease, arginine, deaminase, alanyl aminopeptidase, and lysyl-alanyl aminopeptidase increased, but the activities of β -N-acetyl-glucosaminidase and leucine aminopeptidase were found to decrease in a spruce forest under reduced N deposition conditions.

It is evident that the direction and magnitude of the effect of N deposition and N fertilization on N mineralization are separately and/or interactively affected by soil C/N ratios, C availability, and soil pH. To gain a mechanistic understanding on the changes of forest soil N mineralization under N deposition and fertilization, besides soil variables, it is necessary to

make investigations on soil microbial characteristics and microbial extracellular enzymes and their links with soil C and N cycling.

3.3 Nitrification

Whether net and gross nitrification in forest soils can be stimulated by N deposition and fertilization is associated with N mineralization (Corre et al. 2007), the importance of autotrophic nitrification and heterotrophic nitrification (Jordan et al. 2005; Perakis et al. 2005; Wertz et al. 2012), soil N content and pH (Jordan et al. 2005), soil C availability (Corre et al. 2007), acid tolerance of autotrophic nitrifiers and heterotrophic fungal nitrifiers (Corre et al. 2007), and the density of nitrifiers (Bengtsson and Bergwall 2000). In general, increased gross N mineralization, autotrophic nitrification and C availability, acid-tolerant autotrophic nitrifiers, and heterotrophic fungal nitrifiers are conducive to gross nitrification (Corre et al. 2007). However, it should be noted that only when soil nitrification is dominated by autotrophic nitrification, gross nitrification will increase with increasing autotrophic nitrification (Jordan et al. 2005).

In the past, it is long assumed that the main pathway for soil NO_3^- production is autotrophic nitrification, which is driven by AOB and NOB (De Boer and Kowalchuk 2001; Kowalchuk and Stephen 2001). Thus, in early and even in recent studies, the absence of stimulated effect on potential nitrification is usually attributed to that AOB populations are not activated in fertilized forest soils (Jordan et al. 2005; Perakis et al. 2005). In addition, the activity of AOB may be somewhat repressed by soil acidification in fertilized soils since AOB populations tend to be restricted in pH-neutral site of acidic soils or in soils with pH neutral or close to neutral (Prosser 1989). For instance, in acidic forest soils of southern China, low soil pH led to the low rate of autotrophic nitrification (Zhang et al. 2013a). Despite the fact that Wertz et al. (2012) found that fertilization increased the abundances of AOB and *Nitrobacter*-like NOB, rather than ammonia-oxidizing archaea (AOA) and *Nitrospira*-like NOB abundances, there is increasing evidence that AOA, with a higher affinity for low concentrations of NH_3 in acidic environment, leads to AOB in ammonia oxidation in acidic forest soils (Levy-Booth et al. 2014; Zhang et al. 2012b). However, rates of autotrophic nitrification in acidic forest soils are generally reported to be low even in the case of N input (Schmidt et al. 2007; Zhang et al. 2013a). We speculate that low NH_3 availability in low pH soils may greatly restrict the rates of ammonia oxidation performed by both AOA and AOB in fertilized forest soils.

It has been reported that nitrification may be dominated by heterotrophic nitrification in acidic forest soils (Jordan et al. 2005; Zhang et al. 2013b). For example, a study from Zhang et al. (2013a, b) confirmed that the rates of heterotrophic

nitrification were significantly higher than those of autotrophic nitrification in the acidic forest soils of southern China, which are naturally N rich while an opposite trend was observed in the boreal forest soils. One reason for the high heterotrophic nitrification could be that acid-tolerant heterotrophic fungal nitrifiers are less prone to soil acidification (Corre et al. 2007), thus increasing heterotrophic nitrification linearly (Zhu et al. 2013). If decreased soil C/N ratios are taken into account, it is not difficult to understand why there is increased heterotrophic nitrification in certain fertilized forest soils (Booth et al. 2005; De Boer and Kowalchuk 2001; Kowalchuk and Stephen 2001).

It is noteworthy to mention that the kinetics of nitrification may affect the degree to which N addition impacts on nitrification in forest soils. For example, a report from Zhao et al. (2007) shows that NH_4^+ addition initially reduced soil pH but did not affect nitrification in an acidic subtropical forest soil, implying its relation with the zero-order kinetics of nitrification in acidic conditions. In other words, if nitrification in soils follows zero-order kinetics, substrate availability is not a limiting factor for nitrification.

In brief, it seems that gross N mineralization and C availability are two important factors influencing gross nitrification, and soil pH as a key regulator affecting the role of autotrophic nitrification and heterotrophic nitrification in forest soils under N deposition and fertilization. The low rates of ammonia oxidation (autotrophic nitrification) in acidic forest soils even in the case of high NH_4^+ input may primarily be a result of low NH_3 availability in acidic conditions. On the contrary, heterotrophic nitrification may be favored if soil pH as well as soil C/N ratios decrease with N inputs in forests. In the future, a special emphasis and attention should be given to the soil nitrification kinetics when examining the effects of N deposition and fertilization on net and gross nitrification in forest soils.

3.4 Denitrification and N_2O emission

Compared to nitrification, the mechanisms behind N deposition- and fertilization-induced modifications in denitrification are poorly understood. At site level, the denitrifier community activity and denitrification processes may be greatly influenced by soil moisture and O_2 partial pressure (Gundersen et al. 2012; Pilegaard et al. 2006; Russow et al. 2009), organic C and soil pH (Bárta et al. 2010; Gundersen et al. 2012; Levy-Booth et al. 2014; Pilegaard et al. 2006), and oxidation capacity (OXC) (Zhang et al. 2009). In addition, the accessibility of NO_3^- ions to denitrifiers on soil particles can also exert an influence on denitrification (Bengtsson and Bergwall 2000). At ecosystem levels or in a regional scale, N deposition, together with land use change, forest management, and climate change, plays an important role in shaping the denitrification capacity (e.g., N_2O emission) of forest soils

via inducing changes in soil internal drivers (e.g., N availability, pH, water content (diffusion), and temperature) (Gundersen et al. 2012).

Increased denitrification in N-deposited and N-fertilized forest ecosystems may be a result of stimulation of N on denitrify populations (Booth et al. 2005; Xu et al. 2013). Despite the fact that 16 years of reduced N deposition in spruce forest soil increased NH_4^+ availability but did not affect denitrification genes (Kandeler et al. 2009), Levy-Booth et al. (2014) still pointed out that the abundance of certain denitrification genes (*napA*, *nirS*, *nirK*, and *nosZ*) in forest soils will increase with increasing total N and NH_4^+ concentrations through exogenous N input if soil pH, moisture, and organic C favor or facilitate denitrification. In a highly acidic spruce forest soil, Bárta et al. (2010) found that there were exponential correlations between the amount of *nirK* denitrifiers and DOC and pH, showing two important threshold values being 4.8 mol kg^{-1} and 5, respectively, and below these two values, the amount of *nirK* denitrifiers decreased rapidly. Therefore, decreased soil pH and C availability may mitigate the stimulation of N deposition and fertilization on denitrification in forest ecosystems (Šimek et al. 2002), which may provide explanations for the reversed trends in denitrification (N_2O emission) of forest soils over time under fertilization (Aronson and Allison 2012; Bengtsson and Bergwall 2000).

Although increased N_2O emission under N deposition and fertilization is a widespread phenomenon in forest ecosystems, the mechanistic links between denitrification process and N_2O emission are still not well understood. One of the main challenges is that N_2O can be produced from many N transformation processes in soils, and the contribution of N_2O -genic processes to total N_2O production are not easily quantified. Traditionally, heterotrophic denitrification and autotrophic nitrification are viewed as the main sources for N_2O production in soils (Barnard et al. 2005; Wrage et al. 2001). In fact, processes such as heterotrophic nitrification by fungi (Eylar and Schmidt 1959), anaerobic oxidation of NH_4^+ (Santoro et al. 2011), and codenitrification by fungi and actinomycetes (Laughlin and Stevens 2002; Spott et al. 2011; Spott and Stange 2011) have been identified to produce N_2O . However, in humid environments, heterotrophic denitrification is widely accepted as the dominant source of N_2O production, followed by autotrophic nitrification (Davidson et al. 1986). Therefore, identification of the sources of N_2O in N-deposited and N-fertilized forest sites is a key step to reveal and predict the long-term response of soil N_2O emission to chronic N deposition. Correspondingly, different approaches and techniques, including inhibition of low concentration of acetylene on nitrification, ^{15}N trace methods, natural abundance of ^{15}N in N_2O , and ^{15}N tracing model, are applied to identify the pathways and rates of soil N_2O production, which have been well summarized by Müller et al. (2014) and Kulkarni et al. (2014). For example, Ambus

et al. (2006) found the main source of N_2O emitted from temperate European forests characterized by various climatic regimes and forest types (seven coniferous sites and four deciduous sites) is nitrification following the application of laboratory ^{15}N labeling of intact soil cores and linear mixing model. Furthermore, a low-concentration ^{15}N -labeled ammonium-nitrate solution was applied to a temperate beech and spruce forest to simulate N deposition and thus to assess the direct contribution of N deposition to N_2O emissions in temperate forests, with the results showing that stimulated N loss as N_2O was mainly driven by denitrification (Eickenscheidt et al. 2011). In addition, soil temperature (Schindlbacher et al. 2004; Skiba et al. 1998; Smith et al. 1998) and moisture (Schindlbacher et al. 2004) exert strong controls over N_2O emission from forest soils via modifying rates of enzymatic processes. For example, forest N_2O emission increases with increasing water-filled pore space (WFPS) (Schindlbacher et al. 2004) or soil moisture (Zhang et al. 2008). Besides soil temperature and moisture, a range of processes and factors, such as rates of nitrification and denitrification, NO_3^- availability, redox conditions, and labile C pools, exert strong controls over N_2O production (Tiedje et al. 1982), making it difficult to identify the main controls, pathways, and mechanisms affecting N_2O production and emission under N deposition and fertilization.

Large N_2O emission from bacterial denitrification and fungal denitrification in soils is thought to be a failure of the reduction of N_2O to N_2 that is highly regulated by N_2O reductase (N_2OR), the activity of which is affected by copper (Cu) (Richardson et al. 2009). High levels of N deposition and fertilization may stimulate rapid microbial growth to make Cu limited, thus impeding N_2O reduction to promote N_2O emission from forest soils (Richardson et al. 2009). In addition, the activity of N_2OR is sensitive to pH showing more active at $\text{pH} > 7$ in vitro, while NO_3^- , NO_2^- , and NO reductases are generally more active at $\text{pH} < 7$, providing an alternative explanation for the higher ratios of N_2O to N_2 from denitrification in soils with low pH (Richardson et al. 2009; Šimek et al. 2002). At the ecosystem level, increased N_2O emission from fertilized forest soils may be a result of Al_3^+ toxic effects on mycorrhizal fungi in the process of soil acidification. This is mainly because loss of mycorrhizal fungi function plays a key role in increasing nitrification and NO_3^- mobility (Aber et al. 1998) and, thus, greatly facilitating N_2O emission from soils (Ernfors et al. 2011). If root systems are damaged in the process of soil acidification, we further want to know if more soil moisture will be retained in ecosystems to favor denitrification and N_2O emission.

However, N deposition- and fertilization-induced soil acidification may not favor N_2O emission from forest soils. On the one hand, there will be smaller amounts of organic C, as well as mineral N, available to the denitrification population under acidic conditions (Šimek et al. 2002). On the other hand, more

NO_3^- will be immobilized in soils with low pH (Fang et al. 2004), effectively affecting the amounts of substrate available for denitrification (Zhang et al. 2013b).

For field studies, it should monitor a wider set of parameters, including the soil variables (e.g., soil moisture, C availability, N content, and soil pH), soil microbes (e.g., denitrifying bacteria and denitrifying fungi), and soil rate processes (heterotrophic denitrification and autotrophic nitrification), to allow identification and ranking of various factors that govern the effects of N deposition and fertilization on denitrification process and N_2O emission in forest soils. In addition, more research is required to clarify the links between rate processes such as nitrification, denitrification, and N_2O emission and how these rate processes in acidic forest soils are affected by N deposition and fertilization (Levy-Booth et al. 2014).

4 Environmental consequences of N-addition-induced modifications in N transformations

Higher rates of N mineralization, lower rates of nitrification, higher nitrate (NO_3^-) immobilization, and less N loss from denitrification and leaching are responsible for mineral N production and conservation in forest soils (Templer et al. 2008; Vitousek et al. 1979; Zhang et al. 2013a). However, excessive accumulation of mineral N may stimulate nitrification and denitrification to promote N losses, such as N_2O emission and NO_3^- leaching, from forest ecosystems (Vitousek and Howarth 1991), impeding climate change mitigation and contributing to soil acidification and eutrophication. Thus, N deposition- and fertilization-induced modifications in soil N transformations have important implications for N enrichment, N loss, N retention, and soil acidification in forest ecosystems.

4.1 N enrichment in forest soils

N transformations play an important role in forest soil N enrichment. In native forest ecosystems, the main pathway for soil NH_4^+ production is N mineralization (Gundersen and Rasmussen 1995). Dissimilatory nitrate reduction to ammonium (DNRA) process is also considered as a possible pathway for NH_4^+ production in forest soils (Bengtsson and Bergwall 2000). However, the occurrence of DNRA is generally favored by low and fluctuating redox conditions, such as humid tropical forest soils with high rainfall (Tiedje 1988). Produced NH_4^+ in soils can be consumed via microbial assimilation, plant uptake, and autotrophic nitrification (Fig. 1). NO_3^- produced from autotrophic nitrification, as well as from heterotrophic nitrification, can be consumed either through microbial assimilation, plant uptake and DNRA, or loss from

denitrification to gaseous N and leaching (De Boer and Kowalchuk 2001; Templer et al. 2008). NO_3^- can also be immobilized into soil organic nitrogen (SON) and become available only after remineralization (Huygens et al. 2007).

Generally, N mineralization and N immobilization are the two most important processes affecting forest soil N enrichment. For example, the low rates of N mineralization as a result of low soil temperature, low soil pH, and low quality of litterfall make boreal forest soils naturally N poor (Fang et al. 2004), and thereof, plant growth is generally limited by soil N (Nasholm et al. 1998). Moreover, soil microbes in those soils also lack N and are more effective than plants at competing for N (Kuzakov and Xu 2013). Thus, N added to these soils will be firstly used to remove microbial N immobilization. When soil microbes in these ecosystems are not short of N, net N mineralization will increase, which further increases plant N uptake and decreases the C/N ratios of soil organic matter. Soil organic matter with decreased C/N ratios, in return, facilitates the net microbial N mineralization that favor the net accumulation of inorganic N (Hodge et al. 2000; Kaye and Hart 1997).

Increased N mineralization and decreased N immobilization may be in favor of soil N enrichment from various types of fertilized forest ecosystems, including temperate forests (Bengtsson and Bergwall 2000; Gundersen and Rasmussen 1995; Smolander et al. 1994), boreal forests (Gao et al. 2013), and subtropical forests (Fang et al. 2004). In addition, it is likely that increased heterotrophic nitrification may mitigate the negative effects of decreased autotrophic nitrification on net NO_3^- accumulation in fertilized forest soils that are acidic.

4.2 N loss and retention in forest soils

N leaching (NO_3^- and DON) and denitrification (N_2O) are important N loss pathways (forms) of added N to forest ecosystems. This has been receiving considerable concern. However, NO is another important N loss species from forest soils (Butterbach-Bahl et al. 2002; Hall and Matson 1999; Horváth et al. 2006; Pilegaard et al. 2006; Venterea et al. 2003), and in some cases, the NO emission rate is even larger than N_2O emission rate in N-deposited and N-fertilized forest sites (Butterbach-Bahl et al. 2002; Pilegaard et al. 2006; Venterea et al. 2003). As summarized in Table 3, NO emission rates from European coniferous forests are highly correlated with N deposition, with the highest average annual emission rate up to $81.7 \mu\text{g NO-N m}^{-2} \text{ h}^{-1}$ (Pilegaard et al. 2006). Also, estimated N loss as NO could reach up to 24.5–34.5 % of N deposited or added to forests (Butterbach-Bahl et al. 2002; Pilegaard et al. 2006). Furthermore, it has been reported that the main source for NO in forest soils is nitrification (autotrophic nitrification) (Pilegaard et al. 2006; Venterea et al. 2003), and the key factors regulating its emission could be soil

moisture, soil temperature, litter layer properties (e.g., water content and thickness), N deposition (at least for European coniferous forests), and soil pH (Pilegaard et al. 2006; Venterea et al. 2003).

One of the strategies to avoid N loss in forest ecosystems is to keep low concentrations of NO_3^- via reducing the rate of autotrophic nitrification (Vitousek et al. 1979). It is the case in N-poor soils that are characterized by a high C/N ratio. In these soils, there usually have no net release of NH_4^+ and no occurrence of autotrophic nitrification (Hodge et al. 2000; Schimel and Bennett 2004), effectively conserving N and avoiding N loss. By contrast, soils with ample N availability, such as humid tropical forest soils, have high rates of N mineralization and nitrification, creating the potential for high N losses from leaching and denitrification (Vitousek and Matson 1988). Therefore, in forest soils where NO_3^- production is dominated by autotrophic nitrification, the negative effects of N deposition and fertilization on autotrophic nitrification may reduce the risk of NO_3^- leaching as well as NO and N_2O emissions. However, this may be somewhat offset if heterotrophic nitrification is activated in these soils.

High NO_3^- immobilization is also suggested to be an effective mechanism avoiding N loss (Vitousek et al. 1979). However, by using $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ tracers, together with traditional chloroform fumigation extraction method to measure microbial biomass C and N, the amounts and rates of NO_3^- and NH_4^+ immobilization were found to be low in N highly deposited forest sites or in forest sites that have long been fertilized (Bengtsson and Bergwall 2000; Corre et al. 2003, 2007). Changes in microbial N immobilization could have large influences on N loss, as well as N retention and the fate of N imported to forest ecosystems due to the facts that for most soil microbes, they are short-lived and the immobilized N can be released into soils again in a short time (Kuzaykov and Xu 2013); however, N transferred to plants usually remain unavailable for months to years (Hart et al. 1993; Kuzaykov and Xu 2013). A fact important to be noted is that the method (Tables 1 and 2) used by Corre et al. (2003) and Corre et al. (2007) to estimate immobilization rates of NH_4^+ and NO_3^- is only suitable for short-term measurements, which require no appreciable remineralization of immobilized N occurred during the 1-day incubation experiment. Recently, a ^{15}N tracing technique developed by Müller et al. (2007) overcomes the above limitations and can simultaneously quantify the rates of NH_4^+ and NO_3^- immobilization as well as gross N mineralization, autotrophic nitrification, heterotrophic nitrification, gross nitrification, gross N immobilization, and DNRA. This method has been successfully employed to estimate process-based soil N transformation rates from various types of ecosystems, including grassland (Müller et al. 2007, 2011, 2014; Rütting and Müller 2008), forest (Huygens et al. 2007; Zhang et al. 2013a; Zhu et al. 2013), and agricultural ecosystems (Inselsbacher et al. 2013; Zhang et al. 2012a), showing the

potential usefulness of this technique to investigate the mechanisms responsible for N retention and loss in N-deposited and N-fertilized forest sites.

Rütting et al. (2011) have pointed out that future investigations on the soil N cycle in various terrestrial ecosystems (forest, agricultural land, grassland, and wetland) should pay an attention to DNRA process because of its important role in N retention. For example, in a *Nothofagus betuloides* forest soil of southern Chile, NH_4^+ produced from DNRA ($0.355 \pm 0.016 \mu\text{g g}^{-1} \text{day}^{-1}$) was approximately ten times higher than that from direct mineralization of recalcitrant soil organic matter ($0.039 \pm 0.021 \mu\text{g g}^{-1} \text{day}^{-1}$) (Rütting et al. 2008). Templer et al. (2008) also found that the rate of DNRA (~35 % of gross nitrification rate) in a humid tropical forest soil was much higher than the rate of N_2O production from denitrification process, which agrees with a previous report by Silver et al. (2001) in the same forest soil, showing that the average rate of DNRA ($\sim 0.6 \mu\text{g g}^{-1} \text{day}^{-1}$) was three times as high as the total fluxes of N_2O and N_2 produced from nitrification and denitrification, accounting for 75 % of the turnover of total NO_3^- pool. The above results indicate that DNRA may lead to denitrification in some forest ecosystems. At the ecosystem level, if N losses from NO_3^- leaching and denitrification are less than the rates of DNRA and NH_4^+ uptake, N retention would occur (Templer et al. 2008). However, as Templer et al. (2008) suggested, only the NH_4^+ produced from DNRA is assimilated into biotic biomass (plants and microbial biomass), and DNRA can serve as one of N retention mechanisms.

Despite the importance of DNRA in forest soil N retention, there is a knowledge gap about the processes, mechanisms, and factors controlling DNRA. DNRA is the anaerobic microbial reduction of NO_3^- and NO_2^- to NH_4^+ (Silver et al. 2001). Conditions required for the occurrence of DNRA are similar to denitrification, such as anaerobic and reductive environments, and high NO_3^- availability (Tiedje et al. 1982). Generally, redox potential and C/NO_3^- are considered to be the two most important regulators affecting DNRA process (Rütting et al. 2011), suggesting that this process can be greatly modified by increased N deposition. Additionally, Huygens et al. (2007) have proposed that ecosystem state variables, such as DNRA, should be used to evaluate the influence of anthropogenic perturbations on ecosystem N dynamics. Unfortunately, there are not yet studies examining the impacts of N deposition and fertilization on the DNRA process in forest ecosystems.

4.3 Forest soil acidification

A lot of studies have proven that N deposition contributes to forest soil acidification (Fluckiger and Braun 1998; Hogberg et al. 2006; Liu et al. 2010). In general, soil acidification caused by N deposition is mainly attributed to increased ammonia oxidation and NO_3^- leaching (Bergkvist and Folkeson

1992). In fact, hydrogen ions (H^+) can be produced from and consumed from many N transformation processes in forest soils. For example, H^+ can be generated in the processes of plant NH_4^+ uptake, autotrophic nitrification, and heterotrophic nitrification, while it can be consumed in the processes of organic N mineralization, NO_3^- uptake by plants, and denitrification. In addition, bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), and cation exchange play a buffering role in net accumulation of H^+ in forest soils. For the N-limited temperate ecosystems, it is suggested that strong plant demand for N can slow down the rate of soil acidification caused by N addition since fewer protons are released from plant NH_4^+ uptake than NH_4^+ oxidation (Matson et al. 1999). However, for the N-unlimited subtropical and tropical ecosystems, whether exogenous N input will exacerbate soil acidification via NH_4^+ oxidation remains controversial (Zhao et al 2007). Furthermore, in the N-unlimited stage or in forest soils that are naturally N rich, it is strongly required to know whether or not less NH_3 from decreased N mineralization contributes to soil acidification in fertilized forest ecosystems and to what extent soil acidification is relieved by increased denitrification.

5 Conclusions

In this paper, based on the analyses of related literature, we review the effects of N deposition and fertilization on multiple soil N transformations, such as N immobilization, N mineralization, nitrification (autotrophic nitrification and heterotrophic nitrification), and denitrification, in forest ecosystems. N deposition and fertilization have various effects on microbe-mediated N mineralization in forest soils, which are greatly affected by N status, C/N ratios, C availability, and soil pH. Additionally, changes in microbial extracellular enzymes involved in N transformations may play an important role in affecting the degree to which N mineralization is modified by N deposition and fertilization. The change in N mineralization may exert influences on microbial N immobilization, autotrophic nitrification, and denitrification both directly and indirectly, highlighting the necessity to accurately quantify as many the simultaneously occurring gross N transformations (autotrophic nitrification, heterotrophic nitrification, NH_4^+ immobilization, NO_3^- immobilization, and DNRA) that are pool specific as possible in a single study. It should be noted that heterotrophic nitrification may be favored if soil pH and soil C/N ratios decrease in fertilized forest soils. N added to forest ecosystems usually stimulates N_2O emission. However, due to the difficulties in identifying the role of denitrification in N_2O emission and the factors controlling N_2O production, reduction, and emission, the relationships between denitrification, N_2O emission, and N deposition are still not well understood. N deposition- and fertilization-induced modifications in soil N

transformations have important implications for N enrichment, N loss, N retention, and soil acidification in forest ecosystems. In the future, key research is required to link these rate processes with microbial community characteristics and functional roles of microbial extracellular enzymes in forest ecosystems to provide mechanistic insights into these extraneous N-added modifications.

Acknowledgments This research is supported by the National Natural Science Foundation of China (Grant No. 31130009) and the National Key Project of Scientific and Technical Supporting Program (Grant No. 2013BAC03B03). We would like to express our sincere appreciation to the two anonymous reviewers and the editor for their insightful comments, which have greatly aided us in improving the quality of our paper.

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