Insights into the invasiveness of non-native plants under atmospheric nitrogen deposition

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Abstract
Increasing human activities are causing global changes, such as elevated atmospheric nitrogen deposition and increased biological invasions. Both atmospheric nitrogen deposition and biological invasions are recognized as increasingly prominent features of ecological landscapes throughout the world, and their interactions affect the structure and function of global ecosystems. Thus, there is considerable interest in understanding the mechanism of the invasion of non-native plants under atmospheric nitrogen deposition, specifically in terms of global nitrogen cycling and its potential contribution to the ongoing global change in coming decades. We reviewed the invasiveness of non-native plants under atmospheric nitrogen deposition. We discuss gaps in this research topic in an effort to guide further research.

Keywords
Atmospheric Nitrogen Deposition, Global Changes, Invasiveness, Non-Native Plants

1. Introduction
Continuing increases in human activities in recent decades induce global climate and environment changes such as elevated atmospheric nitrogen (N) deposition (Galloway et al. 2008; Schlesinger 2009; Chen et al. 2012; Wei et al. 2012). Atmospheric N deposition is the major source of anthropogenic N in ecosystems in many regions, such as Northeastern United States, Europe, and Asia (Wang et al. 2007) and is expected to accelerate in the coming decades (Galloway et al. 2008; Schlesinger 2009). Ecosystems even in unpopulated regions are subject to anthropogenic N via long-distance transport and scatter (Wolfe et al. 2006). Atmospheric N deposition in natural ecosystems may exceed the biological demand and assimilation capability, inducing "N saturation" (van den Berg et al. 2011; Chen et al. 2012), which poses a serious threat to the functioning of ecosystems (Wang et al. 2010, 2011; van den Berg et al. 2011; Armitage et al. 2012; Chen et al. 2012; Wei et al. 2012). Therefore, the ecological effects of atmospheric N deposition on ecosystems have stimulated considerable interest in recent years (Wang et al. 2010, 2011; Wei et al. 2012).

Human activities have had impacts on the natural environment besides increased N deposition. For example, many plant species have been carried far from their natural habitats and introduced into new areas, where they often establish invasive populations and significantly change the properties of native ecosystems (Weber and Li 2008; Si et al. 2013; Gruntman et al. 2014). Non-native species have become increasing concerns worldwide because the breakdown of biogeographic barriers blurs the regional distinctiveness of Earth's biota, making non-native species a significant component of anthropogenic environmental change (Gurevitch et al. 2011; Gruntman et al. 2014). Non-native plants threaten ecosystems worldwide because these invaders can alter the structure and/or functioning of the ecosystems in which they occur; these species do not just compete with or consume organisms in their new habitats, they change the rules under which all organisms exist (Crossman et al. 2011; Gruntman et al. 2014). Furthermore, human-induced climate and environment changes, such as
elevated atmospheric N deposition, can affect species distribution and resource dynamics in both terrestrial and aquatic ecosystems, and this might exacerbate the threat of non-native plants on native ecosystems (Crossman et al. 2011). Therefore, understanding how non-native plants invade ecosystems is a major challenge to ecologists, especially in an environment of rapid, anthropogenic global change.

The objective of our research was to review the invasiveness of non-native plant under the condition of elevated atmospheric N deposition to predict the effects of future invasions.

2. The Invasiveness of Non-Native Plants under Atmospheric N Deposition

2.1. The Ecological Effects of Non-Native Plants on Native Ecosystems

At present, natural systems are subjected to unprecedented rates of change and unique pressures from a combination of anthropogenic environmental change drivers (Brooker et al. 2006; van Kleunen et al. 2010). In fact we have, as most ecologists readily acknowledge, always lived in a changing world, and its species and ecosystems have always had to cope with and adapt to the changes in global scope (Brooker et al. 2006; van Kleunen et al. 2010).

Non-native plants pose serious threats to the functioning of native ecosystems. The ecological effects of these invaders on native communities and the factors that influence their invasion have received attention from ecologists and others (Gurevitch et al. 2011). The degradation of natural habitats and the destruction of biodiversity can be the first noticeable change induced by non-native plants (Huntly et al. 2011), especially on islands and ecological islands (Guézou et al. 2010). Many studies have provided evidence that non-native plants alter soil properties (Niu et al. 2007; Si et al. 2013), soil microbial communities (Niu et al. 2007; Si et al. 2013), soil enzyme activities (Niu et al. 2007), soil nutrient cycling (Liao et al. 2008a, b; Feng et al. 2009; Sanon et al. 2012; Si et al. 2013), resources allocation (Hautier et al. 2009), and disturbance regimes (Clark and Johnston 2011; Baker and Murray 2012). In addition, the invasion of non-native plants causes economic damage and raises management challenges, since native biodiversity has a direct value to society through the provision of life sustaining ecosystem goods and services as well as ecological resilience (DeLange et al. 2012). The global damage inflicted by invasions amounts to $1.4 trillion per year, which constitutes 5% of the global economy approximately (Mitchell and Power 2003; Pimentel et al. 2005). The ecological and economic costs of uncontrolled invasions by non-native plants have stimulated interest in the invasion mechanisms of non-native plants, and especially in the core question: Why are some plants more invasive than others? (Schmidt and Drake 2011).

2.2. The Invasion Mechanism of Non-Native Plants

Over recent decades, ecologists have become increasingly interested in the invasion mechanism of non-native plants. Invader success has been attributed to many factors, such as morphological characteristics (Feng et al. 2008; van Kleunen et al. 2010), hereditary properties (Roman and Darling 2007; Müller-Schäer and Schaffner 2008), reproductive ability (van Kleunen et al. 2010), high nutrient use efficiency (Feng et al. 2008, 2009; Laungani and Knops 2009), high rates nutrient cycling (Feng et al. 2008, 2009; van Kleunen et al. 2010; Jones and Chapman 2011), plastic resistance to disturbance and competition (Davis et al. 2000; Blumenthal et al. 2009; Davidson et al. 2011; Desurmont et al. 2011), allelopathy (Hierro et al. 2005; Lankau et al. 2010), escape from natural enemies (Desurmont et al. 2011; Kempel et al. 2011), and plant-soil feedbacks (Kulmatiski et al. 2008; te Beest et al. 2009; Kiers et al. 2011; Wardle et al. 2011).

Invasion success is the consequence of extrinsic changes in the new environment that favor the invading species, without any intrinsic change of the invasive species (Hierro et al. 2005). However, any hypothesis is far from being general. The reason may be due to the difference in species traits and/or biotic and abiotic characteristics of the recipient habitat.

2.3. The Invasiveness of Non-Native Plants under Atmospheric N Deposition

Some investigators found that plant biomass production is limited by N (Hautier et al. 2009; Laungani and Knops 2009), and N is a key factor determining the outcome of interspecific competition in many terrestrial ecosystems (Laungani and Knops 2009; Sanon et al. 2012). Thus, the efficiency of N use or acquisition by non-native plants can maximize their invasiveness in N-limited ecosystems. In general, photosynthetic tissue allocation, photosynthetic N use efficiency, N fixation, N leaching losses, gross N mineralization, and/or plant N residence time may all have an appreciable impact on the efficiency of N use or acquisition of non-native plants (Laungani and Knops 2009; Sanon et al. 2012). Thereby, the question of whether atmospheric N deposition allows non-native plants to gain a competitive advantage over native species has stimulated considerable interest in recent years. Therefore, the question of whether elevated atmospheric N deposition enables non-native plants to gain a competitive advantage over native species has stimulated interest in recent years.

There is a growing body of evidence that plant-plant interactions are an important part of the mechanism by which environmental change drivers affect plant species and communities (Brooker et al. 2006; Blumenthal et al. 2009). Meanwhile, competition is commonly cited as one of the processes determining the response of plant communities to
environmental change drivers, such as N deposition (Brooker et al. 2006) which can alter the nutrient status of plants as well as their relative competitive abilities (Brooker et al. 2006; Blumenthal et al. 2009; Dukes et al. 2011). The conventional wisdom is that plants are only able to acquire soil nutrients like N from the soil solution after microbial mineralization from organic (e.g. amino acids, proteins, chitins, and urea) to mineral forms (ammonium and nitrate) (Lu et al. 2005), although this conventional view has been revised to include direct plant access to organic N pools, particularly in infertile ecosystems (Reynolds et al. 2005; Leduc and Rothstein 2010). However, Reynolds et al. (2005) found no evidence of plant N preferences. Atmospheric N deposition can lead to increased N availability in soil subsystem for plants and increased dominance of competitive plant species (van den Berg et al. 2005) or reduced water availability during critical stages of the growing season (Zavaleta et al. 2003). Interestingly, both native plants and non-native plants were able to acquire more N with exogenous N addition in several lab field studies, but non-native plants grew more than native plants under N addition (Reynolds et al. 2005; Dukes et al. 2011; Jones and Chapman 2011). In addition, non-native plants tend to have faster growth rates and respond more opportunistically to nutrient (especially N) addition than higher phenotypic plasticity (Davidson et al. 2011). The results of Ehrenfeld (2003) showed that the invasion degree of non-native plant was positively correlated with soil nutrient (especially N) through meta-analysis. Such a shift in N availability may be the primary mechanism controlling invasive establishment and persistence in many ecosystems (Ochoa-Hueso et al. 2011). In addition, native plants displayed different changes in response to various N components and that organic N may less detrimental to native species compared to inorganic N (Jones and Chapman 2011). Thus, non-native plants increase their relative dominance over native plants in organic N fertilized soils compared to inorganic-N fertilized soils especially (Jones and Chapman 2011). More even that exogenous N addition had no effects on the productivity of native plants, but greatly increased the growth of non-native plants (Abraham et al. 2009). Thus, the asymmetry of the competition results may confer a competitive advantage to non-native plants over native plants (Ochoa-Hueso et al. 2011). The reason may be that the supply of unused resources for invaders may be increased and resident species may be less competitive under conditions with high resource availability than many non-native plants (Brooker et al. 2006; Wang et al. 2012), which in turn can lead to species loss, with plants of higher growth rate and taller stature shading other slow growing plants out of a system (van den Berg et al. 2005). Moreover, increased N availability may directly change competitive dynamics for N directly, and it may create a situation via changes in the limiting availability of another resource (e.g., phosphorus, water, and light) indirectly (Hautier et al. 2009). Unfortunately, both processes can shift competitive dynamics between native plants and non-native plants and in favor of invading species (Davis et al. 2000).

The fluctuating resources availability theory suggests that a community with surplus available resources is more vulnerable to the invasion of non-native species (Davis et al. 2000). Meanwhile, the environmental constraints hypothesis suggests that limited resources can restrict the invasion of non-native plants and the restriction can be alleviated when nutrient levels rise (Rickey and Anderson 2004). And fertilization experiments across a wide variety of ecosystems have supported those theories, finding that increased soil N leads to an increase in non-native biomass and suppression of native plants (Rickey and Anderson 2004; Wang et al. 2012). Thus, the ecological effects of atmospheric N deposition on the competition between native plants and non-native plants may be affected by site or forest. For example, increased N availability can lead to increased biodiversity in N-limited systems, while increased external N can lead to the competitive dominance of particular species and thus a loss of biodiversity from the community in systems where N availability is already at intermediate levels (Brooker et al. 2006). Meanwhile, no significant differences among ecosystem effects of native and non-native trees in nutrient-poor ecosystems were found (Burns 2004; Kueffer et al. 2008). Base on this, non-native plants are likely to out-compete native species for resources and space only in N enriched systems due to their preferred investment in N uptake and utilization (Feng et al. 2007; Wang et al. 2012). Thus, environments under N addition from anthropogenic sources, even N-limited, can create environmental conditions more favorable for non-native plants than native plants that are adapted to nutrient-deficient soils (Lu et al. 2005; Davidson et al. 2011). The reason might also be the nitrophilous characteristic of non-native plants (Gross et al. 2005; Steers et al. 2011). Dassonville et al. (2008) found strong increases in nutrient concentrations with invasion of seven non-native plants primarily on sites that were initially nutrient poor, but decreases typically occurred in soils that initially were nutrient rich. In other words, high N availability favors non-native plants and low N availability favors native plants (Laungani and Knops 2009; Drenovsky et al. 2012). Thus, the ecological effects of non-native plants on native ecosystems, especially under N deposition, can be aggravated if they introduce a novel function in the invaded area, such as N-fixation. Non-native N-fixing species have been shown to increase the amount of N in soils (Hughes and Denslow 2005; Marchante et al. 2009). The increased N availability may in turn favor the invasion of other non-native plants, particularly in previously N poor ecosystems (Hughes and Denslow 2005; Simberloff 2006; Flory and Bauer 2014).

Accumulating evidence suggests that soil organisms play a considerable role in accelerating the invasion of non-native plants exerting both direct and indirect species specific effects on their growth (Jordan et al. 2008; te Beest et al. 2009). Previous studies suggest that, in general, most plants create plant-soil feedbacks that decrease subsequent conspecific performance (Kulmatiski et al. 2008). An increasing number of studies suggest that non-native plants tend to either be unaffected by plant-soil feedbacks or create plant-soil
feedbacks that increase subsequent conspecific performance (van Grunsven et al. 2007) and decrease subsequent heterospecific performance (Jordan et al. 2008). For example, non-native plants may indirectly facilitate their own performance in the non-native habitat by accumulating soil organisms that are adverse to native plants (Klironomos 2002; Kulmatiski et al. 2008). In other words, non-native plants can benefit from the altered interactions with soil biologic communities as well as by interfering with mutualistic interactions between soil organisms and native plants (van Grunsven et al. 2007; Vogelsang and Bever 2009). However, non-native plants often have weak or no dependence on mycorrhizal fungi, and can gain a competitive advantage by degrading the mycorrhizal networks on which many native plants rely (Wolfe et al. 2008; Vogelsang and Bever 2009). In addition, non-native plants often have higher litter N concentrations and lower C:N (Liao et al. 2008a, b). Thus, the rates of litter decomposition of non-native plants are typically higher than for native plants (Liao et al. 2008a, b; Feng et al. 2009; Sanon et al. 2012). Meanwhile, non-native plants can also create microclimates that facilitate the processes of litter decomposition by increasing soil temperature and moisture (Yelenik et al. 2004). A meta-analysis by Liao et al. (2008a) showed that plant invasion increased litter decomposition rates by 117% in invaded ecosystems. Based on this, non-native plants with higher rates of litter decomposition coupled with higher concentrations of leaf N can be expected to release N into soil subsystem at a more rapid rate than native plants (Kuzyakov 2010). The increased soil N can in turn accelerate the succession of soil microbial communities and then strength microbial functioning to facilitate the further invasion process of non-native plants (Kulmatiski et al. 2008; Wardle et al. 2011). More importantly, there may be legacy effects of the invasion process of non-native plants on soil microbial communities in native ecosystems (Pyšek et al. 2010; Essl et al. 2011), which continue to have negative effects on the establishment and growth of the next generation of native plants (Lankau 2010) through the release of allopathic compounds, changes in resource availability or nutrient cycling (Orr et al. 2005), and/or accumulation of pathogens (Klironomos 2002).

But it is important to note that long-term atmospheric N deposition can also elicit both compositional and functional changes in microbial communities (van den Berg et al. 2011), i.e., soil microbial changes may be a direct consequence of N deposition, but they may also be attributed to the indirect changes in the composition of the plant community caused by non-native plants as well as atmospheric N deposition because plants provide the substrate for growth of soil organisms. Although there is increasing recognition that plant species have a pronounced effect on the structure of microbial communities, the effects may be masked by exogenous high N inputs (i.e. >30 kg N ha⁻¹ a⁻¹) (Zechmeister-Boltenstern et al. 2011). Thus, it is important to investigate the direct and indirect effects both of atmospheric N deposition and non-native plants on soil subsystems, especially through field studies.

3. Discussion

Recent studies have investigated the ecological effects of atmospheric N deposition and non-native plants on ecosystems. Listed here are some shortcomings of recently published studies and opportunities for further research.

(1) Natural atmospheric N deposition contains various N components including inorganic N (e.g., ammonium and nitrate) and organic N (e.g., urea, amino acids, aliphatic amines, peroxyacyl nitrates, N heterocyclic compounds, alkyl nitrates, and methyl cyanide) (Jones et al. 2004; Galloway et al. 2008). Inorganic N is the main type of N in atmospheric N deposition, although the ratio of organic to inorganic N differs greatly between ecosystems (10%–69%, and averages 36.1% globally) (Galloway et al. 2008). In addition, N deposition varies in its form and changes in the form of N deposits are expected in the future (Galloway et al. 2008). Thus, a single N fertilization experiment cannot be a precise reflection of the ecological effects of atmospheric N deposition on the invasiveness of non-native plants. Current studies focus on monitoring and simulated experiments with incremental additions of N (Jones and Chapman 2011), while neglecting the fact that the invasiveness of non-native plants might differ in response to various N forms. For example, some plants are particularly sensitive to NH₃ (Krupa 2003), while others are more sensitive to NOₓ (Nordin et al. 2006). Therefore, future research also should focus on the invasiveness of non-native plants (especially leguminous plants) under mixed N deposition containing various N components.

(2) Atmospheric N deposition into soils has several pathways, such as wet- or dry- deposition (Schlesinger 2009). These pathways might vary in their influence on the invasiveness of non-native plants. However, an overwhelming majority of N deposition simulation studies have focused solely on the effects of nitrogenous fertilizers with direct input into soils instead of ground parts. In addition, natural atmospheric N initially contacts over-ground parts (leaves, branches) and then falls into the soil subsystem. In contrast, nitrogenous fertilizers in most simulation experiments were added in high doses, one-off, or periodically to elicit ecosystem responses within short experimental timescales (Armitage et al. 2012). Moreover, Silvan et al. (2005) found that only 15% of added high-pulse N was assimilated into microbial biomass and 15% was emitted in a gaseous form, while plants used up to 70% of added N in a simulated N fertilization experiments. Thus, it is important to characterize the effects of atmospheric N deposition with different pathways into soils on the invasiveness of non-native plants and to determine which factors influence the processes of their invasion.

(3) Although there has been dramatic growth in research on biological invasions over past decades, mature understanding in this field has been blocked by the tendency of invasion biologists to be concerned with individual taxon and of different ecological environments to adopt different model frameworks for the invasion process. Both factors have contributed to a confusing range of concepts, terms and
definitions (Blackburn et al. 2011). In addition, the factors that regulate invasion success vary by spatial scale, e.g., at neighborhood and community scales. Where environments are homogenous, biotic interactions can influence invasions, but at larger scales where environments are heterogenous, abiotic extrinsic factors will determine plant invasions (Fridley et al. 2007). Thus, study of the ecological effects of non-native plants on native ecosystems might benefit from focus on comparative study between non-native plants and native plants within the same taxon in the same or similar ecological environments.

(4) Soil organisms can play a key role in accelerating the invasion of non-native plants (Jordan et al. 2008; te Beest et al. 2009). Thus, it is important to assess the effects of non-native plants on the metabolic activities and community composition of soil microorganisms under atmospheric N deposition, especially the soil microorganisms which take part in N cycling (e.g., N-fixing bacteria, nitrifying bacteria, nitrosifying bacteria, ammonia oxidizing bacteria, and denitrifying bacteria), to forecast the potential invasiveness of non-native plants in the coming decades.

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