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REVIEW

ECOLOGICAL EFFECTS OF NITROGEN DEPOSITION ON URBAN FORESTS: AN OVERVIEW

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KEYWORDS

biodiversity, carbon sequestration, nitrogen deposition, nutrient imbalance, soil acidification, urban forest

HIGHLIGHTS

- Patterns and effects of N deposition on urban forests are reviewed.
- N deposition generally shows an urban hotspot phenomenon.
- Urban N deposition shows high ratios of ammonium to nitrate.
- N deposition likely has distinct effects on urban and natural forests.

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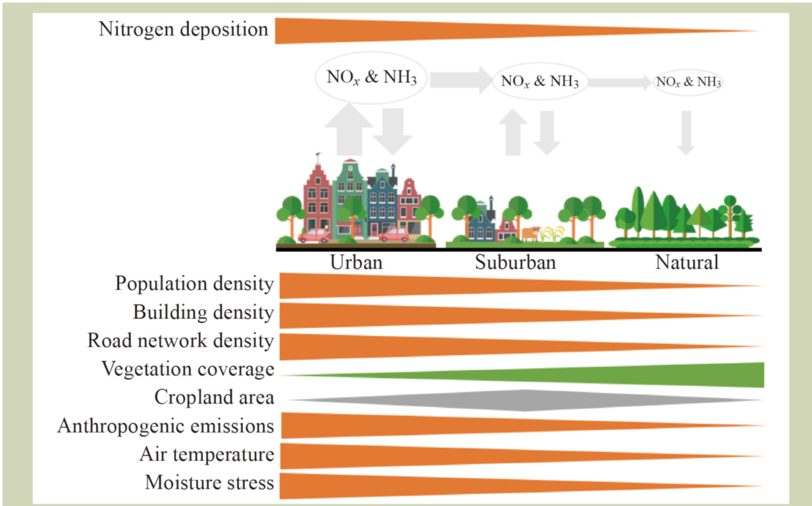
GRAPHICAL ABSTRACT



ABSTRACT

The global urban area is expanding continuously, resulting in unprecedented emissions and deposition of reactive nitrogen (N) in urban environments. However, large knowledge gaps remain in the ecological effects of N deposition on urban forests that provide key ecosystem services for an increasing majority of city dwellers. The current understanding of the spatial patterns and ecological effects of N deposition in urban forests was synthesized based on a literature review of observational and experimental studies. Nitrogen deposition generally increases closer to cities, resulting in an urban hotspot phenomenon. Chemical components of N deposition also shift across urban-suburban-rural gradients, showing higher ratios of ammonium to nitrate in and around urban areas. The ecological effects of N deposition on urban forest ecosystems are overviewed with a special focus on ecosystem N cycling, soil acidification, nutrient imbalances, soil greenhouse gas emissions, tree growth and forest productivity, and plant and soil microbial diversity. The distinct effects of unprecedented N deposition on urban forests are discussed in comparison with the common effects in natural forests. Despite the existing research efforts, several key research needs are highlighted to fill the knowledge gaps in the ecological effects of N deposition on urban forests.

1 INTRODUCTION

The global urban area has expanded rapidly over the past three decades[1,2]. The unprecedented growth of the urban population intensifies fossil fuel consumption, vehicular traffic, waste treatment in urban areas, and agricultural activities in peri-urban regions, resulting in accelerated emissions of nitrogen oxides (NO_x)[3] and NH_3 into the atmosphere[4–6]. The enhancement of reactive nitrogen (N) emissions and deposition has resulted in cascading environmental effects such as air pollution (e.g., haze and elevated tropospheric O_3 concentrations), soil acidification, water eutrophication and damage to human health[7,8]. Urban forests provide key ecosystem services for city dwellers such as regulating the microclimate, removing air pollutants, maintaining urban biodiversity, and benefiting human health[9–13]. However, major knowledge gaps remain in the ecological effects of N deposition on urban forests.

Nitrogen deposition has been found to exert both beneficial and deleterious effects in natural forests[14] such as a stimulation of forest growth and carbon sequestration under N-limited conditions[15,16] but a loss of species diversity[17], an alteration of non-CO_2 greenhouse gas emissions (N_2O and CH_4)[18,19], soil acidification[20] and nutrient imbalances[21] in response to excessive N loads. Unlike natural forests, urban forests consist of less diverse plant species and are subject to distinctive urban environments and considerable horticultural interventions (e.g., irrigation, pruning, cultivation and fertilization)[22,23]. Urban forests generally receive much higher N deposition than natural forests[24–27]. However, the urban heat island effect, high moisture stress via evaporation, high-level atmospheric CO_2 and air pollutant concentrations (e.g., O_3) have a potential to alter tree growth and biogeochemical cycling in urban forests[28–32]. Therefore, the ecological effects of N deposition are likely to be distinct in urban forests as compared with natural forests.

The ecological effects of N deposition in urban environments are of rising concern given that urbanization continues globally and an increasing majority of people live in cities[27]. Based on a literature review of observational and experimental studies, we developed a new perspective on (1) the spatial pattern of N deposition across urban-suburban-natural gradients as well as the interactions with atmospheric deposition of other elements, and (2) ecological effects of N deposition on urban forest ecosystems with a special focus on ecosystem N cycling, soil acidification, nutrient imbalances, soil greenhouse gas emissions, tree growth and forest productivity, and plant and soil microbial diversity. Instead of using a more quantitative approach (e.g., meta-analysis), our review is based mainly on a qualitative synthesis of the literature because there are limited research results in this emerging field. Finally, we discuss major knowledge gaps and recommend future research efforts that will gain further insights into the consequences of N deposition in urban forests. We also highlight a need to develop integrated forest management approaches to amend negative effects of high-level urban N deposition.

2 NITROGEN DEPOSITION IN URBAN ENVIRONMENTS

2.1 Urban hotspots of nitrogen deposition

Urbanization creates a typical landscape with apparent urban-suburban-natural transitions of land cover and environmental factors (Fig. 1). Building density, population density, and road network density generally decrease from urban areas, while vegetation cover increases toward natural areas[33]. Urban areas with high population density are hotspots of anthropogenic emissions of multiple air pollutants including NO_x and NH_3, due to intensive energy production, motor traffic, waste treatment and industrial activities[34]. As a result, atmospheric NO_x and NH_3 both show the highest concentrations in the central urban areas as indicated by ground measured data and satellite retrieved data[35,36] (Fig. 2(a)).

Observational studies generally suggest that N deposition shows a strong spatial trend across urban-suburban-natural gradients[25,39,40] (Fig. 2(b)). Based on a spatial analysis of field-measured data on N deposition in Chinese forests, Du et al.[38] found that N deposition generally showed a power-law increase closer to large cities, i.e., urban hotspots of N deposition

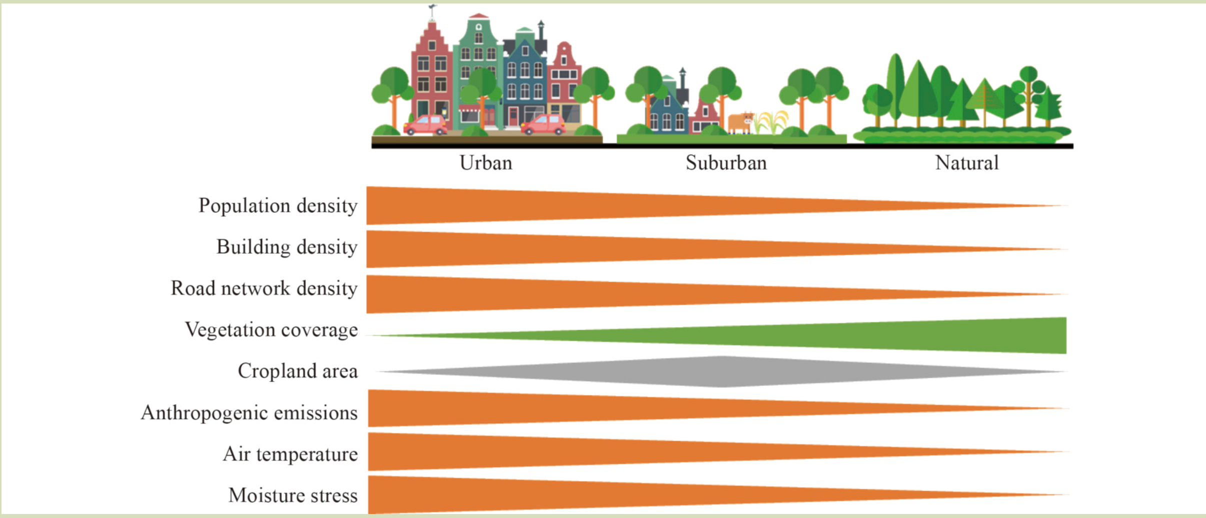


Fig. 1 Spatial changes in population density, land cover, air pollution and climatic conditions across urban-suburban-natural gradients. Arrows indicate a decreasing trend.

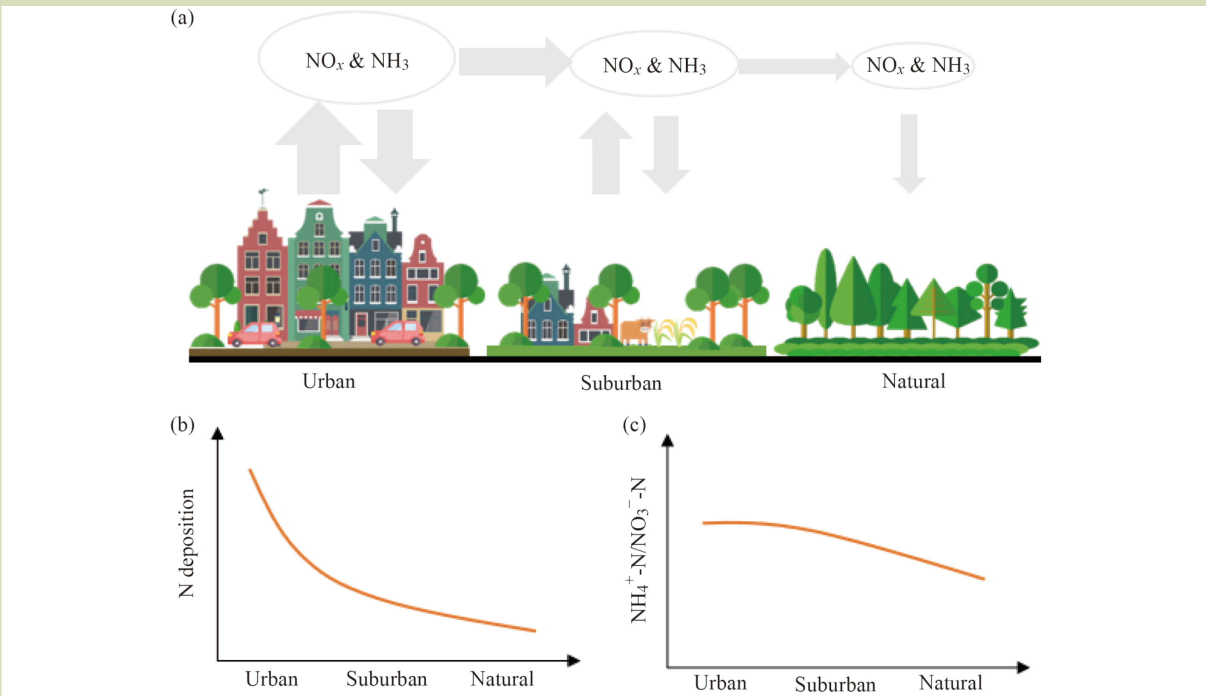


Fig. 2 Changes in atmospheric emissions (a), deposition (b)[37,38] and components (c)[27,38] of reactive N across urban-suburban-natural gradients.

(Fig. 2(b)), being in line with the observed urban hotspots of atmospheric reactive N concentrations[35,36]. Recently, a global meta-analysis further confirmed the occurrence of urban hotspots of N deposition in global cities and showed that N deposition in urban areas was on average twice as high as in nearby rural areas[27]. Urban forests are thus subject to extremely high levels of N deposition compared with their natural counterparts.

Chemical components of N deposition also shift across urban-suburban-natural gradients (Fig. 2(c)). In contrast to the conventional view that oxidized N dominates total N emissions and deposition in urban areas, Du et al.[38] found that the ratios of ammonium (NH_4^+) to nitrate (NO_3^-) in bulk precipitation and throughfall in Chinese forests both showed a significant increase closer to large cities. This shift in components of N deposition toward the urban area is further confirmed by a global synthesis, demonstrating that urban N deposition is predominately composed of chemically reduced (e.g., NH_3 and NH_4^+) rather than oxidized N forms (e.g., NO_x and NO_3^-)[27]. The prevalence of reduced N forms in urban N deposition is likely due to three causes. First, cities are hotspots of NH_3 emissions because of excessive vehicular traffic, sewage treatment, waste disposal and/or fertilizer applications in lawns[4,5,36,41]. Second, atmospheric NH_3 has a shorter residence time than NO_x and thus ammonium deposition is accelerated in urban areas[42,43]. Third, NO_x emissions have been substantially curbed in most countries but NH_3 emissions remain largely unregulated, thus contributing to the dominance of reduced N forms in and around urban areas[44–46].

2.2 Interactions with atmospheric deposition of other elements

Nitrogen deposition is an important component of acid deposition with an additional contribution from sulfur (S) deposition. Although NH_3 neutralizes sulfuric and nitric acids in cloud water and precipitation, deposited ammonium has a strong potential to generate soil acidification[47,48]. By synthesizing chemical fluxes in bulk precipitation and throughfall in forests of southern China, Du et al.[26] proposed the concept of an urban acid island and demonstrated that atmospheric deposition of nitrate, ammonium and sulfate all showed a power-law increase toward the urban areas, whereas rainwater pH showed a logarithmic decline closer to large cities. The emerging industrial clusters in suburban areas under transitional economies may cause increasing S deposition in suburban areas[49], thus changing the spatial pattern of SO_2 emissions at local scale. Given that S deposition has declined globally due to a decline in anthropogenic SO_2 emissions in recent decades[50], the contribution of N deposition to acid deposition and thereby to urban acid islands is thus of increasing importance.

Atmospheric inputs of base cations (e.g., K^+, Ca^{2+} and Mg^{2+}) can partially buffer the effect of acid deposition by N and S compounds. A synthesis of bulk deposition data across Chinese forests showed a power-law increase in base cation deposition closer to large cities. The urban hotspots of base cation deposition thus neutralize a considerable proportion of the potential acid load due to acid deposition and partially replenish the leaching loss of soil base cations[51]. Also, a synthesis of field-measured data in Chinese forests indicates high N:P ratios in bulk deposition and throughfall deposition, being 2–3 times of that in plant leaves[37]. The imbalanced N and P deposition thus likely enhances P limitation in urban forests over time. However, P deposition also exhibits an urban hotspot pattern, partially alleviating the N-induced P limitation in urban environments[37].

3 EFFECTS OF NITROGEN DEPOSITION ON URBAN FOREST ECOSYSTEMS

Insights into the ecological effects of N deposition on urban forests are mainly derived from manipulative N addition experiments and field-based monitoring studies across N deposition gradients. However, such studies are rare in urban forests compared with those conducted in natural forests. Here, we describe a new perspective on the effects of unprecedented urban N deposition on ecosystem N cycling, soil acidification, nutrient imbalances, soil greenhouse gas emissions, tree growth and forest productivity, and plant and soil microbial diversity (Fig. 3).

3.1 Effects on nitrogen cycling

Urban forests are important sinks of N inputs from atmospheric deposition[59,60]. Similar to the effects in natural forests[52,53], N deposition directly increases N availability and thereafter alters ecosystem N cycling in urban forests. For example, field studies along an urban-rural gradient in the Pearl River Delta of southern China indicate that N deposition significantly increased soil available N concentrations in urban and suburban forests as compared with that in rural forests[39,61]. Across an urban-rural tropical forest gradient in Puerto Rico, higher soil nitrate concentrations were found nearer to the urban core in parallel with higher atmospheric N deposition[62]. A study of Mediterranean ecosystems across an N deposition gradient in proximity to urban Los Angeles shows that N deposition strongly shaped regional soil N availability, resulting in an increase in soil nitrate and ammonium concentrations and a decrease in soil C:N ratios toward the urban area[63]. Also, a field study across the greater Boston area indicates that the soil nitrate concentration increased with throughfall nitrate inputs while the soil ammonium

	Potential difference in urban forest	Common effects in natural forest
N cycling	Likely cause N saturation due to urban hotspots of N deposition	Increase N availability and accelerate ecosysterm N cycling[52,53]
Soil acidification	Likely cause stronger soil acidification due to urban acid island effect	Increase soil acidification and the toxicity of metals (e.g., Al and Fe)[20]
Nutrient balance	Likely cause stronger nutrient imbalances due to urban hotspots of N deposition	Induce imbalances of N in relation to other nutrients[54]
Soil GHGs fluxes	Likely reduce soil respiration and CH_4 uptake and cause stronger N_2O emission due to urban hotspots of N deposition	Have nonlinear effects on soil respiration and CH_4 uptake; mostly increase soil N_2O emission[18,19,47]
Forest growth	Likely cause neutral to negative effects on forest growth due to urban hotspots of N deposition	Mostly favor forest growth and carbon sequestration; increase aboveground biomass allocation[16,55]
Biodiversity	Less likely cause direct plant diversity loss but may increase other risks such as plant invasion	Decrease understory plant diversity; decrease total microbial biomass and the fungi to bacteria ratio[56–58]

Fig. 3 The effects of N deposition in urban forests in comparison to natural forests. Given the paucity of relevant research on urban forests in the literature, the potential effects in urban forests are partially based on expert opinion.

concentration was not correlated with throughfall N inputs[64].

Urban hotspots of N deposition likely reshape a regional pattern of N cycling across urban-rural-natural forests. For example, net N mineralization was found to decrease significantly from urban to rural forests in the New York City metropolitan area with a larger proportion of the mineralized N being nitrified in urban and suburban forests whereas net nitrification was mostly below the detection limit in rural forests[65]. Field studies across urban-rural forests in the Pearl River Delta showed an increase in soil nitrification and a decrease in soil and plant foliage $\delta^{15}N$ values with the higher N deposition, implying a significant alteration of regional N cycling[39,66]. Generally, high-level N deposition likely results in faster N cycling and an easier N saturation in urban forests than in rural forests[39,65]. Consequently, nitrate leaching to stream water was found to increase with N deposition and showed high levels in urban forests, potentially contributing to the eutrophication of urban waterbodies[25,39].

3.2 Effects on soil acidification

Nitrogen deposition has been found to increase soil acidification and the toxicity of metals (e.g., Al and Fe) in natural forests[20]. In view of the urban acid island hypothesis[26], high-level N deposition may contribute to stronger soil acidification in urban forests than in rural and natural forests. Based on field investigations across urban-rural forests in the Pearl River Delta, soil pH decreased significantly with higher N deposition[39,61]. Although base cation deposition also shows urban hotspots and partially buffers acid deposition[51], the field evidence given above implies a stronger effect of the urban acid island. Also, high-level N deposition likely causes accelerated leaching of base cations and further increases concentrations of soluble aluminum and/or iron over time, causing negative effects on plant growth and biodiversity[20].

3.3 Effects on nutrient imbalances

Nitrogen deposition in natural ecosystems frequently causes imbalances of leaf N in relation to other nutrients due to increased N availability[54]. Urban hotspots of N deposition likely result in stronger nutrient imbalances in urban forests due to increased soil N availability and acidification. Soil calcium and potassium concentrations were found to decrease significantly with N deposition from rural forests to urban forests in the Guangzhou metropolitan area, China[61], potentially causing a deficiency of base cationic nutrients in urban forests due to soil acidification. Long-term N deposition has been demonstrated to increase leaf N:P ratios in two forests close to urban centers in subtropical China, resulting in an enhancement of P limitation[67]. Also, a field monitoring study of soil nutrient leaching across urban parks in Saint Paul, Minnesota, United States, found that urban trees substantially reduced leaching of P but not N to groundwater[68], implying a risk of N saturation and P deficiency driven by high-level urban N deposition.

3.4 Effects on soil greenhouse gas fluxes

Urban forest soils are both sinks of CH_4 and sources of N_2O and CO_2 that are strongly regulated by N availability[69–71]. High-level N deposition is conventionally thought to increase soil N_2O emissions and suppress soil heterotrophic respiration and CH_4 uptake in many natural ecosystems[18,72,73]. In contrast, positive effects of low-level N deposition on soil heterotrophic respiration and CH_4 uptake are also suggested in N-limited natural forests[15,19]. In view of the urban hotspot effect, N deposition tends to reduce soil respiration and CH_4 uptake and cause stronger soil N_2O emissions in urban forests. A strong urban heat island effect may cause lower soil moisture contents in urban environments, potentially causing an increase in soil CH_4 uptake and a decrease in N_2O emissions[74,75]. Watering practices, frequently conducted in urban forests, likely increase drying and rewetting cycles with periods of high N_2O and CO_2 emissions[75,76]. These processes might mediate the fluxes of soil greenhouse gases in response to N deposition in urban forests.

Field monitoring studies across urban-rural forests generally showed a lower capacity of soil CH_4 uptake in urban forests relative to rural forests and this decline in soil CH_4 uptake in urban forests was partially attributed to high-level N deposition[69,77]. Fertilizer applications may also increase N_2O emissions in urban garden systems[78]. Experimental N additions in three forests along an urban-rural gradient in Hefei city, east China, suggested an increase in soil respiration by N deposition[79]. In contrast, a monitoring study across the greater Boston area, Massachusetts, United States, indicates that soil respiration was not associated with N deposition[64]. These inconsistent results based on limited studies highlight key knowledge gaps in the effects of N deposition on soil greenhouse gas emissions in urban forests.

3.5 Effects on tree growth and forest productivity

Nitrogen deposition favors tree growth in most natural forests and tends to increase the aboveground biomass allocation[16,55]. Urban forests are likely less limited by N than natural forests in view of high-level urban N deposition. In that case, N deposition is likely to exert only minor stimulatory effects on tree growth in urban forests and other factors will be more important. For example, cottonwood (*Populus deltoids*) was found to grow faster in an urban area of New York City than in surrounding rural areas and this difference was attributed to the effect of O_3 (i.e., higher O_3 concentrations in rural areas) instead of N deposition[80]. A field study along an urban-rural transect from the central area of New York City indicates a strong growth stimulation of red oak (*Quercus rubra*) seedlings at urban sites relative to those grown at rural sites but this effect was mainly due to higher temperatures at urban sites[81]. In contrast, high-level N deposition may suppress urban forest growth over time due to an increase in P limitation, soil acidification and a decrease in water use efficiency[67]. Also, high-level N deposition can increase tree leaf N contents and decrease resistant metabolites, potentially increasing the risk of pest outbreak and consequent damage to urban forests.

3.6 Effects on plant and soil microbial diversity

Urban forests are key to maintaining plant biodiversity in urban areas. In line with the well-recognized negative effects on plant biodiversity in natural ecosystems[17,56], high-level N deposition also likely alters understory species composition and decreases plant species richness in urban forests, especially those with less management. By evaluating the plant species richness of Mediterranean-type ecosystems across a strong gradient of N deposition with proximity to Los Angeles, California, USA, Valliere et al.[63] found a significant decline in species richness of native forbs and shrubs with higher N deposition, while N deposition had no effect on the richness of introduced species but significantly increased their cover. A field study across urban-rural forests in metropolitan Guangzhou, south China, demonstrated a decline in understory herb-layer diversity with higher N deposition due to N-related changes in soil properties (i.e., decreasing pH and loss of Ca^{2+} and K^{+})[61]. These results indicate that the selection and arrangement of N-tolerant plant species are important in urban forest planning.

Nitrogen deposition generally exerts a negative effect on total microbial biomass and decreases the fungi-to-bacteria ratio in natural ecosystems[57,58]. Nitrogen deposition also likely results in a profound effect on soil microbial diversity in urban forests and surrounding lawns. In an urban green space covered by Bermuda grass (*Cynodon dactylon*), simulated N deposition (NH_4NO_3 at 50, 100 and 150 $kg \cdot ha^{-1} \cdot yr^{-1}$ N) significantly changed the bacterial community composition and caused a loss of bacterial diversity in soils[82]. A field study along an urban-rural N deposition gradient in combination with N addition experiments indicates distinct effects of N deposition on arbuscular mycorrhizal and nonmycorrhizal fungal abundance, i.e., lower mycorrhizal colonization at sites with higher N deposition and plots with N fertilization[83], being consistent with the effects in natural forests[58]. Future research efforts are recommended to reveal the interplay of aboveground plant diversity and belowground microbial diversity in the context of high-level N deposition in urban forests.

4 CONCLUSIONS AND OUTLOOK

4.1 Concluding remarks

By reviewing existing observational and experimental studies in the literature we conclude that N deposition has profound impacts on urban forests and highlights several potential detrimental effects that threaten the health and function of urban forest ecosystems. High-level urban N deposition can accelerate soil acidification, activate the toxicity of metals, induce imbalances between N and other nutrients, and cause N saturation over time. Although N deposition provides external N sources for urban forests it may cause a decline in tree growth when a certain threshold N load is exceeded. High-level urban N deposition likely increases soil N_2O emissions and suppresses soil CH_4 uptake in urban forests. Also, the urban hotspots of N deposition can exert negative effects on plant and soil microbial diversity, including a facilitation of introduced species and a suppression of native species.

4.2 Future research needs

Despite the existing research efforts, large knowledge gaps remain regarding the ecological effects of N deposition on urban forests. For example, the dominance of ammonium in and around cities indicates a need to separate the effects of ammonium deposition from those of nitrate deposition in urban forests, considering that atmospheric deposited ammonium and nitrate have distinct fates and ecological consequences in natural ecosystems[84–86]. Also, terrestrial plants can either directly take up available N from soils via roots that are frequently in association with mycorrhizal fungi or absorb reactive gaseous and ionic N via the leaves[87–89]. Compared with natural plants, urban forests might utilize considerable atmospheric reactive N via canopy uptake in view of the high concentrations of atmospheric NO_x and NH_3 and rain water ammonium and nitrate in urban environments. However, the role of canopy N uptake has been rarely considered when evaluating the effects of N deposition in urban forests.

Unlike natural forest ecosystems, urban forest fragmentation is prevalent due to multiple socioeconomic drivers[90], resulting in a strong increase in forest edges. As indicated by studies in natural forests there are significant changes in light, temperature and soil moisture from the forest edge to the center[91,92]. Also, forest edges are found to be nutrient concentrators of airborne nutrients, especially N[93–95]. As an overall result, the edge effect tends to accelerate nutrient (especially N) cycling, favor tree growth and enhance carbon sequestration, and alter plant community structure[92,96–98]. However, these consequences have been rarely investigated in urban forests and a knowledge gap thus remains concerning how forest edges interact with the effects of N deposition.

Nitrogen deposition occurs simultaneously with various air pollutants and soil contaminants in urban environments. High-level N deposition has a potential to interplay with other anthropogenic contaminants and affect their biogeochemical cycles. For example, a mesocosm experiment found that N additions significantly decreased soil leaching of phenanthrene (a polycyclic aromatic hydrocarbon; PAH) and exerted a positive effect on phenanthrene retention in retention in the plant–soil system but did not cause significant effects on the dynamics of pyrene (another PAH)[99]. More research is needed to determine the effects of N deposition on the retention of soil contaminants such as potentially toxic metals, PAHs and microplastics, in urban forest ecosystems that are important sinks of atmospheric pollutants[13,100].

Given that urban forests are subject to strong urban heat island effects and moisture stress, high-level CO_2 and ozone concentrations, and frequent horticultural interventions[23,33,81], further research is needed to evaluate the combined effects of urban N deposition and these factors. Also, there is a need to develop integrated forest management approaches[101] to amend negative effects of high-level N deposition in urban forests with the potential for N saturation. These efforts will increase our understanding of urban forest dynamics and have important implications for urban forest management which are closely linked to sustainable development[102].

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Compliance with ethics guidelines

Enzai Du, Nan Xia, Yuying Guo, Yuehan Tian, Binghe Li, Xuejun Liu, and Wim DE Vries declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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