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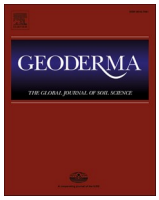

Artificial light at night triggers negative impacts on nutrients cycling and plant health regulated by soil microbiome in urban ecosystems

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ABSTRACT

Artificial light at night (ALAN) is a hallmark anthropogenic disturbance to urban ecosystems in the Anthropocene. However, the potential effects of ALAN on urban soil microbial community structure and functions are unclear yet. Here we combined amplicon sequencing and high-throughput qPCR to catalog the structure and functions of microbiomes in urban turf soils subjected to varying levels of nocturnal light. Our results showed that ALAN was an important factor influencing the structures of bacterial, fungal, and protist communities in urban soils. Moreover, ALAN potentially changed the microbial functional profiles involved in nutrients cycling and urban health. Specifically, nocturnal light significantly reduced the relative abundances of key functional genes involved in methanotrophic and denitrifying pathways in bacteria, including *mmoX*, *mxa*, *nirK* and *nosZ*. Further, ALAN exposure may marginally influence the abundances of fungal phytopathogen, which could increase odds of adverse effects on plant health in urban green spaces. Our findings highlight the significant effects of ALAN for soil bacterial and fungal communities, nutrient cycling and urban plant health. Moreover, our results suggest that vanishing darkness due to the expanded artificial illumination are likely to have long-term consequences for soil microbiomes and ecological functioning in urban ecosystems.

1. Introduction

Artificial light at night (ALAN) is a hallmark of urbanization and becomes an important new global change disturbance influencing urban terrestrial ecosystems (Gaston et al., 2013). ALAN illuminates more than a quarter of the land surface between 75°N and 60°S, and is still rapidly spreading globally at an estimated rate of 6% per year (Hölker et al., 2010). ALAN persists typically from dusk until dawn in the entire year with a broad range of wavelength between 400 and 700 nm peaking in the blue and green light in urban (Elvidge et al., 2010). The nocturnal light directly irradiates on urban surface soils which are the "living skin" to support biological diversity in urban areas. The long-term ALAN exposure on urban soils can disrupt natural light patterns and potentially exerts impacts on urban soil dwellers that rely on light as energy source or regulation signal of circadian rhythm (Sanders et al., 2021).

ALAN may harm individual organisms living in the urban soil ecosystems and perturb their interspecies interaction. ALAN is well known to cause plenty of environmental impacts on physiology and ecological communities of plants and animal in cities (Gaston et al., 2013; Bennie et al., 2016; Sanders and Gaston 2018; Liu et al., 2022), including reducing populations of aphid (Sanders et al., 2015), advancing reproductive time of birds (Dominoni et al., 2013), leading to earlier spring greening of trees (Meng, 2021), and influencing phytobiome through direct and indirect effects (Heinen, 2021). These results clearly show that ALAN is an important anthropogenic pressure for animals and plants living in urban soil ecosystems (Sanders et al., 2021). In contrast, microorganisms sourced from soils have rarely been studied in the context of ALAN. We are far from understanding the effects of ALAN on

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urban soil microbiomes in cities which are mostly disturbed by human activities.

The effects of visible light (main component of ALAN) on bacterial growth and fungal pathogenicity have been documented for a few species. Firstly, light can exert detrimental effects on the viability of bacteria, and such adverse impacts depend on the intensity and wavelengths of light (van der Horst et al., 2007). For instance, strong light intensity and blue light irradiation have been shown to suppress the growth rate of *Poterioochromonas malhamensis* and *Porphyromonas gingivalis*, respectively (Holen, 1999; Fukui et al., 2008). These phenomena may be attributed to light-induced generation of reactive oxygen species (ROS), leading to bacterial cell death (Lubart et al., 2011). Based on the impaired effects, light can further influence bacterial activities, including the inhibitions on methane oxidation of *Methylosinus* (Dumestre et al., 1999) and denitrification of *Pseudomonas* (Barak et al., 1998). To avoid harmful effects of light, some bacteria could produce protective pigments, 'run away' or form biofilm to adapt to the unfavorable external environments (van der Horst et al., 2007). In addition, visible light can intensify fungal pathogenicity. On one hand, light upregulates toxic effects of fungal pathogens on hosts through activating photosensors (i.e., phytochromes, rhodopsins, and flavoproteins), which are directly linked to virulence (Idnurm et al., 2005). Deletion of the respective photosensor genes led to less virulence of *Cryptococcus neoformans* on mouse (Idnurm et al., 2005; Liu et al., 2008). On the other hand, light can also induce H_2O_2 production in pathogenic fungi, which triggers hypersensitivity, cell death, and tissue necrosis in hosts (Mittler et al., 1997). For example, high intensity and prolonged time of light enhanced the endophyte pathogenicity of *Diplodia mutila* on the palm tree *Iriartea deltoidea* (Alvarez-Loayza et al., 2011). Taken together, these findings suggest a strong potential for light to affect microbial activities and functions at species level, but the specific effects of ALAN on microbial communities are not yet understood.

Urban soil microbiomes are related to a wide range of ecosystem functioning such as biogeochemical elemental cycling, organic matter turnover and plant productivity (Delgado-Baquerizo et al., 2020). Furthermore, urban soil microbiomes are linked with all components of the "urban health" framework, including human, plant, and ecosystem health (Banerjee and van der Heijden, 2023). Actually, soil microbes are sensitive to anthropogenic perturbations, which may weaken the ecological services including changes of soil carbon transformations and increases of pathogenic abundances (Banerjee and van der Heijden, 2023). Pervasive, long-term ALAN could act as one of perturbations influencing microbial community and triggering cascade effects in urban ecosystems. However, little attention is paid to understand the ALAN ecological effects on urban soil microorganisms. To date, ALAN is known to increase photoautotrophic richness, and decrease heterotroph diversity and microbial community respiration in aquatic sediments (Hölker et al., 2015). To fully unravel the ecological consequences of ALAN on urban soil ecosystems, it is essential to investigate the effects of ALAN pressure on the urban soil biodiversity and ecosystem functions.

To fill the knowledge gap of ecological effects of ALAN in urban environments, here we performed urban turf soil survey to explore the impacts of ALAN on urban soil microbial community and potential functioning. We aimed to address the following questions: (1) To what extent of ALAN could drive variations of urban soil microbial community? (2) How does ALAN influence soil microbial functions in relation to nutrients cycling? (3) Does ALAN promote pathogenic threats to urban ecosystems?

2. Material and methods

2.1. Soil sampling

We obtained the artificial light at night (ALAN) data of Ningbo city in China, from "Luojia No.1" satellite which is the professional luminous remote sensing satellite launched on 2018 (Jiang et al., 2018). Next, soils were sampled based on latitude and longitude data (WGS01984 standard) to get the accurate ALAN intensity values in Ningbo. To minimize the impacts of spatial heterogeneity on soil microbial community, we selected 29 sampling sites scattered across ten urban turfgrass parks, which are all located in the Ningbo urban area under different levels of long-term nighttime light pressures (Fig. 1 and Table S1). The sampling points were less than ten meters away from the adjacent arbors or shrubs (Fig. S1). Besides, to quantify and correct for plant diversity in all sampling sites, the normalized difference vegetation index (NDVI) was used as a proxy for plant species diversity. Then, we downloaded NDVI for Ningbo of September 2020 from the NASA website (https://search.earthdata.nasa.gov/search). The NDVI data are generated monthly with spatial resolution of 1000 m, and NDVI data in each sampling sites were obtained by matching the corresponding latitude and longitude (Table S1).

Then the turf surface soils (0–10 cm in depth) without tree or shrub shading were sampled with soil auger (diameter, 5 cm) in September 2020. At each sampling site, three surface soil samples with two-meter intervals were gathered independently and completely homogenized into a composite sample. Finally, a total of 29 soil samples were analyzed in this study (Table S1). To minimize potential contamination during the sampling process, several precautions were taken including wearing masks and gloves, and disinfecting sampling tools with 75% rubbing alcohol after each sampling spot. After sampling, soils were sieved (<2 mm) and separated into two parts, one part was air-dried for soil physicochemical analyses, and the remaining part was immediately frozen at −20 °C for molecular analyses.

2.2. DNA extraction and Illumina sequencing

DNA was extracted from 0.5 g soil samples using the FastDNA™ SPIN Kit for Soil (MP Biomedicals, USA). DNA was diluted to 50 ng/μL and quantified by Nanodrop 2000 (Thermo Fisher Scientific, USA). Additionally, all materials, such as pipettes and tubes, were autoclaved during the soil DNA extraction process to prevent environmental contaminations. The diversity of urban turf soil bacteria, fungi, and protists was measured by amplicon sequencing using Illumina HiSeq platforms (2×250 with a paired-ends configuration) at Novogene Corporation. The primer sets were chosen as 515F (5′-GTG CCA GCM GCC GCG GTA A-3′) and 806R (5′- GGA CTA CHV GGG TWT CTA AT-3′) for prokaryotic 16S V4 rRNA gene (Peiffer et al., 2013), 5.8S-Fun (5′-AAC TTT YRR CAA YGG ATC WCT-3′) and ITS4-Fun (5′-AGC CTC CGC TTA TTG ATA TGC TTA ART-3′) for fungal ITS2 gene (Taylor et al., 2016), TAReuk454FWD1 (5′-CCA GCA (G/C)C(C/T) GCG GTA ATT CC-3′) and TAReukREV3 (5′-ACT TTC GTT CTT GAT (C/T)(A/G)A-3′) for protist 18S V4 rRNA gene (Stoeck et al., 2010), respectively.

Bioinformatics processing was performed by USEARCH (Edgar, 2010) and UNOISE (Edgar, 2013). Sequences were clustered into phylotypes (Amplicon Sequence Variant, ASV) using a 100% identity level. Annotation of the representative sequences of ASV was performed against the RDP training set v16 (16S gene) (Cole et al., 2014), UNITE (ITS gene) (Kõljalg et al., 2013), and PR2 (18S gene) (Guillou et al., 2012) databases by SINTAX algorithm (Edgar, 2016). The ASV abundance tables were rarefied at 48,021 (bacteria, 16 s rRNA gene, 16,964 ASVs), 40,243 (fungi, ITS rRNA gene, 1,092 ASVs), and 8,710 (protist, 18S rRNA gene, 2,619 ASVs) reads per sample to ensure an even sampling depth. Protists were defined as all eukaryotic taxa, except fungi, invertebrates, and vascular plants.

To determine the community functions, ASV tables and taxonomy files of bacteria and fungi were used to predict functions through the Functional Annotation of Prokaryotic Taxa database (FAPROTAX, version 1.2.4) for bacteria (Louca et al., 2016) and FUNGuild database (version 1.2) for fungi (Nguyen et al., 2016). Fungal trophic modes were assigned into seven groups pathotroph, pathotroph-saprotroph, pathotroph-saprotroph-symbiotroph, pathotroph-symbiotroph, saprotroph, saprotroph-symbiotroph and symbiotroph. The trophic functional

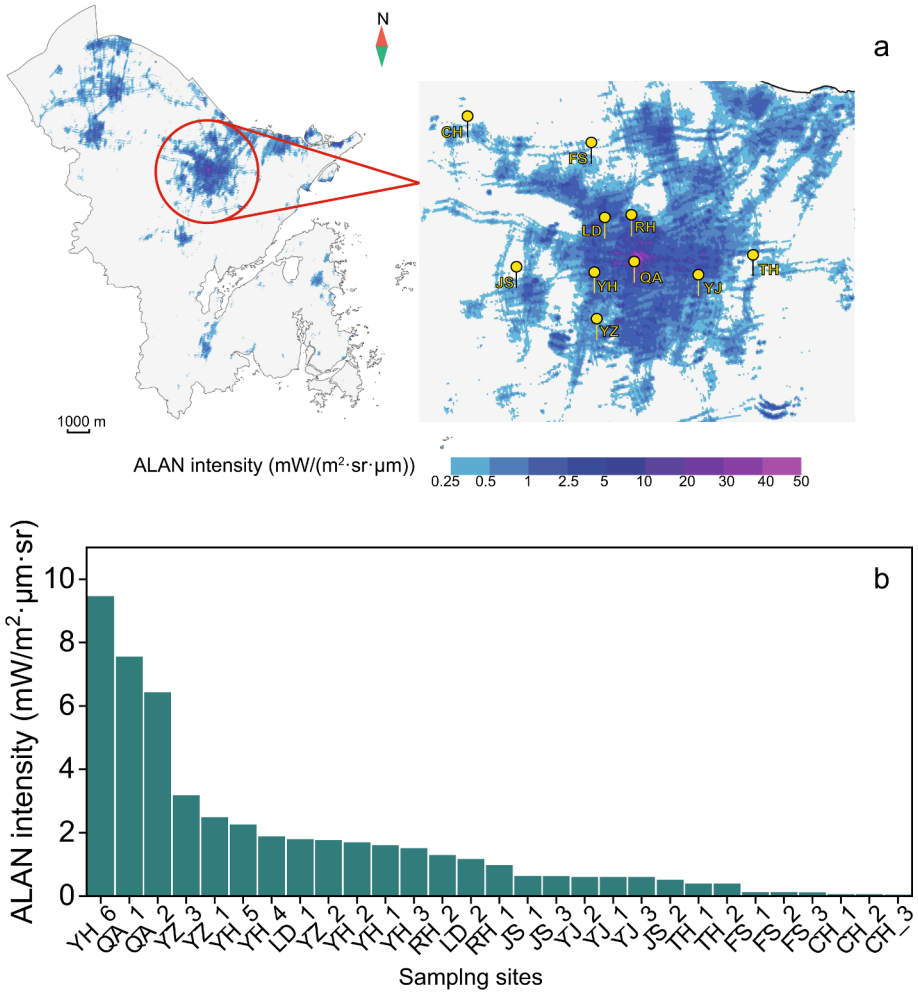

Fig. 1. Overview of ALAN in Ningbo city and geographic locations of sampling parks (a), and the ALAN intensity at different sampling sites in urban parks (b). Abbreviations of parks: YH: Yuehu park; QA: Qing'an park; YZ: Yinzhou park; LD: Lvdao park; RH: Rihu park; JS: Jishi park; YJ: Yujin park; TH: Taihe park; FS: Feishi park; and CH: Cihu park. The numbers following the abbreviation represent sampling sites within the same park.

groups of major protists lineages were also assigned as phototrophic, parasitic and consumers following the classification in Oliverio et al. (Oliverio et al., 2020). The proportions of each functional group reads out of total sequence reads were defined as functional relative abundances and used for further analysis for urban soil microbial community functions.

2.3. High-Throughput quantitative PCR

The abundance of functional genes related with nutrient cycles were calculated via a high-throughput quantitative PCR (HT-qPCR) carried by the SmartChip real-time PCR system (WaferGen Biosystems, Fremont, USA). This method can simultaneously detect the abundances of 16S rRNA gene and 71 functional genes associated with bacterial nutrients cycling in maximum 72 soil samples (Zheng et al., 2018). In detail, 3.1 μL of primers (5 μM), 24.8 μL of mix, and 3.1 μL of DNA solution were injected to each hole of the chip and detected by a SmartChip. The detailed qPCR conditions were as follows

initial heating at 95 °C for 10 min, followed by 40 cycles at 95 °C for 30 s, annealing for 30 s at 58 °C, extension for 30 s at 72 °C. Each sample was amplified with two technical replicates. Effective results included a single melting peak, 80–120% amplification efficiencies and threshold cycle (C_T) <31. Genes with effective amplification results in both replicated samples were regarded as positive and for following data analysis. The relative gene copy number (*R*) and normalized functional gene abundance (*NR*) were calculated as follows:

$$R_{16SrRNAgene}\text{or}R_{\text{functionalgene}} = 10^{(9.3-0.33C_T)} \quad (1)$$

$$NR = R_{\text{functional gene}}/R_{\text{16S rRNA gene}} \quad (2)$$

2.4. Soil properties

Soi characteristics were determined using standardized protocols (Lu, 1999). pH was measured in all soil samples using a pH meter in a 1:2.5 mass:volume suspension of soil and water without CO_2. Total carbon and nitrogen in soil were measured using an element analyzer (VARIO Macro, Elementar, Germany). Dissolved soil carbon was extracted at a soil to water ratio of 1:5 (w:v) and determined by a TOC analyzer (VARIO TOC, Elementar, Germany). Soil NH_4^+ and NO_3^- were extracted with 1 M KCl and determined by a continuous flow analyzer (SEAL AA3, Seal, Germany).

2.5. Statistical analysis

The statistical analyses were based on 29 soil samples and performed with R (R Core Team, 2019). The α diversity indices of Chao1, Shannon, and PD_whole_tree, and Bray-Curtis dissimilarity-based PCoA analyses were performed by vegan package (Oksanen et al., 2013) based on the rarefied ASV table. The *envfit* command in the "vegan" package was used to select the significant factors related with microbial community

variation. Random forest, a machine-learning model, was applied to examine the strengths of the associations between environmental variables and microbial variations (representing by PCo1 and PCo2 data) using randomForest R package (Liaw and Wiener, 2002). The importance of each variable was calculated as the percentage of increase in the mean square error (InMSE) from multiple regression trees. To test the pure effects of ALAN on community variations, random forest adjustment model (RFA model) was used for estimating relationships between ALAN intensity and microbial structure represented by PCo1 and PCo2, after partialing out the variations explained by covariates (i.e., plant diversity) using "RFA" package (Williams, 2023).

Then, significant factors were calculated the contributions of community changes with adjusted R-square in the "rdacca.hp" package (Lai et al., 2022). Correlations between ALAN and functional genes/groups were tested by spearman analysis through the corrplot package (Wei and Simko, 2017). To control confounding effects of habitat biodiversity on soil microbial functional profiles, NDVI index was included as a covariate into the partial spearman correlation analysis through "ppcor" package (Kim, 2015). Relative abundances of each ASV (minimum reads $\geq$1) of microbial communities in all sampling soils were selected to correlate with long-term ALAN intensity by spearman analysis using "agricolae" package (Mendiburu and Yaseen, 2020). Benjamini-Hochberg method to multiple correlation analyses was used to yield adjusted *p*-values (*q*-values) through p.adjust function to control the false positive rate (Benjamini and Hochberg, 1995), and the relationship between ALAN intensity and sampling sites was used by Kruskal-Wallis test (Hollander and Wolfe, n.d) in stats package.

3. Results

3.1. Environmental factors of soils

Soil samples (n = 29) were collected from 10 urban parks, sparsely distributed across Ningbo city of China. The sampled soils exhibited a high variability in physicochemical properties, including soil pH, total C and N content (Table S1). Despite the geographic proximity, the sampling sites receive varying levels of ALAN, with estimated intensities ranging from 0.03 to 9.44 mW/(m^2·sr·μm) (Fig. 1 and Table S1). No significant correlations by spearman were detected between ALAN and the soil physiochemical properties (Table S2), but the average ALAN intensity significantly (Kruskal-Wallis test, $p = 0.002$) differed among sampling sites (Fig. 1b). These results suggested ALAN intensity was different among sampling sites, and its variation was independent of other environmental factors measured in our studies.

3.2. ALAN shaped the microbial community of the urban turf soils

Chao1, Shannon and PD_whole_tree indices were calculated to evaluate alpha diversity of soil microbial communities along the ALAN gradient (Fig. S2). Higher fungal richness ($p = 0.01$, $q = 0.11$) and phylogenetic diversity ($p = 0.002$, $q = 0.02$) were observed in soils with strong ALAN (Table S3). On the contrary, no significant correlations were detected between ALAN and alpha diversity of bacterial and protist communities. Diversity of bacterial and protist groups was primarily influenced by the absolute latitude of sampling sites and/or soil organic carbon contents and pH (Table S3).

To assess the contributions of long-term ALAN on microbial community structure, we performed principal coordinates analysis (PCoA) based on Bray-Curtis dissimilarity distances along ALAN intensity (Fig. 2a – c). PCoA yielded the top two major coordinates, totally representing 31.8% of all variation in bacteria, 19.1% in fungi, and 26.7% in protists (Fig. 2). ALAN also consistently correlated with major axes of community variations across all microbial domains (Tables 1). In addition to ALAN, latitude, longitude, and pH were the additional variables to structure the microbial compositions (Tables 1).

Consistently, random forest regression analyses revealed that at least 5% importance of intensive ALAN was significant for driving the microbial compositions along PCoA1 and/or PCoA2 axes in urban soils (Fig. 3a – f). These results inferred ALAN might significantly influence the soil microbial community variations, which was then quantified through variance partitioning analysis (VPA). Then, VPA results showed pure effects of ALAN were around 3%, 3% and 1% of bacterial, fungal, and protist variations, respectively (Fig. 3g – i), which contributed less than geographical factors or pH. Altogether, these analyses emphasized long-term ALAN is an overlooked yet important driver on the underground communities in urban ecosystems.

3.3. Effects of ALAN on microbiomes at finer phylogenetic scale (ASVs)

The impacts of nighttime light on microbial community structures varied considerably at different community levels. Strong ALAN affected the bacterial compositional variations at ASV scale, but limitedly impacted the ASVs of fungi and protist. Relative abundances of 72 bacterial ASVs, 6 fungal, and 4 protist ASVs were significantly correlated with ALAN intensity through spearman analysis (Fig. 4, Tables S4 and S5). Specifically, stronger ALAN intensity significantly reduced the abundances of more than 68% of bacterial ASVs, which were mainly affiliated in Proteobacteria (25 out of 35 ASV) and Actinobacteria (12 out of 14 ASVs) phyla but enriched the ASVs belonged to Acidobacteria (9 out of 14 ASVs) (Fig. 4).

In addition, Ascomycota phylum is the most abundant species (abundance >98%) in the fungal community across different soils, and 6 ASVs almost in Ascomycota significantly ($q \leq 0.04$) were increased along ALAN intensity (Table S4). Similarly, only 4 ASVs belonging to Rhizaria supergroup of protist were significantly ($q \leq 0.04$) enriched by ALAN intensity (Table S5). Thus, these results indicated that strong ALAN had

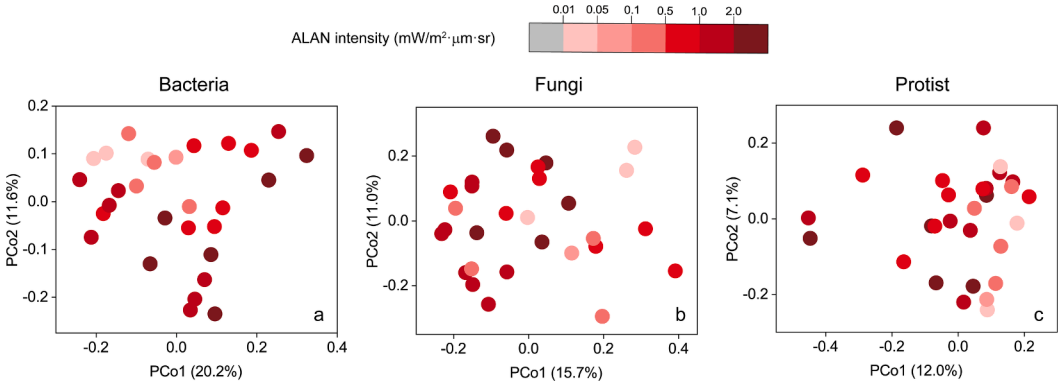

Fig. 2. PCoA (Bray-Curtis dissimilarity) for bacterial, fungal, and protist communities in all sampling sites. The dots of PCoA plots were color-coded along the intensity of ALAN in sampling soils.

Table 1
Results of environmental factors and soil microbial community variations (representing first two axes of PCoA) through *envfit* analysis.

Environmental factors	Bacteria			Fungi			Protist		
	R^2	*p*	*q*	R^2	*p*	*q*	R^2	*p*	*q*
latitude	0.46	0.002	0.01	0.18	0.07	0.26	0.56	0.001	0.01
longitude	0.02	0.78	0.83	0.37	0.001	0.01	0.10	0.25	0.34
ALAN	0.47	0.001	0.01	0.23	0.035	0.19	0.40	0.005	0.02
TC	0.17	0.09	0.20	0.02	0.72	0.82	0.12	0.18	0.33
TN	0.18	0.07	0.19	0.04	0.59	0.82	0.10	0.24	0.34
C/N	0.06	0.48	0.59	0.02	0.82	0.82	0.13	0.17	0.33
DOC	0.11	0.21	0.33	0.03	0.71	0.82	0.15	0.12	0.33
NH_4^+	0.14	0.13	0.24	0.06	0.48	0.82	0.03	0.70	0.77
NO_3^-	0.06	0.44	0.59	0.02	0.81	0.82	0.06	0.43	0.53
NO_2^-	0.01	0.83	0.83	0.06	0.48	0.82	0.02	0.85	0.85
pH	0.25	0.027	0.10	0.03	0.66	0.82	0.40	0.002	0.01

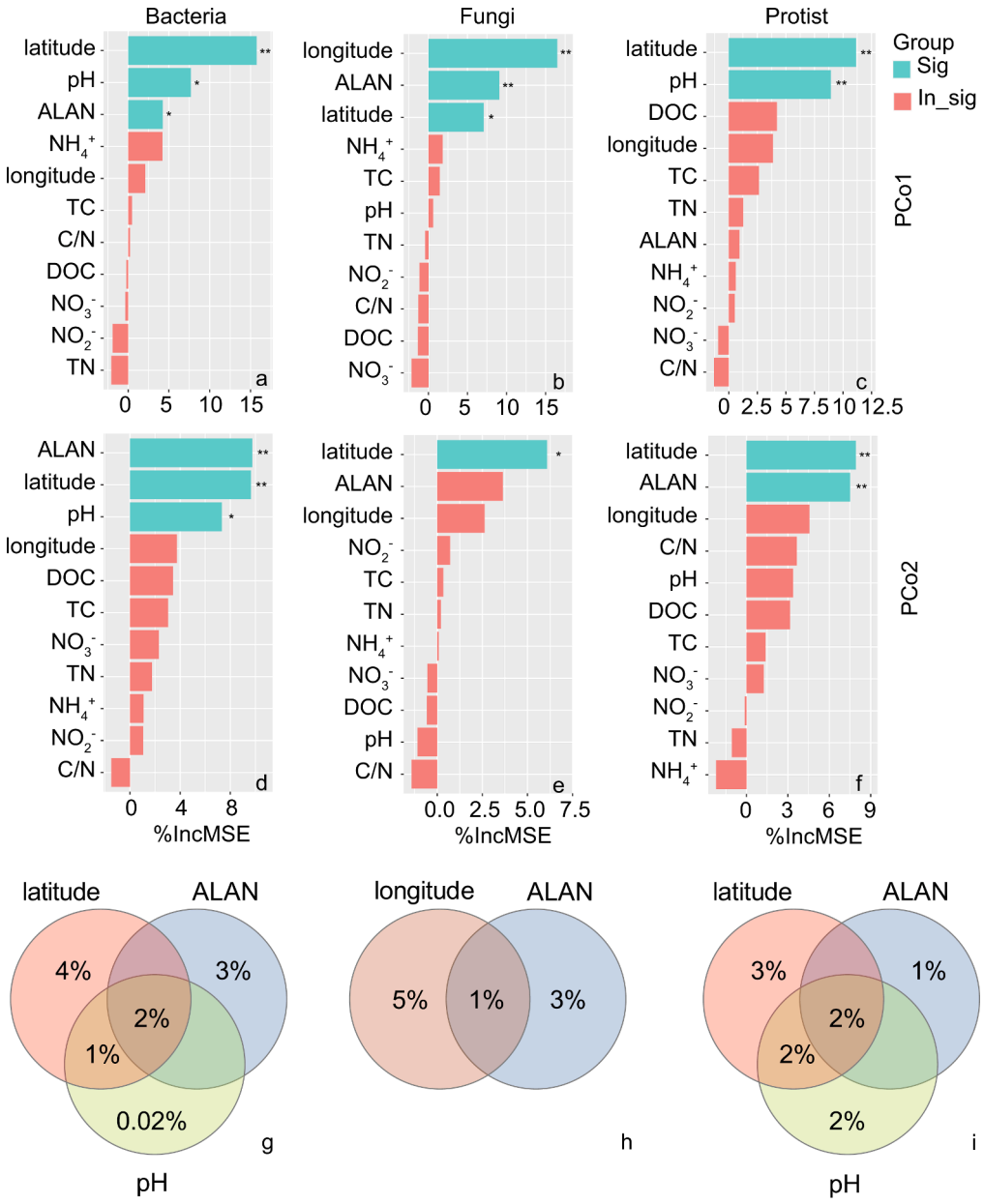

Fig. 3. Random forest analysis (a-f) and variation partitioning analysis (VPA, g-i) against significant environmental factors were analyzed for bacterial, fungal, and protist communities in sampling soils. The top 2 components of microbial compositional variation obtained from PCoA analysis were used as dependent variables in random forest models. * $p < 0.05$; ** $p < 0.01$.

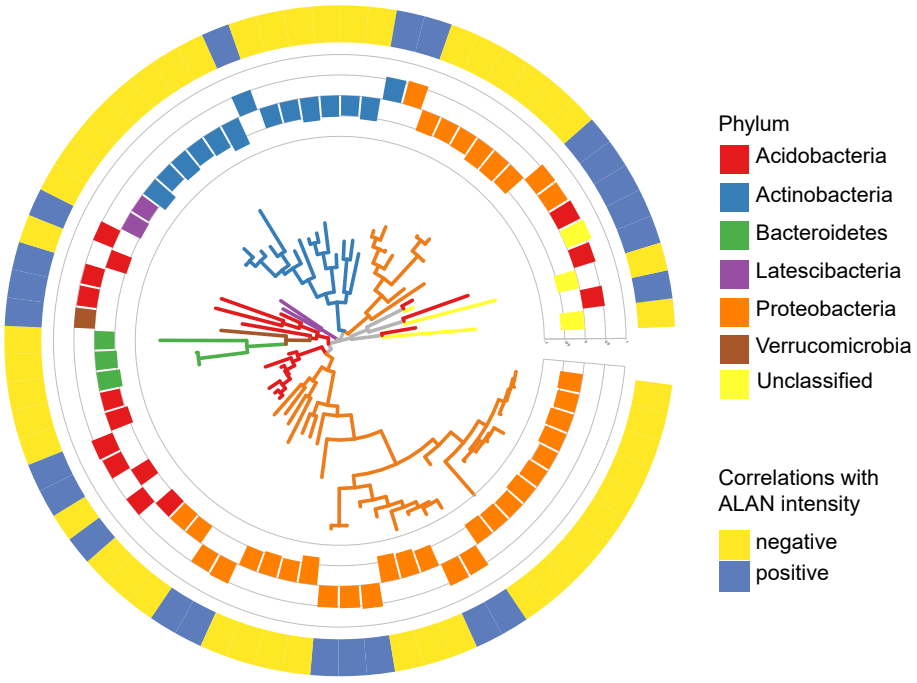

Fig. 4. Effects of ALAN on the phylogenetic relationships of individual bacterial ASVs abundances. Only ASVs (minimum reads number ≥ 1 in all soil samples) with a significant response ($q < 0.05$) to ALAN intensity were included in the trees. Colors of the branches in the first ring and bars in the second ring correspond to individual phyla, and length of bars indicated spearman's R value. Colors in the outer ring represent ASVs with significant increase (blue) or decrease (yellow) under ALAN pressure.

negative effects on the abundances of bacterial ASVs, and minor positive impacts on fungal and protist composition at ASV scale. However, relative abundances of dominant phyla in bacteria, fungi and protist were not significantly affected by ALAN disturbances (Fig. S3).

3.4. Long-term ALAN impacted soil microbial functions

The nighttime light-induced impacts on soil microbial diversity might affect urban nutrient cycling. Firstly, potential bacterial activities involved in C, N, P and S cycling processes were further tested by HT-qPCR. Among 71 functional genes examined, a total of 61 functional genes were effectively detected by HT-qPCR, and used for correlation analysis. Normalized relative abundances of 26 genes showed negative ($q < 0.05$) correlations with ALAN intensity (Fig. 3 and Table S6), and no significant positive correlations between genes and ALAN were observed (Fig. S4 and Table S6).

Furthermore, the bacterial functional assemblages relating with nutrients cycling were predicted by the FAPROTAX database. 1,966 ASVs were effectively assigned to 38 functional groups according to the bacterial taxonomy. The most abundant functional groups were chemoheterotrophy (14.8%) and aerobic chemoheterotrophy (13.1%) linked with C cycling, which was followed by the functions related to N cycling, including N fixation (1.78%), nitrate reduction (1.41%) (Table S7). Spearman analyses showed that relative abundance of 17 functional groups associated with C, N and S cycling, were marginally correlated ($p \leq 0.04$, $q = 0.089$) with nighttime light intensity (Table S7). Both HT-qPCR and FAPROTAX prediction results indicated that ALAN reduced the bacterial potential for methanotrophy/methylotrophy and denitrification (Fig. 6). Functional genes (*mmoX* and *mxa*) for methanotrophy/methylotrophy and a well-known methanotrophic/methylotrophic genus *Methylobacterium* were both negatively correlated with intensities of ALAN (Fig. 6a – c). Similar trends were observed for the denitrification process as deduced from abundances of functional genes (*nosZ* and *nirK*), predicted functional groups by FAPROTAX database, and abundances of denitrifying bacteria *Rhodoplanes* along ALAN intensity (Fig. 6d – f).

On the contrary, long-term ALAN disturbance may increase the abundances of soil phytopathogenic fungi. 329 ASVs out of 1092 fungal ASVs were assigned into various trophic modes by FUNGuild database with high probable or probable confidence (Table S8). Saprotrophic fungi were the most abundant (average 16.19%) of the annotated trophic modes, followed by pathotroph (average 9.07%) and pathotroph-saprotroph (average 2.61%), and approximately 70.2% of fungal functions were undefined (Table S8). Then, ALAN intensity was marginally and positively correlated with the relative abundances of pathogenic fungi ($p = 0.04$, $q = 0.30$), which are dominated by *Curvularia* and *Devriesia* genera (Fig. 7). While there were no significant correlations between saprotroph/symbiotroph and environmental factors other than ALAN (Table S8). At last, the relative abundances of protist trophic modes (consumer, phototroph, and parasite) were not impacted ($q \geq 0.32$) by ALAN intensity (Table S9).

4. Discussion

Our results showed that ALAN influenced the structure and function of microbial communities in urban soils. Negative correlations were observed between ALAN intensity and relative abundance of functional genes involved in nutrient cycling. Further, ALAN exposure appeared to increase the abundances of plant pathogenic fungi, which could potentially pose a risk to plant health in urban green spaces. These results demonstrate that ALAN could be a previously overlooked but important factor for shaping soil microbial communities, influencing soil microbial ecological functions and increasing the potential risks to urban health. It hints that anthropogenic activities and management (i.e., ALAN) might significantly affect the underground communities, which may perturb nutrient cycling or ecosystem stability in urban areas.

4.1. ALAN as a selection pressure on microbial community of urban soils

The relationships between soil microbial community and environmental factors had received substantial attentions. In previous studies, soil pH and geological factors were the important factors shaping microbial community variations (Bahram et al., 2018; Karimi et al., 2018; Zhang et al., 2020; Oliverio et al. 2020), but ALAN has rarely been considered as a driver of microbial community variation. In fact, the pure effects of ALAN on soil microbial communities were evident and significant in this study. ALAN could explain more than 3% variations of soil bacterial and fungal communities (Fig. 3 and Table S3), which

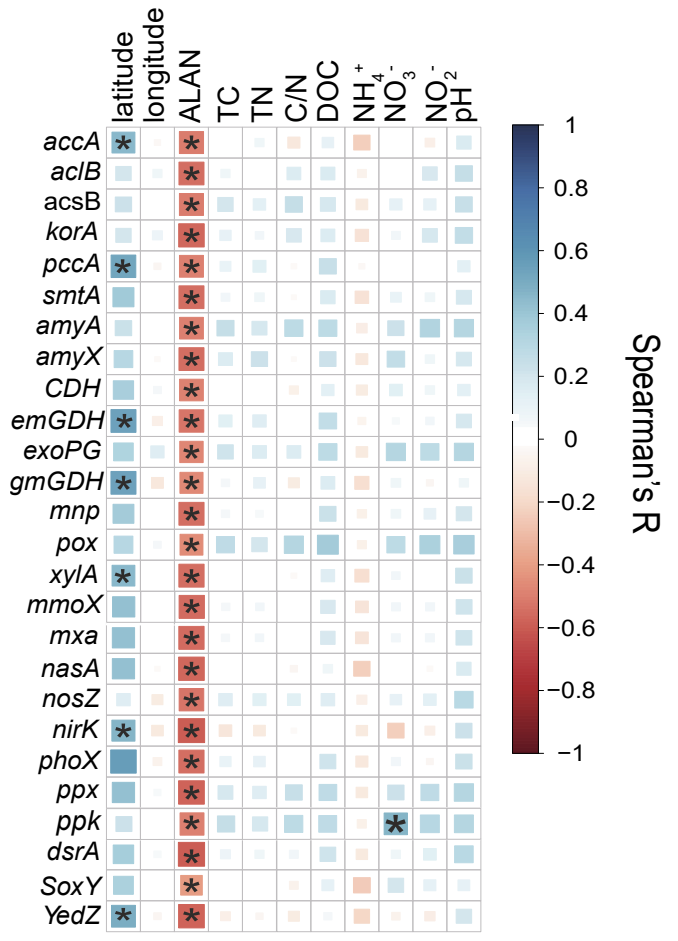

Fig. 5. Spearman correlations between ALAN intensity and relative abundances of functional genes involved in C, N, P, and S cycling. Multiple correlations were adjusted by Benjamini-Hochberg method to yield q values. *, $q < 0.05$.

approximates roughly half the variance explained by soil pH. ALAN reduced abundances of bacterial species belonging to Proteobacteria and Actinobacteria (Fig. 4), but increased fungal richness mainly in Ascomycota (Table S5). They implied the hidden influences of ALAN on soil microbial communities in urban systems. Some previous studies also shed light on the impacts of ALAN on microbial communities in other ecosystems. For instance, ALAN could affect microbial compositions living in the sediment of seashore (Hölker et al., 2015), coral (Baquiran et al., 2020), and human gut (Wei et al., 2020). These observations together with our findings indicate that ALAN could act as a potential strong global change driver, affecting both organisms in aboveground and belowground compartments in diverse environments.

4.2. ALAN as an inhibitor on functional potential of soil microbiota

Changes in soil microbial composition induced the shifts of urban soil microbial functions under ALAN disturbance. Abundances of functional groups involved in methane-oxidation and denitrification processes had significantly negative correlations with ALAN intensity across urban turf soils (Figs. 5 and 6). Methane-oxidizing methylotrophs use single-carbon compounds such as CH_4 and methanol as sources of carbon and energy. These microbes lessened methane and methanol emission in terrestrial ecosystems, and thereby affected gross greenhouse gas emission and ozone stability (Galbally and Kirstine, 2002; Kuloyo et al., 2020). It has been reported that soil methylotrophic community was influenced by soil pH, temperature, salinity, and plant diversity (Stacheter et al., 2013). Here we showed long-term ALAN, a potentially new abiotic factor, may inhibit the growth and activity of methanotrophic/methylotrophic bacteria (Fig. 6). In fact, the growth of methanotroph/methylotroph has been observed to be suppressed by visible light in mesotrophic lake or reservoir, and such bacteriostatic effects increased with light intensity (Murase and Sugimoto, 2005; Dumestre et al., 1999; Thottathil et al., 2018). Moreover, methane monooxygenase could be inhibited by blue region of spectrum that is richly emitted by LEDs used widely as outdoor lighting (Lubart et al., 2011). In addition to this "killing effect" of light on bacteria, ALAN has been proposed to control the methane oxidation process via regulation of oxygen concentration in microenvironments. For example, increasing O_2 level at night induced by ALAN-stimulated photosynthesis in plant (Segrestin et al., 2021) may further inhibit the activity of methanotroph in microaerobic environments. Such inhibition phenomenon on methanol/CH_4 oxidation and the underlying mechanisms may have critical impacts on controlling dynamics of carbon cycling in urban soils. Generally, an urbanized environment is a hotspot for CH_4 emissions which accounts for around 21% of total global CH_4 emissions (Hopkins et al., 2016), and urban lawn contributes to about 5% of soil CH_4 consumption through methanotrophic activities in some regions (Kaye et al., 2004). Therefore, the inhibitory effect of ALAN on methanotrophy/methylotrophy possibly can influence the CH_4 flux in urban greenspaces. Discerning interactions between methanotrophic/methylotrophic microbes and ALAN are essential to predict future CH_4 flux in urban soils.

On the other hand, ALAN may also suppress the denitrification activities in urban turf soil. In the present study, the abundances of *nirK* and *nosZ* genes, targeting the key steps of denitrification process, as well as the highly abundant denitrifying bacteria *Rhodoplanes* were negatively correlated with ALAN intensity in this study (Fig. 6). Similarly, light was shown to influence denitrification process at community and cellular level in previous studies. Visible light apparently reduced the richness of denitrifying bacterial community in river sediment (Jiang et al., 2022), and inhibited the nitrite reduction of *Rhodobacter* or *Pseudomonas* (Barak et al., 1998). The possible mechanism was that light may impair the electron transfer from cytochrome *c* to nitrite reductase. Additionally, decline of denitrification by ALAN may be relevant to biogeochemical cycles. Indeed, N intensities in urban land were higher than forest and rural landscapes (Li et al., 2022), and amounts of inorganic N (i.e., NO_3^-) received in urban areas were much more than the suburban and rural sites through deposition (Lovett et al., 2000; Pickett et al., 2011). Thus, the decreasing denitrification potential by ALAN may result in NO_3^- accumulation and less N_2O and N_2 emissions in urban areas, exaggerating N disequilibrium between urban and agricultural/natural ecosystems. Hence, quantitative studies of ALAN on denitrification are warranted in future, which would help to track N flux and transformations among different ecosystems.

In addition, the chemoheterotrophic activity, occupying 14.8% of all known functions, was negatively ($p = 0.01$, $q = 0.089$) related with long-term ALAN intensity (Table S7), indicating chemoheterotrophic bacteria may be sensitive to nighttime light. In previous studies, heterotrophs were losing competitiveness along light gradients and retreated to low-light zones compared to autotrophs and mixotrophs (Fischer et al., 2017; Fitter and Hillebrand, 2009). This implies that heterotrophs as the most abundant microbes in soils may have lower growth rate and metabolic activities under long-term ALAN disturbance in city. Besides, heterotrophic potentials in soil were strongly related with inorganic N and organic carbon (D'Angelo and Reddy, 1999), so the inhibition of heterotrophic processes by ALAN maybe a reason for the reduced abundances of key genes involved in C and N transformations. Thus, changes in microbial activities caused by long-term ALAN may have cascade effects to disturb the biogeochemical element cycling and ecosystem functions across the urban areas.

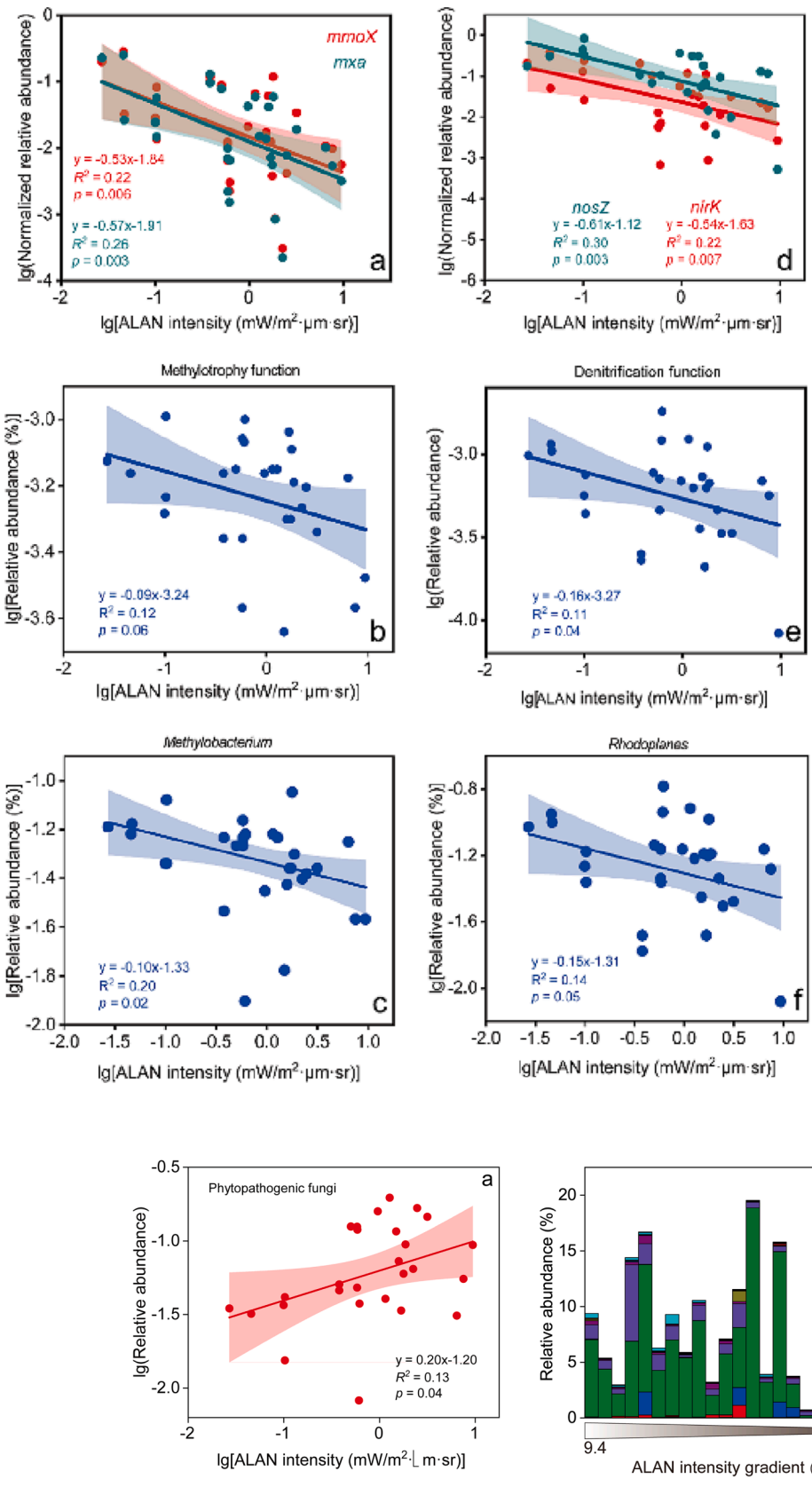

Fig. 6. The linear relationships between ALAN intensity and functional gene abundances or predicted functional group abundances or genera abundances related with methane oxidation (**a**, **b** and **c**) and denitrification (**d**, **e** and **f**) in different sampling soils. The normalized relative abundances of functional genes were obtained by HT-qPCR, and the functional group abundances were predicted by the FAPROTAX database. The data were transformed by log10 for normal distribution, and the shades represented 95% confidence intervals.

Fig. 7. (a) Linear correlation between ALAN intensity and the predicted abundances of phytopathogens by FUNGuild database. The data were transformed by log10 for normal distribution, and the shades represented 95% confidence intervals. (b) The relative abundances of fungal pathogenic genera along ALAN intensity of all sampling sites.

4.3. ALAN as a putative threat for urban plant health

In addition to urban elemental cycles, long-term ALAN may potentially affect urban plant health by increasing abundances of plant pathogenic fungi in soil. In our study, relative abundances of *Curvularia* and *Devriesia* genera increased along ALAN intensity in different urban soils (Fig. 7b). Indeed, it was reported that some fungal pathogens had higher growth rates in illuminated cultures than dark ones (Idnurm et al., 2009). Possible reasons include that light can up-regulate fungal virulence and guide them to infect more hosts to compete for resources (Gomelsky and Hoff, 2011). The enrichment of *Curvularia* and *Devriesia* by ALAN in the urban soil reservoir may jeopardize plant productivity and human health and raise public health issues. These pathogenic genera have high dispersal abilities (Barberán et al., 2015), and are associated with numbers of diseases in plants, such as foliar spots, seedling rot, and sooty blotch in grasses or trees (Santos et al., 2018; Limtong et al., 2020; Seifert et al., 2004; Li et al., 2013). Moreover, these two genera of fungal pathogens could possibly harm human health including skin and nail infection (Madrid et al., 2014; Fu et al. 2021). Abundances of fungal pathogens have also been observed to accumulate in street, residential quarter, household dust, and polluted urban environments (Li et al., 2021; Ding et al., 2020; Bearchell et al. 2005). Together, these suggested that ALAN is a previously unrecognized factor influencing the richness of fungal pathogens, and thereby increasing urban health risks. Given more intensive ALAN perturbations in the near future, fungal pathogens are expected to become more prevalent in urban ecosystems. Thus, it is required to develop scientific and efficient policies for defending fungal-related health risks in urban ecosystems.

4.4. Potential confounders in studies of ALAN and soil microbiomes

It is important to acknowledge that several potential confounding factors be correlated with soil microbiomes and/or ALAN levels. For instance, ALAN has been shown to correlate inversely with urban plant diversity (Stanhope et al., 2021), and to affect various plant traits such as nutrients partitioning, rooting patterns and chemical profiles of root exudates (Folta et al., 2015). The shifted diversity and physiology of plant communities induced by ALAN could impose environmental filtering effects on soil microbiota, and trigger variation in their compositions and functions (Liu et al., 2020; Berg and Smalla, 2009). Besides, aerobiome may be an additional confounding factor influencing the structure of soil microbial community (Robinson et al., 2021). In our study, the sampling points were less than ten meters away from the adjacent arbors or shrubs (Fig. S1), where the microbial composition could be affected by tree-associated aerobiomes via wind dispersal.

To partly control the confounding effects, "park of origin" and "NDVI" were included as covariates in random forest (RF), random forest adjustment (RFA), and partial correlation-based analyses to adjust for the between-park heterogeneity of habitat biodiversity. RF results reaffirmed ALAN as a significant factor predicting the primary axes (PCo1 and 2) of variations in the structure of soil microbiomes (Fig. S5). Furthermore, influences of ALAN on bacterial and fungal structures were still significant ($p < 0.05$, $q < 0.05$) while setting aside the contributions of confounders such as plant diversity using RFA analysis (Table S10). These supported "pure" effects of ALAN on soil microbiota, beyond those could be explained by the adjacent habitat heterogeneity (i.e., vegetation biodiversity). Consistently, partial correlation analyses that accounted for the influences of NDVI still detected significant correlations between ALAN and key functional genes (*nosZ, nirK, mxa*, and *mmoX*), as well as phytopathogens (Fig. S6). These results indicated the observed associations between ALAN and soil microbiomes in our study is not solely driven by the confounding effects of regional biodiversity. It also supported ALAN may be an important but overlooked factor driving soil microbial variation, in addition to the most influential geographic locations.

Furthermore, there are some confounders that could not be controlled in our study, such as regional temperature and ALAN spectrum in urban areas. These factors may also play a role in shaping soil microbial compositions. A significant positive relationship existed between land surface temperature and ALAN in urban areas (Howlader and Islam, 2020). It indicated variations of temperature across sampling sites may collaboratively impact soil microbiomes along ALAN intensity gradient. Except for ALAN intensity, different light wavelengths can have specific effects on microbes by activating corresponding pigments in different species (Nishida et al., 2018). For example, blue light irradiation has been shown to suppress bacterial growth rate (Holen, 1999; Fukui et al., 2008) and inhibit methane monooxygenase (Lubart et al., 2011). However, due to lack the information of regional temperature and ALAN spectrum data, the effects of these two confounders on soil microbiomes could not be quantified in present study. Therefore, manipulative (incubation) studies are needed to distinguish the effects of regional climate and ALAN wavelength on microorganisms in the future.

Given the multitude of factors present in natural environments, incubation experiments are essential to determine the pure impacts of ALAN on soil microbial compositions, processes, circadian rhythm, and underlying mechanisms while controlling for confounding factors. Besides, additional research is necessary to elucidate the complex interactions between ALAN and other environmental factors (i.e., plant diversity) affecting soil microbial communities in urban environments.

5. Conclusions

Together, our work characterizes the features of urban turf soil microbial community and potential ecological functions under ALAN disturbance. ALAN played an important role in altering structures of bacterial community and increasing fungal richness but had only minor influence on protists in urban soils. Lower abundances of key genes involved in nutrients cycling under stronger ALAN suggested potential adverse effects on microbial activities related to elemental cycling in urban areas. Moreover, the potential positive relationship between ALAN intensity and phytopathogenic abundances may increase the challenges of urban plant health under long-term ALAN exposure. These would guide us to reconsider long-term ALAN effects and environmental issues in urban ecosystems. Integrating ALAN's ecological effects into urban microbial ecology is a targeted and powerful alley to better understand the capacity of life to adapt to an increasingly urbanized world.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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