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# Linking street-level greenery to environmental microbial diversity: A multiscalar analysis in the Taipei metropolitan area

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## HIGHLIGHTS

- Integrating GVI with eDNA profiling links urban greenery and microbial diversity.
- Street-level GVI correlates with microbial richness, not diversity, across urban habitats.
- Significant GVI–microbial correlations occur only in hotspots, not in pavements or entrances.
- Biodiversity hotspots host higher microbial diversity than entrances and pavements.
- Provides a scalable framework to assess greenery–microbiota relationships across cities.

## ARTICLE INFO

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## ABSTRACT

Urbanization has led to a significant reduction in green spaces, altering microbial habitats and potentially contributing to the growing prevalence of immune-mediated diseases. Urban greenery may serve as a reservoir for more diverse environmental microbiota, yet the links between street-level vegetation and environmental microbial diversity remain poorly understood. This study investigates how the visibility of greenery, measured through the Green View Index (GVI), relates to microbial richness and Shannon's diversity across urban habitat gradients in the Taipei metropolitan area. Environmental DNA samples and Google Street View panoramas for calculating GVI were collected from three sublocation types: biodiversity hotspots featuring urban green spaces, residential building entrances, and pavements linking biodiversity hotspots and entrances. Our findings show that biodiversity hotspots support greater microbial diversity, and significant GVI–microbial correlations occur only in biodiversity hotspots, not in pavements or entrances. This positive correlation observed in biodiversity hotspots suggests that street-level vegetation can reflect the diversity of environmental microbial communities. These results highlight the importance of incorporating green infrastructure into urban planning to enhance microbial habitat heterogeneity and promote microbial diversity. As urbanization continues to sever citizens' contact with nature, this initiative helps maintain the environmental microbiota essential for immune regulation and support public health. Future research should incorporate longitudinal and cross-seasonal studies to evaluate the durability of GVI-microbial relationships, examine the influence of vegetation types and structural complexity, and explore how urban greenery can act both as a scientific indicator and a public engagement tool in biodiversity-aware urban design.

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## 1. Introduction

By concentrating a wealth of resources for living, working, education, healthcare, entertainment, and many other essential activities, cities attract people to migrate to urban areas. As urban areas expand and lifestyles shift increasingly indoors, city dwellers now have significantly fewer interactions with soil, flora, and fauna, which has been reported to be associated with declines in both psychological and physiological well-being (Colléony et al., 2022; Gong et al., 2024). At a macro scale, humans possess an innate predisposition to connect with nature and other living organisms, a concept known as the Biophilia Hypothesis (Wilson, 1984). Empirical studies have consistently demonstrated the importance of exposure to natural scenes and green spaces, resulting in reduced stress, improved mood and attention, and lower rates of depression and other psychiatric disorders (Li & Sullivan, 2016; Lu et al., 2021; Hung & Chang, 2022). At a micro scale, human immune function is supported by exposure to diverse environmental microbial communities, a relationship described in the Biodiversity Hypothesis. Thus, reductions in environmental biodiversity can diminish human microbiome diversity and weaken immune regulation (Haahtela et al., 2021).

To strengthen human–nature interaction across multiple scales, from perceptible landscape features to microbial processes, researchers and urban planners have increasingly turned to expanding urban green spaces, which not only reconnect citizens to nature but also achieve multiple benefits. These benefits, referred to as ecosystem services, include managing stormwater, mitigating the urban heat island effect, reducing air pollution, sequestrating carbon, and enhancing urban biodiversity (Roslund et al., 2020; Zhang & Qian, 2024).

When discussing urban green infrastructure, studies have often relied on biodiversity-related metrics to characterize ecological patterns of plants, birds, and invertebrates (Beninde et al., 2015; Zhao et al., 2022; Hu & Lima, 2024). These approaches provide systematic ways to capture patterns of species richness, evenness, and community composition, enabling comparisons across sites, temporal monitoring, and evidence-based evaluation of biodiversity outcomes (Pierce et al., 2020; Ye et al., 2025). However, these metrics primarily reflect ecological conditions that are not directly perceptible to non-experts in everyday urban environments. Without specific training, ordinary citizens are unable to perceive or interpret such ecological information their own sensory experiences, thereby limiting their capacity to meaningfully engage in or contribute to urban biodiversity conservation efforts (Novacek, 2008; Bele & Chakradeo, 2021).

Therefore, the Green View Index (GVI, Yang et al., 2009) was developed as an alternative, more comprehensible indicator that captures street-level greenery (Li et al., 2015; Kumakoshi et al., 2020). Unlike widely used satellite-based indices such as the Normalized Difference Vegetation Index (NDVI), which quantify vegetation from a top-down, remote sensing perspective, GVI reflects greenery as experienced at street level and is therefore more directly aligned with human-scale environmental exposure (Villeneuve et al., 2018; Kumakoshi et al., 2020). As such, GVI offers an effective and efficient means of quantifying the visual impact and vegetation configuration of urban green infrastructure from the perspective of ordinary citizens walking through urban areas (Li et al., 2015). For example, Hu and Lima (2024) demonstrated the potential of public participation by recruiting non-expert volunteers to photograph urban greenery that attracted their attention, without interference or deliberate guidance. In parallel, large-scale datasets of Street View Imagery (SVI) provide a promising method for quantifying greenery across extensive urban areas, offering scalable and replicable assessments of GVI while continuing to improve in consistency and accuracy (Torkko et al., 2025). Together, citizen-contributed photographs and SVI-based analyses illustrate the diverse data sources through which GVI can be generated. In comparison, calculating biodiversity typically requires trained professionals to conduct systematic fieldwork, generate ecological datasets, and perform rigorous statistical analyses, limiting opportunities for public engagement.

An important but often overlooked component of urban environments is microbial biodiversity. Although invisible to the naked eye, microbial biodiversity supports both human health and ecosystem function. Increasing evidence suggests that exposure to diverse environmental microbiota can positively influence the human immune system, potentially reducing the prevalence of immune-mediated diseases such as allergies, asthma, and inflammatory disorders (von Hertzen et al., 2011; Hanski et al., 2012; Sinkkonen et al., 2025). Studies have demonstrated that the microbiome present in forest soil has a beneficial effect on the immune health of individuals who come into contact with it (Hanski et al., 2012; Roslund et al., 2020). In particular, greater gammaproteobacterial diversity on the skin of children has been associated with enhanced immune regulation and a reduced risk of allergies and atopy (Hanski et al., 2012; Roslund et al., 2020). Engaging in playing within forest environments and interacting with pets has been associated with the promotion of natural immunity and the prevention of autoimmune diseases, allergies, and asthma in children (Hanski et al., 2012; Haahtela et al., 2021). Additionally, exposure to natural microbiota, including soil and plant microbial communities, has been linked to enhanced immune regulation in adults, such as increased microbiota diversity and modulation of anti-inflammatory and pro-inflammatory cytokines (Nurminen et al., 2018; Saarenpää et al., 2024). At the same time, plant-associated microbes in urban soil enhance plant health and resilience by improving nutrient/biochemical cycling, promoting plant growth, and providing protection against pests and pathogens (Xie et al., 2020; Fan et al., 2023; Stewart et al., 2024). Furthermore, microbial diversity interacts synergistically with other components of biodiversity, including plant and insect communities, contributing to ecosystem multifunctionality and stability (Wagg et al., 2014; Delgado-Baquerizo et al., 2016). Recognizing microbial diversity is therefore essential not only for advancing urban biodiversity conservation but also for enhancing the health and resilience of both human and non-human urban residents.

This case study took place in the Taipei metropolitan area, one of the most ecologically vulnerable regions in the world (Chang et al., 2017; Lee & Lin, 2020). Google Street View (GSV) panoramas were obtained to calculate GVI from 90 sublocations belonging to 15 study sites scattered across five districts of Taipei and New Taipei. Meanwhile, environmental DNA (eDNA) samples were collected from three sublocation types: biodiversity hotspots, pavements, and building entrances. Biodiversity hotspots mainly refer to green infrastructure, such as urban park trees, bushes, vertical green walls, and potted plants. Pavements referred to pathways featuring impervious surfaces that connect urban biodiversity hotspots (hereafter hotspots) with residential building entrances (Fig. 3). This design aims to simulate residents' visits to nearby green spaces and the potential transfer of enriched microbes to residential areas (Mhuireach et al., 2016; Parajuli et al., 2018; Kim et al., 2023). We hypothesized that there would be positive quantitative relationships between street-level greenery (assessed via GVI) and microbial biodiversity in urban environments. Since diversity of Proteobacteria (synonym: Pseudomonadota), particularly Gammaproteobacterial diversity, has been associated with enhanced immune regulation and reduced risk of allergies and atopy (Hanski et al., 2012; Roslund et al., 2020), we were particularly interested in the relationship between street-level greenery and Gammaproteobacterial diversity. We further anticipated that this case study would inform future efforts to design resilient and healthy urban environments through the reintegration of nature and biodiversity.

## 2. Materials and methods

### 2.1. Study sites in the Taipei metropolitan area

The study took place in Taipei City and the vicinity metropolitan area of New Taipei City, Taiwan (25.0330°N, 121.5654°E). Home to around 2.5 million residents (Taipei City Government, 2025), Taipei is a congested metropolis area transversed by two rivers and surrounded by high mountain ranges, forming a distinct basin terrain (Chen et al., 2024). With New Taipei City accounting for 4 million residents (New Taipei City Government, 2025), the metropolitan area is the densest area in Taiwan. The urbanized areas have adapted to geographical traits, while the demographic dynamics reflect the mobility of residents there.

Historically, the development of the urban system in Taiwan favored the Taipei metropolitan area due to its strategic location at the northern core of the western corridor (Liu & Dąbrowski, 2024). As a result, this region exhibits a higher building density to accommodate the large population. Many housing projects were hastily built, often disregarding the characteristics of neighboring buildings, which led to a contentious urban sprawl. Moreover, the green system within the Taipei metropolitan area exhibits a fragmented typology (Kim & Li, 2024), hardly adequate to satisfy the increasing population. Most of the green spaces and parks within the city are less than 2 ha, leaving urban residents reliant on this fragmented green provision.

The eDNA sampling and GSV calculation were carried out in selected study sites in Da'an, Songshan, Xindian, Zhongshan, and Zhongzheng districts, with the focus on Da'an (Table 1). Each study site included three sublocation types: near the hotspot, entrances of residential buildings, and pathways linking hotspots and entrances (Fig. 1). The sampling of the materials took place between 4 January and 11 January 2024. In Da'an District, six study sites in residential neighborhoods (A-F), one in Da'an forest park (G), and three around the National Taiwan University (NTU) campus and dormitories (H-I) were chosen, each with six sublocations including all sublocation types, except the study site in Da'an forest park with only six hotspots (Fig. 1; Supplementary material Table S1). In addition, five more study sites were selected in four other districts: Minsheng Park in Songshan District (K), two residential neighborhoods in Xindian (L) and Zhongshan (M) district, respectively, and an old military dependents' village (N) and NTU dormitories (O) in Zhongzheng district. Each study site also included six sublocations as described above. In total, the study included 90 sublocations, comprising 34 hotspots, 28 pavement areas, and 28 entrances (Fig. 1; Table 1; for details on sampling locations, daily weather during DNA sampling, and coordinates, see Supplementary material Table S1).

## 2.2. Quantification of urban green

We used GVI to estimate the amount of urban greenery in the streetscapes (Yang et al., 2009) by acquiring all available GSV panoramas within a 50-meter spatial buffer around each sublocation (Fig. 1). To ensure an accurate assessment of greenery, we excluded four sublocations that had fewer than five panoramas within the spatial buffer. In total, we collected 2574 panoramas from 2009 to 2025 (Supplementary material Fig. S1). This averaged 47 GSV panoramas per sublocation, ranging from 8 to 124. To calculate the GVI, we semantically segmented all the panoramas using a OneFormer model with a DiNAT-L backbone (Jain et al., 2023), which was pre-trained on the ADE20K dataset (Zhou et al., 2017). We used the aggregated share of the classes *tree, grass, shrub, flower,* and *palm* to calculate GVI for each panorama (Fig. 2). Representative examples of the three sublocation types are provided in Supplementary Fig. S2 to illustrate their spatial and morphological characteristics.

## 2.3. Microbiological sample collection and analysis

The hotspots were soil below or right next to the large trees, bushes, small garden parks, or vertical green walls (Fig. 3A). The pavements were asphalt, cement, or tiles of the walking pathways (Fig. 3B). The entrances were flooring, doormats next to the residential or public building entrance doors. Each microbiological sample was collected by using a sterile cotton swab in a tube (VWR, Radnor, PA, USA), the tip of which was dipped into autoclaved Tween (VWR, Radnor, PA, USA). The samples were then collected by using the moistened swab and sterilized plastic stencil (5 cm x 5 cm) (Fig. 3B & 3C). Three separate replicates were collected by scraping soil particles and dust horizontally and vertically from hotspots, pavements, and entrances (Fig. 3) with the swab, using a standardized 'zigzag' motion and uniform pressure. After sampling, the swabs were immediately placed into their container tubes and stored with cold bags (+0°C) during sampling and transportation to the laboratory, where they were kept frozen for a short-term storage of one week in Taipei, Taiwan (−18°C). Then, the samples were transferred to Helsinki, Finland, in dry ice (−70°C) to long-term storage in −80°C until further processing.

DNA was extracted from swaps with PowerSoil® DNA Isolation Kit (MoBio Laboratories, Inc., Carlsbad, CA, USA) according to the manufacturer's standard protocol. The V4 region within the 16S rRNA gene was amplified by PCR (three technical replicates from each sample) using 505F and 806R primers (Caporaso et al., 2012). Negative controls (sterile water) and positive controls (ZymoBIOMICSTM Microbial Community Standard, Zymo Research Corp., Irvine, CA, USA) were included in DNA extraction and PCR proceсures to ensure analytical quality. Paired-end sequencing of the amplicons (2 × 300 bp) was performed on an Illumina MiSeq instrument using a v3 reagent kit.

Raw paired-end sequence files were processed with DADA2 into amplicon sequence variants (ASVs) (Callahan et al., 2016) using the Silva database version 138 (Quast et al., 2013). ASVs were inferred using the DADA2 pipeline, including quality filtering, denoising, merging of paired-end reads, and chimera removal (Bokulich et al., 2013; Callahan et al., 2016). Following taxonomic assignment, an ASV table was constructed and subsequently preprocessed by removing non-bacterial sequences, such as chloroplast and mitochondrial reads. ASVs observed in negative controls were removed from the ASV table (Roslund et al., 2021). Sequencing depth was assessed for each sample prior to downstream analyses. No samples were excluded based on read count, and all samples were retained for analysis. The final sequencing was 25,808 ± 12,977 (mean ± SD) reads per sample. To account for differences in sequencing depth, the ASV counts were transformed into

**Table 1**
Population size and land area of the sampled districts in comparison with the whole Taipei City and New Taipei City.

| Location | Taipei City / New Taipei City | Districts | | | | |
|---|---|---|---|---|---|---|
| | | Da'an (Taipei City) | Songshan (Taipei City) | Zhongshan (Taipei City) | Zhongzheng (Taipei City) | Xindian (New Taipei City) |
| Urban development area (ha) | 12,478 / 111,779 | 1060.34 | 833.90 | 993.47 | 685.17 | 8454.03 |
| Population count (ten thousand persons) | 249.1 / 404.7 | 28.99 | 19.18 | 21.52 | 14.84 | 30.66 |
| Population density (persons/ha) | 199.6 / 36.2 | 273.4 | 230.0 | 216.6 | 216.6 | 36.3 |
| District population density / City population density ratio | – | 1.37 | 1.15 | 1.09 | 1.09 | 1.00 |
| Study sites (Fig. 1) | 15 (A – O) | 10 (A – J) | 1 (K) | 1 (M) | 2 (N & O) | 1 (L) |

Source: New Taipei City Government (2025); Taipei City Government (2025).

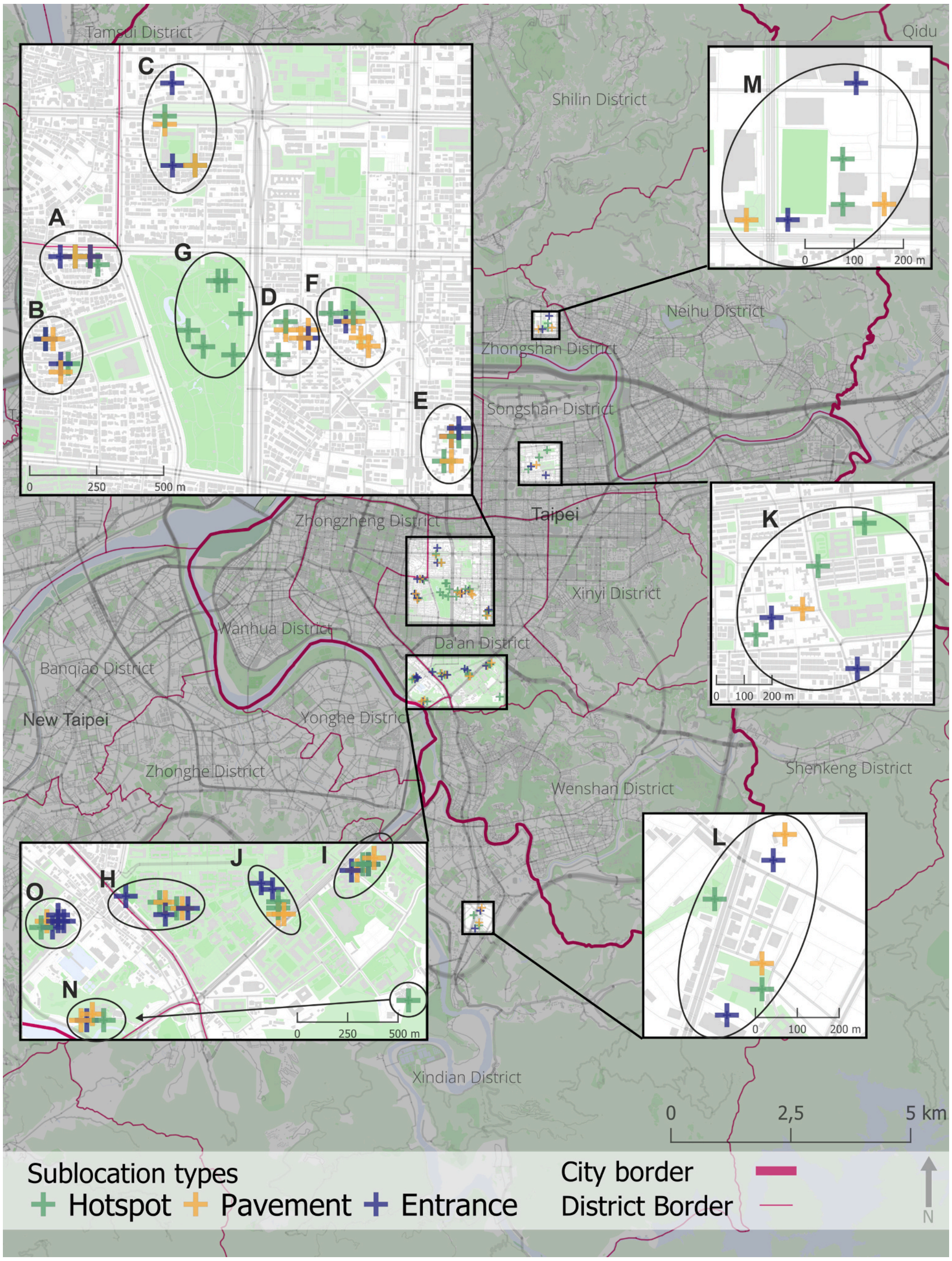

**Fig. 1.** Map of study sites and three sublocation types in the Taipei metropolitan area: near the hotspots (green cross), pavements connecting hotspots and door entrances (blue cross), and door entrances of residential buildings (orange cross). City borders and district borders are highlighted. Detailed information about the study sites (A-O) can be found in Supplementary material Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

proportions to conceptualize the different sequence read depths (McKnight et al., 2019). The Shannon diversity index was determined using the *diversity* function and species richness using the *specnumber* function in the *vegan* package (Oksanen et al., 2019).

### *2.4. Statistical analysis*

Microbial data were analyzed in RStudio v4.3.1 (Posit team, 2025) using the *vegan* package (Oksanen et al., 2019). Differences in microbial community composition between locations were analyzed with Permutational Multivariate Analysis of Covariance (PERMANOVA, *adonis2* function in *vegan* package) using Bray-Curtis distances (Anderson, 2017). Multivariate homogeneity of group dispersions (PERMDISP, *betadisper* function in *vegan* package) was used to examine if the significant differences in PERMANOVA are caused by different within-group variation (dispersion) instead of different centroid positions. Principal coordinates analysis (PCoA) with Bray-Curtis distance was used to visualize the difference in bacterial community composition (*cmdscale* function). Analysis of Variance (ANOVA) (*aov* function) was used to analyze differences in microbial richness and Shannon's diversity. Pairwise analyses were done with pairwise permutation tests in the *rcompanion* package with Benjamini-Hochberg correction to conceptualize the false discovery rate (FDR). Spearman correlation was used to analyze the relationship between GVI and microbial data.

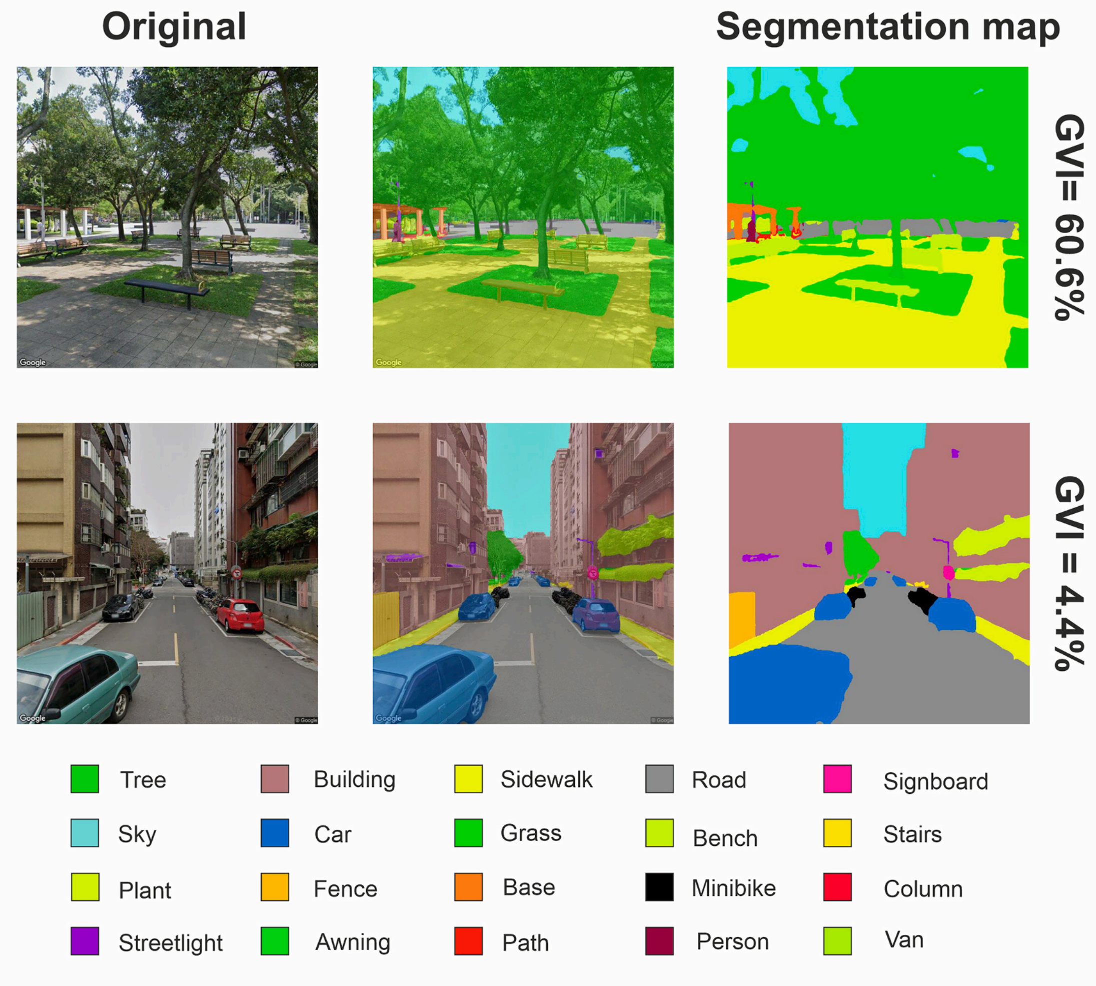

**Fig. 2.** Calculation of GVI to estimate greenery in the streetscapes of the Taipei metropolitan area.

## 3. Results

### 3.1. Urban green view index

The average GVI for all the sublocations was 24% (min = 2.7%, max = 71.4%, σ = 15.7%), with all of them exhibiting at least some vegetation and over 27% having a GVI greater than 30%, indicating a significant presence of street-level greenery (Supplementary material Fig. S3).

GVI varied across different sublocation types within the Taipei metropolitan area (Kruskal–Wallis: H = 8.399, $p = 0.015$). The Dunn's post hoc test with Bonferroni correction revealed that the GVI of hotspots was different from entrance ($p = 0.014$), while the differences between hotspot and pavement ($p = 0.159$), and entrance and pavement ($p = 1.000$) did not exhibit statistical significance. GVI exhibited a declining trend across sublocation types, decreasing from approximately 30% in hotspots to around 20% in pavements and further to 18% at entrances (Fig. 4).

### 3.2. Microbial diversity

The results revealed variation in bacterial richness, indicated by the number of ASVs, and the Shannon diversity index across different locations and sublocations (Supplementary material Fig. S4).

PERMANOVA showed that microbial community compositions differed between the different study sites ($p = 0.01$) and sublocation types ($p = 0.02$) (Fig. 5A and 5B). The microbial community of hotspots differed from entrances ($p = 0.01$; Fig. 5B), but not from pavements ($p = 0.17$; Fig. 5B). No difference was found in microbial community composition between entrances and pavements ($p = 0.1$). These differences were not driven by dispersion effects, as indicated by non-significant PERMDISP results ($p > 0.1$).

Hotspots had higher total richness and diversity compared to entrances (Fig. 6). However, the difference in Proteobacteria between hotspots and entrances was significant only for richness, not for diversity. Such a difference was mainly contributed by Gammaproteobacteria, while there was no difference in Alphaproteobacterial richness. Additionally, the diversity of Gammaproteobacteria was significantly different between hotspots and pavements ($p = 0.026$; Fig. 6B). No difference was found in bacterial richness or diversity between entrances and pavements ($p > 0.3$).

### 3.3. Correlation between urban green view index and microbial diversity

A significant correlation was found between GVI and total bacterial richness ($p = 0.031$), with the highest GVI corresponding to increased richness in hotspots ($p = 0.047$) (Fig. 7A). However, the monotonic relationship between GVI and bacterial richness was not significant in entrances and pavements, which exhibited lower maximum GVI and richness levels. Notably, entrances showed particularly diminished GVI and bacterial richness compared to hotspots.

The relationship between the GVI and the Shannon diversity index was less pronounced than the correlation observed between GVI and bacterial richness ($p = 0.078$) (Fig. 7B). However, a significant

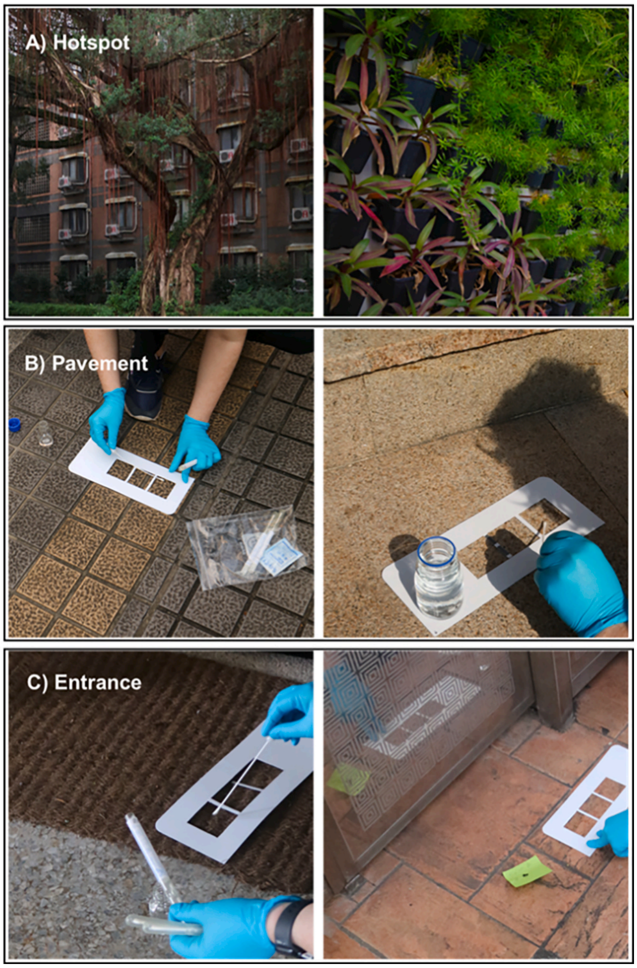

**Fig. 3.** Three sublocation types in the Taipei metropolitan area: near hotspots (A), pavements connecting hotspots and door entrances (B), and door entrances of residential buildings (C).

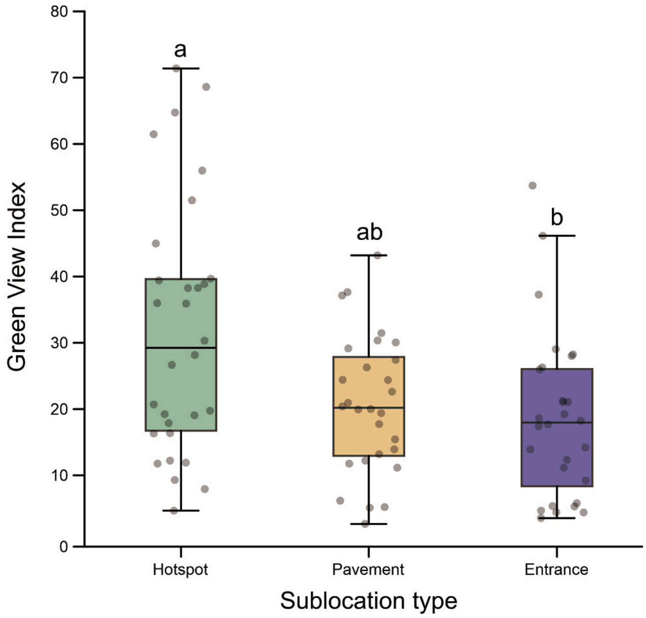

**Fig. 4.** GVI across different sublocation types. The lowercase letters indicate significant differences between sublocation types at $p < 0.05$.

correlation was found between the Shannon diversity index and GVI in the hotspot sublocations ($p = 0.034$).

## 4. Discussion

This study links eDNA-based bacterial data with GVI across urban sites in the Taipei metropolitan area. Our findings suggest that greater street-level greenery supports higher microbial diversity, highlighting the potential of GVI serving as an accessible, less resource-intensive proxy for estimating urban microbial diversity.

### 4.1. Interpretation of the GVI patterns of the study sites

Our findings show that the average GVI across the study sites was 24%, with hotspots exhibiting the highest value (~30%), followed by pavements (~20%) and entrances (~18%). This gradient suggests that street-level greenery decreases when moving from ecologically rich patches toward more heavily built, human-congregated urban spaces. Similar intra-urban gradients have been documented, suggesting that GVI tends to decline near building edges due to limited planting spaces and obstruction by structures (Ye et al., 2019; Zhang et al., 2024).

This pattern reflects how urban greening strategies often prioritize public or semi-public green spaces over spaces immediately adjacent to buildings and entrances. Nevertheless, this pattern can be partially explained by physical and functional considerations near building entrances, where requirements for accessibility, security, and maintenance typically limit the feasibility of dense vegetation (Jim, 2013; Ossola et al., 2019). As a result, the transition from public green spaces to residential areas often represents a shift from high to low level of greenness, suggesting that residents may experience reduced exposure to vegetation in their immediate living environment. This underscores the need to strengthen the continuity of visual greenery throughout the "last meters" of people's daily routes. Integrating small-scale vegetation, such as green walls, side planters, and courtyard gardens, can mitigate this green visual scarcity and enhance ecological connectivity at the same time (Goel et al., 2022; Biljecki et al., 2023).

Furthermore, socioeconomics and urban morphology are also key determinants in GVI values. Wealthier districts/cities with strong urban–ecological planning generally exhibit higher and more evenly distributed GVI due to systematic integration of greenery into streets and public spaces (Ye et al., 2019; Zhang et al., 2025). In contrast, densely populated and land-scarce areas like some of Taipei's inner districts often display fragmented greenery. Urban form further shapes street-level greenery. Narrow street canyons, high building coverages, and minimal setback substantially lower GVI, whereas wider streets, open plazas, and layered vegetation create more visual permeability, thus enhancing measured GVI (Biljecki et al., 2023; Zhu et al., 2025).

### 4.2. Interpretation of urban bacterial diversity

In this study, hotspots exhibited higher bacterial richness and Shannon's diversity than entrances, suggesting a higher bacterial diversity and a more balanced distribution. Vegetated areas typically provide more diverse microhabitats (Fierer, 2017; Delgado-Baquerizo et al., 2018), while impervious surfaces like pavements are homogeneous, resource-deficient, and often exposed to stronger environmental filtering, such as UV light, desiccation, and human intervention, allowing only resilient taxa to persist (Hu et al., 2018; Zhang et al., 2020; Nugent & Allison, 2022). Moreover, the Intermediate Disturbance Hypothesis suggests that moderate disturbance can enhance habitat heterogeneity and support a greater variety of species (Fox, 1979; Moi et al., 2020). Therefore, the lack of a significant difference between pavements and hotspots may be partly explained by the presence of intermediate disturbances and by the fact that approximately 60% of the pavement sampling sites were located closer to hotspots than the entrance sites.

Hotspots supported particularly higher richness and Shannon's

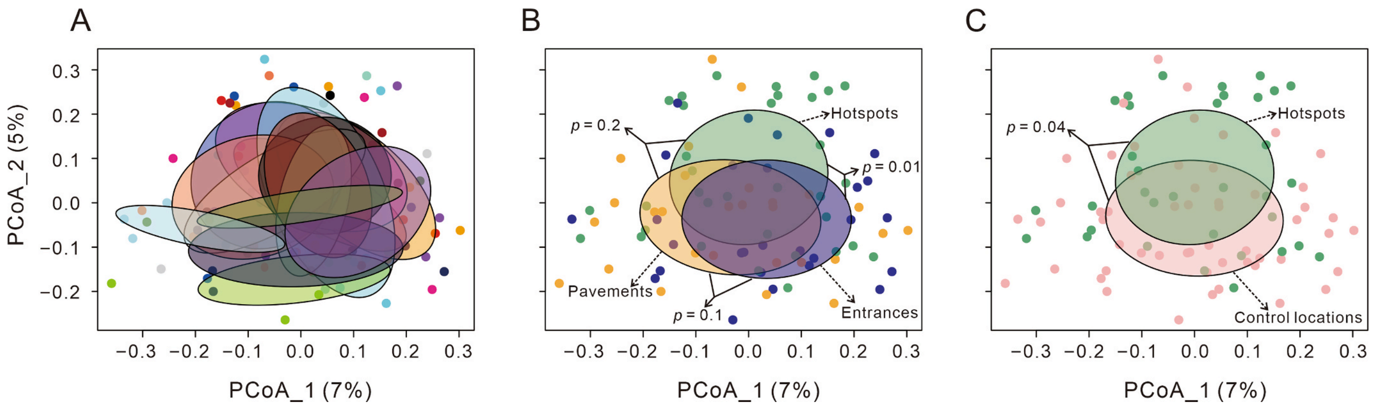

**Fig. 5.** PCoA plots showing ASV variation in microbial community composition between study sites in the Taipei metropolitan area (A); sublocations across all the study sites (spring green for hotspots; light orange for pavements; and blue for entrances) (B); and the hotspots (spring green) vs. control locations that combine pavements and entrances (pink) (C). The percentages in parentheses are the proportion of variation explained by the PCoA axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

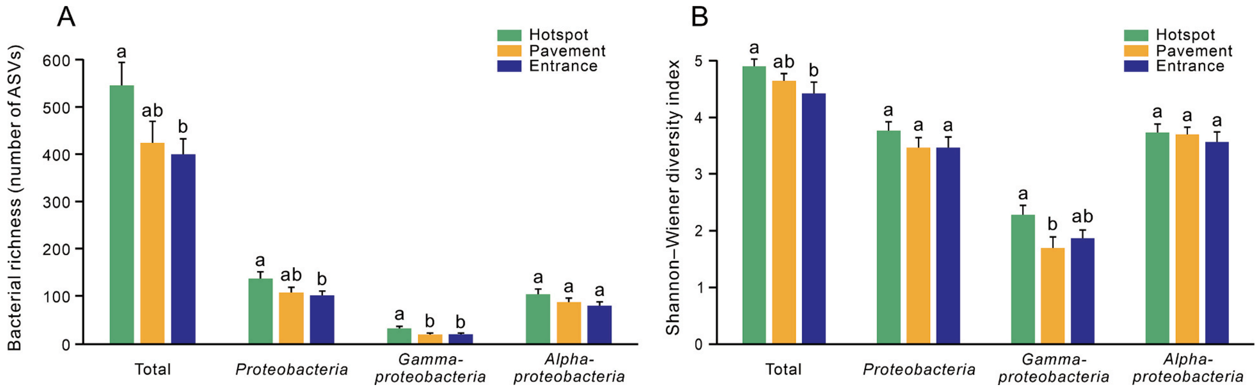

**Fig. 6.** Bacterial richness (A) and Shannon diversity index (B) between hotspots, pavements, and entrances for total bacteria, Proteobacteria, Gammaproteobacteria, and Alphaproteobacteria. The lowercase letters above the bars indicate significant differences between sublocation types at $p < 0.05$.

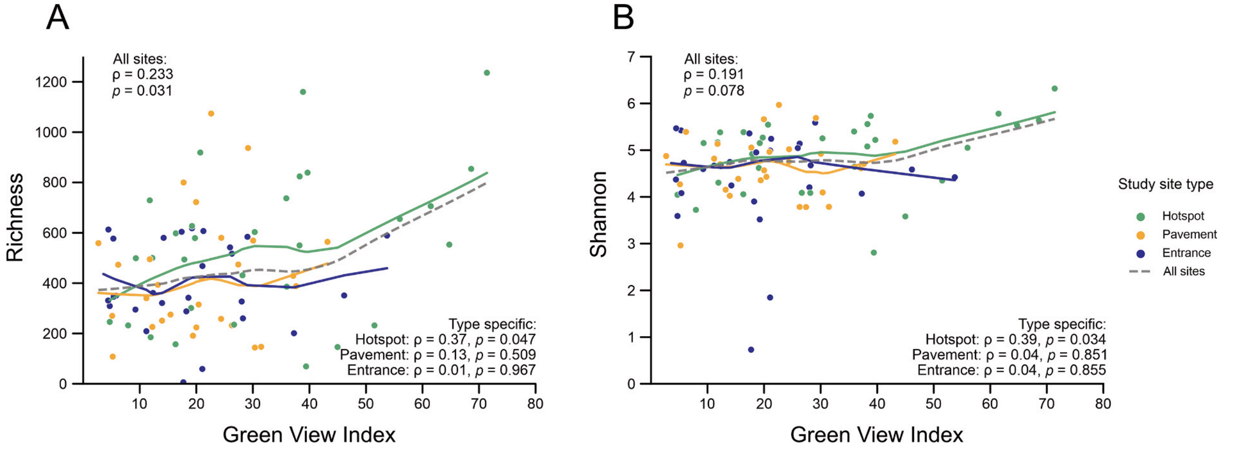

**Fig. 7.** Total bacterial richness (A) and Shannon diversity index (B) as a function of the Green View Index across sublocations in the Taipei metropolitan area. The curves are fitted with the LOWESS method. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diversity in Gammaproteobacteria but not Alphaproteobacteria, both under Proteobacteria. This phylum commonly dominates urban soils and phyllospheres due to its metabolic versatility and stress tolerance (Janssen, 2006; Delgado-Baquerizo et al., 2020). As copiotrophs, Gammaproteobacteria (e.g., *Pseudomonas*, *Serratia*, and *Enterobacter*) thrive in nutrient-rich, moist environments with abundant plant exudates and organic matter (Eilers et al., 2010; Li et al., 2021). In contrast, oligotrophic Alphaproteobacteria, with low rRNA gene copy number and low protein synthesis rate, persist under resource-limited and stable conditions (Yao et al., 2017; Li et al., 2021). Since our samples were collected from material surfaces, the greater nutrient and moisture availability in hotspots likely favored Gammaproteobacteria, compared to impervious surfaces. Meanwhile, Alphaproteobacteria, which preferentially inhabit deeper and more stable soil layers, remained uniformly low with no significant difference among sublocation types.

Although our study did not sample human-associated microbiota, existing literature suggests that several Gammaproteobacteria, such as *Pseudomonas*, *Salmonella*, and *Vibrio*, are immunologically relevant as opportunistic pathogens or modulators of host immune responses (Montero et al., 2023; Letizia et al., 2025). In skin microbiome studies, their relative abundance correlates with immune regulatory gene expression in blood cells, implying a connection between environmental exposures and systemic immune responses (Hanski et al., 2012). Conversely, many Alphaproteobacteria (e.g., *Pelagibacterales*, *Rhizobiales*, *Sphingomonadales*, and *Caulobacter*) are adapted to oligotrophic environments, contributing to nitrogen fixation, organic carbon degradation, and biofilm formation under resource-limited conditions (Waigi et al., 2015; Giovannoni, 2017; Fiebig, 2019; Maisnam et al., 2023). In urban microbiomes, their relatively uniform abundance across surfaces suggests slow-growing, persistent colonizers indicative of long-term ecological stability.

Overall, the contrasting patterns of bacterial richness and diversity among sublocations in the Taipei metropolitan area reflect the combined effects of environmental heterogeneity, vegetation presence, and habitat filtering. Further research integrating functional metagenomics or metatranscriptomics could reveal whether these compositional differences translate into ecological functions along urban gradients.

### *4.3. Greenery as an indicator of bacterial diversity in urban habitat gradients*

Our analyses revealed that GVI was significantly correlated with total bacterial richness across all sublocations, while the correlation with Shannon's diversity was weaker and non-significant. Because Shannon's diversity is sensitive to evenness, dominance of stress-tolerant taxa on hard urban surfaces can reduce evenness and lower Shannon diversity, even when vegetation stochastically hosts rare taxa and consequently increases richness (Jost, 2010; Strong, 2016; Roswell et al., 2021). Therefore, urban microbiome studies frequently report stronger gradients in richness than in Shannon's diversity across green-grey transitions, driven by environmental filtering on impervious surfaces (Hu et al., 2018; Zhang et al., 2020; Gao et al., 2023).

Correlations between GVI and both microbial richness and Shannon's diversity were significant only in hotspot sublocations, not on pavements or at entrances. This result highlights that such correlations are context dependent. Three mechanisms might explain this. Firstly, hotspots contain plant-associated microbiota, especially Alpha- and Gammaproteobacteria that respond to plants' presence, which may contribute to greater microbial richness and evenness as GVI increases (Kurm et al., 2017; Zhalnina et al., 2018; Schäfer et al., 2023; Yang et al., 2025). Secondly, dense foliage in hotspots provides buffered and resource-rich microclimates, supporting more diverse microbial taxa. In contrast, lacking such conditions, pavements and entrances constrain the bacterial community regardless of small vegetation variations nearby (Tecon & Or, 2017; Hu et al., 2018; Yu et al., 2019). Thirdly, a threshold or non-linear effect may exist: only when GVI exceeds a certain level do conditions support both species accumulation and a more balanced community structure. This explains why correlations with GVI occur only in hotspots, consistent with threshold-like microbial responses to vegetation gradients in other urban studies (Hu et al., 2018; Mills et al., 2022; Huang et al., 2023; Koster et al., 2025). Together, these findings suggest that street-level greenery can support microbial diversity under specific habitat conditions, which has important implications for the design and evaluation of urban green infrastructure.

It is important to distinguish between urban greenery as captured by GVI and actual plant diversity when interpreting these relationships. GVI primarily reflects the visual abundance of vegetation at street level, rather than species composition or taxonomic diversity. Many previous studies have shown that plant diversity can be a stronger predictor of microbial diversity and community structure than vegetation quantity or productivity (Yang et al., 2017; Baruch et al., 2021; Yi et al., 2025). However, these relationships are not universal, as microbial communities are also strongly shaped by abiotic factors such as soil properties and climate, which can modulate or interact with plant diversity effects (Yang et al., 2017; Liu et al., 2020; Bierza et al., 2023; Labouyrie et al., 2023). In this study, our sampling targeted surface-associated microbial communities in urban environments that are more relevant to human exposure than belowground microbiota typically examined in ecological studies (Hsu et al., 2016; Joseph et al., 2025). Compared to belowground communities that are more strongly influenced by plant-specific traits such as root exudates (Wei et al., 2025), these surface communities are more immediately shaped by environmental conditions (e.g., light, temperature, and moisture) and the overall presence and structure of surrounding vegetation (Fu et al., 2022; in't Zandt et al., 2025; Panek et al., 2026). From this perspective, GVI captures the visible and experiential dimension of urban greenery that mediates everyday human–microbial interactions. Therefore, the associations observed between GVI and bacterial diversity are more appropriately interpreted as indicator of environmental exposure and urban ecological context, rather than direct effects of plant diversity per se. Moreover, GVI also serves as a practical and scalable indicator that does not require expert taxonomic knowledge.

### *4.4. Implications and future directions*

#### *4.4.1. Integrating urban ecological diversity into design and planning*

Regardless of its aesthetic appeal, urban street-level greenery serves as a tangible ecological asset supporting urban microbial diversity. The positive correlations between GVI and both bacterial richness and Shannon's diversity in hotspots indicate that even small-scale greening, such as street trees, vegetated façades, and pocket gardens, can meaningfully enhance biological complexity in dense urban districts. This aligns with broader evidence that vegetation improves microbial diversity in built environments (Dockx et al., 2021) and with frameworks identifying vegetation cover as a key determinant of urban ecosystem health (Nugent & Allison, 2022). By regulating microclimate and increasing habitat heterogeneity, greenery contributes to essential ecosystem functions and urban resilience (Stewart et al., 2024; Kumar et al., 2025). In addition, variation in vegetation type further shapes microbial functional potential, underscoring the importance of research evidence-based plant selection and site design (Qiu et al., 2025). These insights highlight the need to integrate ecological, biological, and social considerations into urban planning and design (Watkins et al., 2020; Herath & Bai, 2024). At the neighborhood scale, enhancing greenery improves habitat quality and strengthens social cohesion, as residents' satisfaction relates more to the connectivity, diversity, multifunctionality, and accessibility of green spaces than to total green area alone (Jennings & Bamkole, 2019; Ta et al., 2021; Cardinali et al., 2024). Collectively, GVI and microbial indicators can serve as accessible proxies for underlying ecological processes, providing practical tools for integrating biodiversity considerations into urban design and policy, while also supporting environmental literacy and community-based monitoring through sustained stewardship, low-maintenance strategies, and community engagement.

#### *4.4.2. Linking urban biodiversity to human well-being*

Although this study did not directly measure health outcomes, numerous studies have shown that exposure to biodiverse environments can contribute to human immune resilience and wellbeing (Ojala et al., 2019; Roslund et al., 2020). According to the Biodiversity Hypothesis, continuous exposure to diverse environmental microbiota enhances immune tolerance, while reduced microbial contact increases the risk of immune-mediated inflammatory diseases (Haahtela et al., 2021; Sinkkonen et al., 2025). Urbanization, on the one hand, has lowered the chance of exposure to pathogens; on the other hand, it has also decreased beneficial microbial encounters, contributing to immune dysregulation, such as allergy, asthma, and other chronic inflammatory conditions (Haahtela et al., 2021; Matthews et al., 2024). For example, “rewilding” playgrounds with forest soil has been shown to diversify children’s skin microbiota, improving immune regulation and reducing the relative abundance of opportunistic pathogens (Roslund et al., 2020, 2022). Together, the observed correlation in our study suggests that everyday green environments may shape the microbiome of residential neighborhoods that likely contribute to human microbial exposure through air, soil, and surface contact, emphasizing the importance of restoring microbial diversity as both an ecological and a public health priority.

In addition to ecological-immunological linkage, environmental-psychology research has shown that street-level greenery alleviates stress, restores attention, and enhances positive emotions, through even a brief visual exposure (Ojala et al., 2019; Ingabo et al., 2024; Bardhan et al., 2024; Hung, 2025; Gao et al., 2025). Because vegetated environments that host diverse microbial communities also provide cognitive and emotional benefits, enhancing street-level greenery and microbial diversity may therefore represent a dual pathway for promoting population health.

### *4.5. Limitations and suggestions for future reference*

While this study offers novel evidence linking urban street-level greenery and microbial diversity, several limitations should be acknowledged and addressed in future studies.

First, our microbial assessment focused exclusively on bacterial communities, while other major microbial groups, particularly fungi, were not included. This represents an important limitation, as fungi play key roles in ecosystem functioning and contribute to environmental microbial exposure associated with immune-related health outcomes (Dannemiller et al., 2014; Bahram & Netherway, 2022). However, this focus was influenced by both resource constraints and methodological considerations. Bacterial communities are widely distributed and consistently detectable across diverse urban environments, including air and surface samples (Brągoszewska & Mainka, 2024), making them suitable for capturing spatial variation in environmental microbial exposure (Bowers et al., 2011; Grönroos et al., 2024). In contrast, fungal communities are often more strongly associated with specific environmental sources such as soil and vegetation (Štursová et al., 2016; Zhou et al., 2021). Under these constraints, focusing on bacteria provides a practical basis for detecting environmental microbial patterns. Nevertheless, future research should incorporate multiple microbial domains to achieve a more comprehensive understanding of urban microbiomes and their potential health implications.

Second, microbial samples were collected within a limited time window, whereas the GSV panoramas span 17 years. Although this temporal mismatch may introduce potential confounding effects, restricting the analysis to imagery from a single year would substantially reduce spatial coverage and introduce systematic spatial bias, as locations with more frequent updates, typically central or highly accessible urban areas, would be overrepresented (Goel et al., 2018; Fan et al., 2025). Additionally, even within the same street segment or location, GSV panoramas are often captured in different years (Curtis et al., 2013; Kim & Jang, 2023). In our dataset, 98.72% of the images were captured within the most recent decade (2016–2025; Supplementary material Fig. S1), thus largely reflecting contemporary urban conditions. However, if resources permit, panoramic imagery could be collected alongside eDNA sampling to reduce temporal mismatch.

Third, although we used GSV imagery regardless of the seasons and collected eDNA samples once in winter, we acknowledge that seasonality and climatic zones play major roles in influencing both GVI and microbial results (Nugent & Allison, 2022; Zhao et al., 2025). However, in tropical and subtropical regions, GVI variation due to seasonality is weaker than in temperate and cool regions. This is likely because evergreen vegetation dominates the urban landscape, and the sematic segmentation algorithm used for GVI detection can still identify woody components such as branches and trunks as green objects, leading to relatively stable GVI values across seasons (Jim & Chen, 2008; Chan et al., 2024). As for eDNA results, microbial communities are sensitive to seasonal variations in environmental conditions such as temperature and moisture, and even in tropical and subtropical regions these dynamics may influence diversity patterns (Bowers et al., 2011; Štursová et al., 2016). Therefore, sampling at a single time point may not fully capture temporal variability in urban microbial communities. It would be valuable for future research to investigate how seasonality affects the relationship between street-level greenery and microbial diversity in urban areas.

For future reference, research should more explicitly consider the role of urban morphology and socioeconomic conditions in shaping both greenery patterns and microbial outcomes. Characteristics such as street configuration, building density, frontage conditions, and maintenance regimes may influence the distribution and accessibility of street-level greenery (Łaszkiewicz et al., 2022; Zhang et al., 2023), while socioeconomic differentiation has been shown to structure environmental exposure and green space availability (Hoseini et al., 2025; Wei et al., 2025). These factors may mediate the relationships identified in this study and should be incorporated into future analytical frameworks to better understand how urban form and social inequality interact with ecological processes and public health outcomes.

## 5. Conclusions

This study exhibits a significant relationship between urban greenery and microbial diversity, demonstrating that hotspots supported greater microbial richness and Shannon’s diversity. In addition, significant GVI–microbial correlations were observed only in hotspots, not in pavements or entrances. These findings underscore the ecological potential of urban greenery to foster healthier microbial communities and reinforce the importance of incorporating green infrastructure into urban planning to sustain ecological processes across multiple scales, from urban greenery to microbial diversity.

As urbanization continues to reduce access to green spaces, the resulting loss of microbial diversity in cities may contribute to the rising prevalence of immune-mediated inflammatory diseases. Therefore, prioritizing greening initiatives can not only enhance the aesthetic quality and ecosystem services of cityscapes but also mitigate health risks associated with insufficient microbial exposure. A better understanding of these linkages can inform nature-based planning strategies that reconnect residents with diverse microbiota and promote long-term well-being in urban areas.

Future research should focus on longitudinal studies to 1) validate GVI-microbial relationships across climatic, seasonal, and cultural contexts; and 2) investigate the interplay between vegetation type, microbial communities, and genetic predispositions of urban residents. In this way, deeper insights into the ecological and health implications of urban greenery will be elucidated. At the same time, expanding the use of GVI as both a scientific and public engagement tool could encourage greater appreciation for biodiversity, foster citizen participation in greening initiatives, and bridge scientific understanding with community action. A comprehensive understanding of the multiple factors linking urban ecology and public health is essential for shaping sustainable and equitable cities. Evidence from previous studies consistently shows that exposure to greenery is associated with psychological restoration and healthier lifestyles. This reinforces the need for urban planners to integrate ecological and social design into green infrastructure, building more biophilic and resilient urban environments.

## CRediT authorship contribution statement

**Long Xie:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Jussi Torkko:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Marja Roslund:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tzen-Ying Ling:** Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Juulia Manninen:** Writing – review & editing, Validation, Software, Methodology, Investigation, Data curation. **Shih-Han Hung:** . **Aki Sinkkonen:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Tuula Jyske:** Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

## 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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2026.105709.

## Data availability

Data will be made available on request.

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