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Urban green infrastructure for biodiversity and ecosystem services

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Chapter 5

Urban green infrastructure does not show synergies or trade-offs in ecosystem services and invertebrate species richness

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Abstract

Green infrastructure (GI) is widely promoted as a solution to simultaneously deal with urban challenges related to climate, health and biodiversity. However, empirical field evidence supporting this claim is lacking. Our research assessed the relationship between GI, and the role of vegetation density, height and land-use, in driving ecosystem services (ES) and biodiversity across 167 sites in The Hague, the Netherlands. In contrast to expectations, ES and biodiversity did not show trade-offs or synergies, and contributions of GI and its features were remarkably unimportant for explaining biodiversity and ES. Our findings challenge the prevailing paradigm, and suggest that GI is unlikely to be inherently multifunctional, and that specific GI features are essential in promoting ES and biodiversity. Our findings highlight critical limitations in current GI multifunctionality models and tools leading to flawed urban planning, due to a lack of causal drivers, showing a demand for increased urban ecological understanding.

5.1 Introduction

Global urbanization has profoundly disrupted the natural environment, leading to a range of challenges in cities, such as extreme climate, unhealthy living conditions and loss of biodiversity, which will become increasingly severe with climate change (Kim and Brown, 2021). Together, these challenges increase human mortality by millions, drive species extinction and burden the economy by billions USD (Gao et al., 2023; Tomson et al., 2021; WHO, 2018; McKinney, 2008; Maghrabi et al., 2022; Taylor et al., 2015). The urgency of addressing these challenges is becoming increasingly important as 68% of the global population is predicted to live in cities by 2050 (UN, 2019). Key features of urbanization driving these local challenges include impervious surfaces, heat retaining materials, the density of combustion-based engines and the destruction of natural habitat (Kim and Brown, 2021; Gao et al., 2023; McKinney, 2008; Yadav et al., 2023). These drivers combined cause the Urban Heat Island (UHI) effect (Maghrabi et al., 2022; Taylor et al., 2015; Yadav et al., 2023), increase flooding (Gao et al., 2023; O'Donnel and Thorne, 2020), increase air pollutants above healthy thresholds (Tomson et al., 2020; WHO, 2018), and reduce much of the already imperilled local biodiversity (McKinney, 2008). Solving these challenges in dense urban environments requires solutions that provide multiple functions or benefits (i.e. multifunctionality) and do so space-efficiently.

Cities are crucial for human livelihoods and increasingly also for other species (Boakes et al., 2024; Jokimäki et al., 2018; Wenzel et al., 2020). Therefore, as part of the Sustainable Development Goals, governments have globally agreed upon making cities sustainable and liveable (UN, 2015). To do so, natural and semi-natural managed areas, also termed Green Infrastructure (GI), are proposed to space-efficiently execute multifunctionality in form of both ecosystem services (ES) —benefits that humans derive from nature— and enhancing biodiversity (UN, 2015; Haase et al., 2014; Schwarz et al., 2017; Morpurgo et al., 2023). Indeed, evidence shows that GI helps to mitigate the UHI effect by reducing ambient temperatures up to 5°C and enhancing thermal comfort (Balany et al., 2020; Shao and Kim, 2022). GI also aids in water regulation, reducing the volume of water during urban flooding and runoff by 27.7–45.5% and 32.8–96%, respectively (Berland et al., 2017; Zhang and Chui, 2019; Esraz-UI-Zannat et al., 2024). Additionally, GI improves urban air quality, reducing pollutants by up to 60% (Tomson et al., 2021). GI also supports biodiversity by providing habitat for species, including rare and endangered ones, making cities vital for biological conservation (Boakes et al., 2024; Jokimäki et al., 2018; Beninde et al., 2015; Lapoint et al., 2015). Existing research showing the high potential of GI to alleviate these urgent climatic, health and biodiversity challenges, which tends to be interpreted as compelling evidence for GI multifunctionality.

The GI multifunctionality assessment as a solution to urban challenges draws on isolated studies investigating individual ES or biodiversity benefits, which tend to show important relationships with general vegetation indices derived from global remote sensing datasets, creating the impression of worldwide generalizability (Korkou et al., 2023; Charoenkit and Piyathamrongchai, 2019). These general vegetation indices capture some GI characteristics, but they lack information on most of the varied structural and functional features of GI, such as vegetation density, height, and spatial configuration, which are known to be critical for ES and biodiversity. Nonetheless, stacking individual single-function models using a single general vegetation indicators to assess GI multifunctionality is immensely popular and make claims on GI multifunctionality. Tools such as InVEST[®], i-Tree, ARIES (Villa et al., 2009; Nowak, 2021; Natural Capital Project, 2024) are attractive to researchers and policy-makers as they include multiple predicted benefits of GI (Balany et al., 2020; Charoenkit and Piyathamrongchaim 2019; Paulin et al., 2020). Critically, these tools predict ES and biodiversity

synergies and trade-offs, without sufficient validation of (1) whether the included variables are actually key drivers or causal mechanisms, and (2) interactions between ES and biodiversity. This is especially concerning where ES and biodiversity respond to distinctly to GI features (Schwarz et al., 2017; Morpurgo et al., 2023).

As a major consequence of the current modelling-focused approaches to assess GI multifunctionality, we lack empirical evidence on whether ES and biodiversity actually spatially co-occur, as their co-occurrence is only present through model predictions. Moreover, we do not know which features of GI actually simultaneously drive ES and biodiversity individually. Underlying these knowledge gaps is the unexpectedly limited number of field studies assessing the individual relationships between GI, ES, and biodiversity (Ma and Yang, 2025). More importantly, no study exists using field observations on urban ES and biodiversity benefits, assessing their synergies, trade-offs, and links to GI features. A novel framework suggest the simultaneous inclusion of three key drivers for ES and biodiversity —vegetation density, structure and usage—, allowing for the identification of important GI features for biodiversity and ES (Morpurgo et al., 2023). Therefore, gathering in-field empirical evidence while incorporating several GI features are needed to confirm the GI multifunctionality, through co-occurrence of ES and biodiversity benefits, synergies, and trade-offs.

In this study, we investigated the synergies and trade-offs among ES and biodiversity within GI based on field empirical observations in The Hague, The Netherlands. Specifically, we investigated air temperature regulation, air pollution regulation, water infiltration, and invertebrate species richness and evaluated their co-occurrence and determined how much they are driven by a specific urban GI features. To ensure a comprehensive analysis, we included three standardized features of GI: vegetation density, vegetation height and Land-use and Land-cover type, adapted from the recently developed Consolidated Urban Green Infrastructure Classification (CUGIC), allowing for delineation of drivers and a deeper understanding of the urban GI, ES and biodiversity patterns (Morpurgo et al., 2023). Our results do not show synergies or trade-offs between GI, biodiversity and ES, yet the results do show that different features of GI are important for explaining their individual patterns.

5.2. Methods

To assess the synergies and trade-offs between ES and biodiversity of urban GI, we sampled 167 sites comprised of a mix of different types of urban GI in The Hague, The Netherlands (Fig. 5.1, 52°04'57.0"N 4°17'40.3"E). The ES measured were air temperature regulation, air pollution regulation, water infiltration rate. In addition, invertebrate species richness was determined as a biodiversity indicator. The correlation among these services and biodiversity was assessed. Moreover, correlations with GI features and other drivers were assessed individually and in combination to determine sources of variation among ES and biodiversity.

5.2.1 GI sampling and locations

ES and biodiversity were sampled in a broad range of GI types in The Hague. We sampled sites on dry days from the 19th of June until the 25th of August 2023 (Fig. 5.5). The sampling protocol followed an earlier study⁶⁰, which contains a detailed description. In summary, sample locations were decided by using conditional Latin Hypercube Sampling, mimicking the distributions of several variables of interest. These variables contained information on both green and grey infrastructure, across different land-use and land-cover types. Locations were identified through geographic coordinates and photos from the previous sampling year. The sampling followed the chronological order of the earlier study (Morpurgo et al., n.d.) as closely as possible, while being random and aiming to avoid spatial and

temporal autocorrelation. At each location, we measured air temperature regulation, air pollution regulation, water infiltration and invertebrate species richness.

To assess ES of air temperature regulation, we measured the air temperature as this is an important driver of heat stress in human health, especially in urban areas (Liu et al., 2023). At each sample site, we measured air temperature every minute for one hour with five sensors at approximately 1 meter height of the ground, and could be shaded depending on trees, buildings or clouds (Temtop LKC-1000S+), and averaged to reflect the air temperature at the sampling location. We also retrieved hourly air temperature data from a stationary rural governmental temperature sensor at approximately 10km from The Hague city centre (52.12'15.0"N, 4.43'49.9"E).

To assess ES of air pollution regulation, we measured PM2.5 every minute for one hour with a cluster of five sensors (Temtop LKC-1000S+), and averaged to reflect the air pollution at the location of sampling. Typically, low cost air pollution sensors are used to infer reliably the estimates of air pollution (Maag et al., 2018). To assess the reliability of our sensor clusters, we evaluated the correlation between a government sensor and our own stationary sensor cluster ($r > 0.70$, more details in Supplementary file 5.1), and deemed the sensors reliable for comparative analysis amongst our own sensors, as shown by the higher positive correlation values ($r > 0.98$, details in Supplementary file 5.1). The stationary sensor cluster was placed on a roof at approximately 150m from the nearest governmental air pollution sensor (52°07'66.1"N 4°29'12.2"E).

To assess ES of water infiltration, we measured the infiltration rate of water into the soil as this is a crucial soil hydraulic property to regulate and mitigate severe stormwater run-off or flooding (Bagarello et al., 2004). Using the Simplified Falling Head method (SFH), we measured an average water infiltration by recording the time it took for soil to dry after adding 177ml of water, which was replicated five times in separate metal cylinders ($\varnothing = 15\text{cm}$). This amount of water added represent the instant precipitation of approximately 10 mm of rain. After, we took topsoil samples using bulk density rings (100cc), gathering data on bulk density and soil moisture to control for spatiotemporal factors that influence water infiltration. Bulk density was calculated by using a constant of volume (100cc) of soil divided by the dry weight of the soil after 24h at 105°C in an oven. Soil moisture was calculated by 1 minus the dry soil weight over the wet soil weight.

Invertebrate species richness was sampled a year prior to the ES measurements. Details on the sampling procedure and the invertebrate species richness estimation can be found in the earlier study (Morpurgo et al., n.d.). Invertebrate species were estimated using soil environmental DNA. Specifically, soil was sampled with a bleach-sterilised trowel and mixed in a clean plastic bag. In the lab, 15 grams of soil were used for DNA extraction, after which the DNA product was PCR amplified and sequenced using the NOVASEQ. The raw data was analysed in the DADA2 pipeline in combination with VSEARCH to generate Operational Taxonomic Units (OTUs; Elbrecht et al., 2018). This method provides a large amount of DNA data and is known to detect the presence of many species simultaneously (Elbrecht et al., 2018; Cristescu and Herbert, 2018; Callahan et al., 2016). The generated OTUs were assigned to species using the BOLD database (BOLD SYSTEMS, 2023). All OTUs, at 97% similarity, were assigned as an invertebrate species when matched at 70% or greater overlap with the BOLD database on invertebrates. Within every sample, the OTUs matched to an invertebrate species were summed and represent the invertebrate species richness of the site.

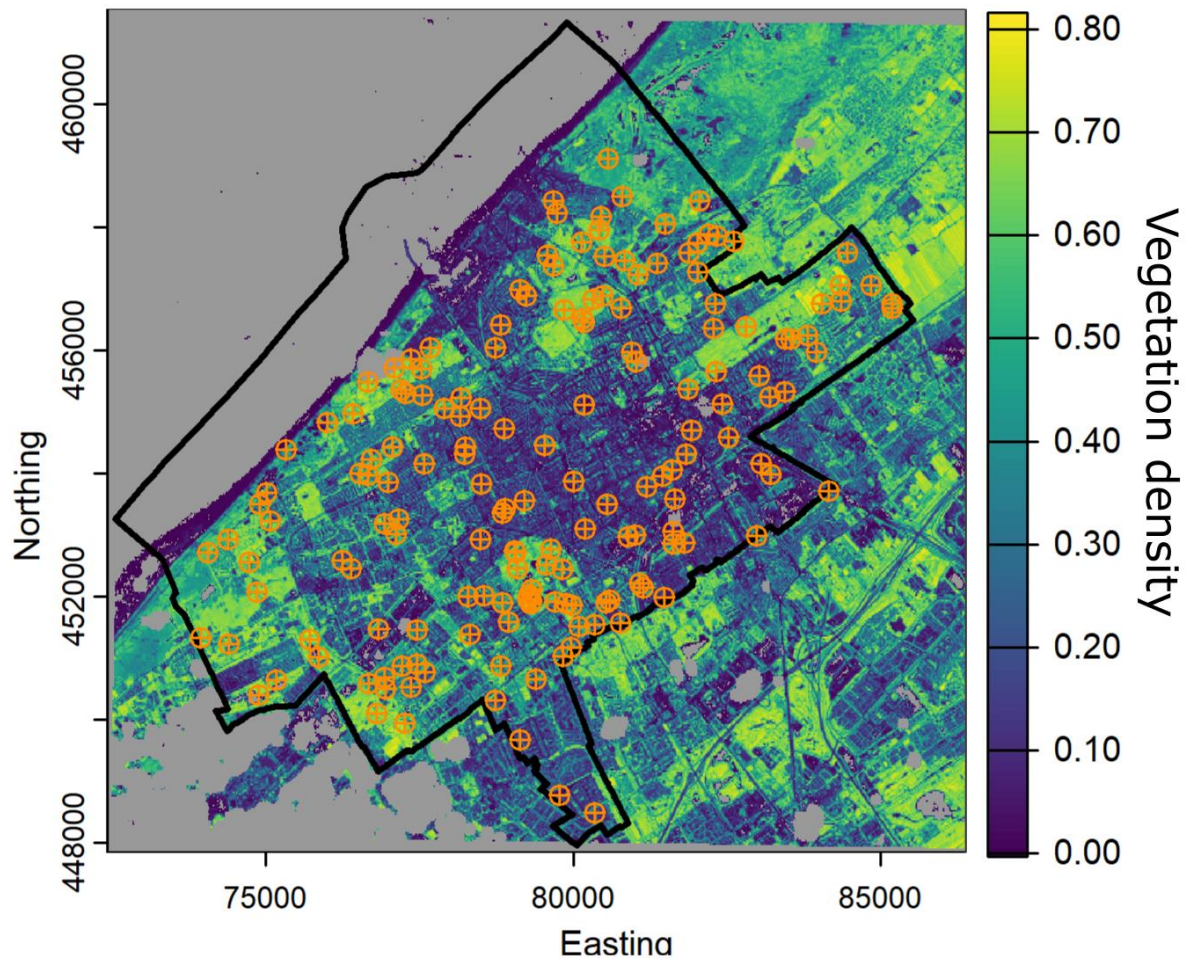


Figure 5.5. Sampling locations (orange crossed circles) against a background of vegetation density in The Hague, The Netherlands.

5.2.2 GI features

We addressed three commonly used indicators to describe urban GI features. These included cover vegetation density, height and the land use. The choice of these indicators is based on an adapted and simplified approach of the Consolidated Urban Green Infrastructure Classification (Morpurgo et al., 2023). The classification system combines remote sensing satellite data on vegetation and LULC maps to disentangle and better understand which GI features drive ES and biodiversity.

Vegetation density contains numerical proportional data that describes the density of vegetation based on NDVI retrieved from Sentinel-2, and scaled by field measurements (Morpurgo et al., n.d.; Carlson and Ripley, 1997). Vegetation height describes the proportion of vegetation that is above 1 meter high, using LiDAR data (i.e. shrubs and trees; Morpurgo et al., n.d.). LULC is a categorical predictor variable containing data describing four categories, being: Park (e.g., parks with recreation opportunities) (n = 39), Natural (e.g., dunes, forest, with passive or no recreation opportunities) (n = 17), Residential (e.g. gardens, public green in residential zones) (n = 81) and Buffer strips (n = 30; vegetated strips next to roads), retrieved from Statistics Netherlands (Morpurgo et al., 2023; CBS, 2017).

5.2.3 Data Analysis

To assess the synergies and trade-offs between the multiple functions of GI, we ran pairwise correlations using the Pearson correlation metric. In addition, a PCA was run on water infiltration rate, invertebrate species richness, the difference in air temperature at sample site compared to a rural stationary sensor and the difference in air pollution at sample site compared to our own stationary sensors. The PCA allows us to visually explore the correlations across several dimensions.

The extent to which these GI features could explain individual ES and invertebrate diversity was evaluated at several spatial scales. For this purpose, the numerical variables, vegetation density and vegetation height, were aggregated bilinearly. The categorical LULC was aggregated by the modal method, selecting the category that was the most dominant in the aggregated cell. We modelled each vegetation indicator at 8 different spatial extents (Supplementary Table 5.2). These multiple different spatial extents were assessed as it is currently uncertain to what degree local ES are dependent on the local or neighbourhood vegetation (Madrigal-Martínez and Miralles, 2020). The aggregations cover the spatial resolutions of 10x10, 20x20, 30x30, 40x40, 50x50, 100x100, 200x200 and 500x500m representing sizes ranging from approximately a large tree up to a small neighbourhood. At each spatial scale, a multiple linear model was run for each GI function. The general formula for these developed models are:

$$GI\ Function = Vegetation\ density + Vegetation\ height + LULC + Covariates + \epsilon \quad (1)$$

In these models, *GI function* is either I) air temperature regulation, II) air pollution regulation, III) water infiltration or IV) invertebrate species richness. While we modelled interaction terms between vegetation density and LULC, we opted to show the parsimonious models without interaction as their performance was statistically equal or better (t-test, $p > 0.40$; Supplementary sheet 5.4). For each of these models, we also assessed the relationship between the estimated effect of a GI feature and the spatial scale of analysis. We analysed the relation with a linear model where the response

variable was the extracted estimated beta coefficient of the respective ES or biodiversity model and used the spatial scale of analysis as predictor.

For the models on air temperature and air pollution regulation, we subtracted values from stationary sensors off the values from the field sensors to offset temporal variation. The remaining variation in both models is likely related to the local environment, including the features of local GI of interest. For the air pollution regulation model, we also included the distance to the nearest roads where cars were allowed speeds of 50km/h or higher. The air temperature regulation model and the invertebrate species richness were only predicted by the features of GI.

For the water infiltration model, soil bulk density and soil moisture were included as covariates to control for local difference in soil properties. We also ran similar models with the addition of the first two axis of a PCoA of the soil invertebrate communities retrieved via soil eDNA. PCoA from invertebrate soil eDNA were assessed for: I) all soil species, II) all invertebrate species and III) all burrowing invertebrate species. These models were used to assess if changes in soil invertebrate communities are related to increases in infiltration rate through bioturbation⁷¹. Yet, we found the models to perform equal and the PCoA did not significantly affect water infiltration (ANOVA, p-value = 0.99; Supplementary sheet 5.5).

For each linear model, we assessed the importance of GI features for ES and biodiversity. The importance was calculated via the R^2 contribution averaged over orderings among regressors (Grömping, 2006).

5.3 Results

5.3.1 Synergies and trade-offs among ES and biodiversity

To investigate the multifunctionality of GI, we assessed the pairwise Pearson correlation among included ES and invertebrate species richness and assessed the first two axis of a Principal Component Analysis (PCA). Across the GI sites (Fig. 5.1; Supplementary Table 5.1), correlations between water regulation ($n = 167$), invertebrate species richness ($n = 154$), air pollution regulation ($n = 128$), and air temperature regulation ($n = 159$) were all found to be low (Fig. 5.1a; $r < 0.30$), with only one significant negative weak correlation - between air temperature regulation and air pollution regulation ($r = -0.26$, $p = 0.004$). The first two axes of the PCA showed that all ES and species richness vary independently (Fig. 5.1b). The general lack of correlations and interdependencies indicate that trade-offs or synergies between ES and biodiversity are unlikely.

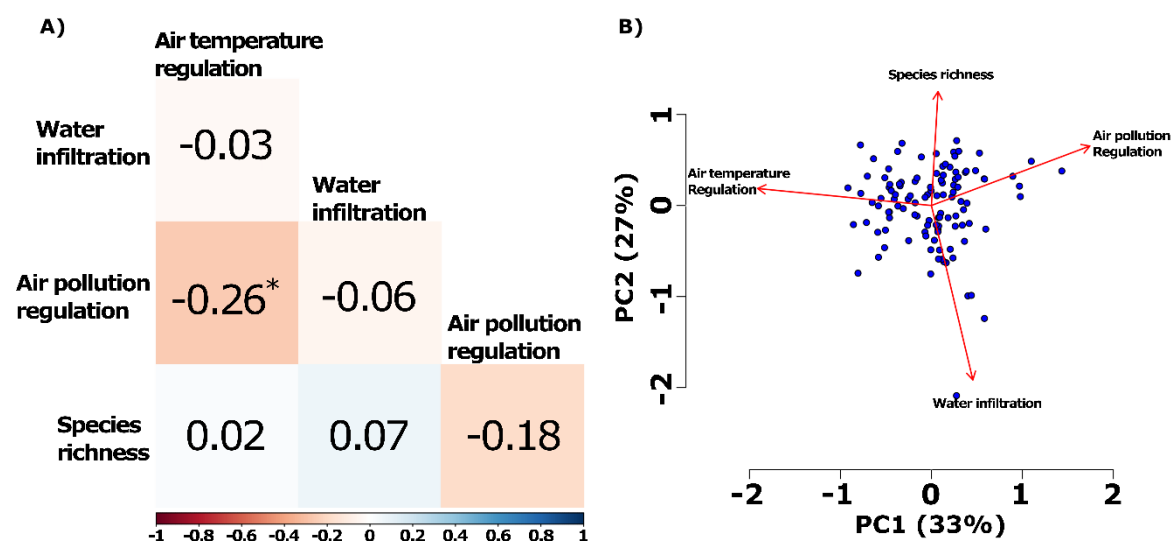


Figure 5.1. A) Pearson correlations and B) Principal Component Analysis assessing synergies and trade-offs of GI functions.

5.3.2 Analysis of GI features relationships with ES and biodiversity.

In order to evaluate the drivers of ES and biodiversity, we used linear models for every ES and the invertebrate species richness. These models contained three features of GI, being vegetation density, composition of vegetation height, land use land cover (LULC) and controlling covariates (Fig. 5.2-3; Equation 1). The explanatory power across models assessing ES and biodiversity was very low ($R^2 < 0.20$; Supplementary sheet 5.1). For every ES or invertebrate species richness, performance was similar across aggregations of spatial scales (10^2 , 20^2 , 30^2 , 40^2 , 50^2 , 100^2 , 200^2 and 500^2 m² resolution). The air temperature and air pollution regulation models showed the poorest fit, explaining on average 2-3% of the regulation (air pollution regulation, $\mu R^2 = 0.03$, $SD = 0.02$; temperature regulation, $\mu R^2 = 0.02$, $SD = 0.03$). The water infiltration and species richness models both explained the data marginally better (water infiltration, $\mu R^2 = 0.07$, $SD = 0.01$; biodiversity, $\mu R^2 = 0.10$, $SD = 0.02$).

The results indicate that GI vegetation density consistently enhances biodiversity across spatial scales and, considering GI at a large spatial scale, enhances air pollution regulation. Yet, the UHI effect and water infiltration rates are unlikely to be meaningfully impacted by vegetation density (Fig. 5.2). Vegetation density of GI showed a significant positive relationships with species richness, across scales, and a positive relationship with air pollution regulation —indicated by the negative regression

coefficients (Fig. 5.2). The models on air pollution regulation showed more pronounced negative regression coefficients when considering large spatial scale of analysis ($p < 0.05$, Supplementary sheet 5.2). Neither air temperature regulation nor water infiltration showed significant relationships with vegetation density. Moreover, the direction of the relationships of air temperature regulation and water infiltration were not consistent when considering larger spatial scales of analysis (Example using water infiltration in Fig. 5.2e-f).

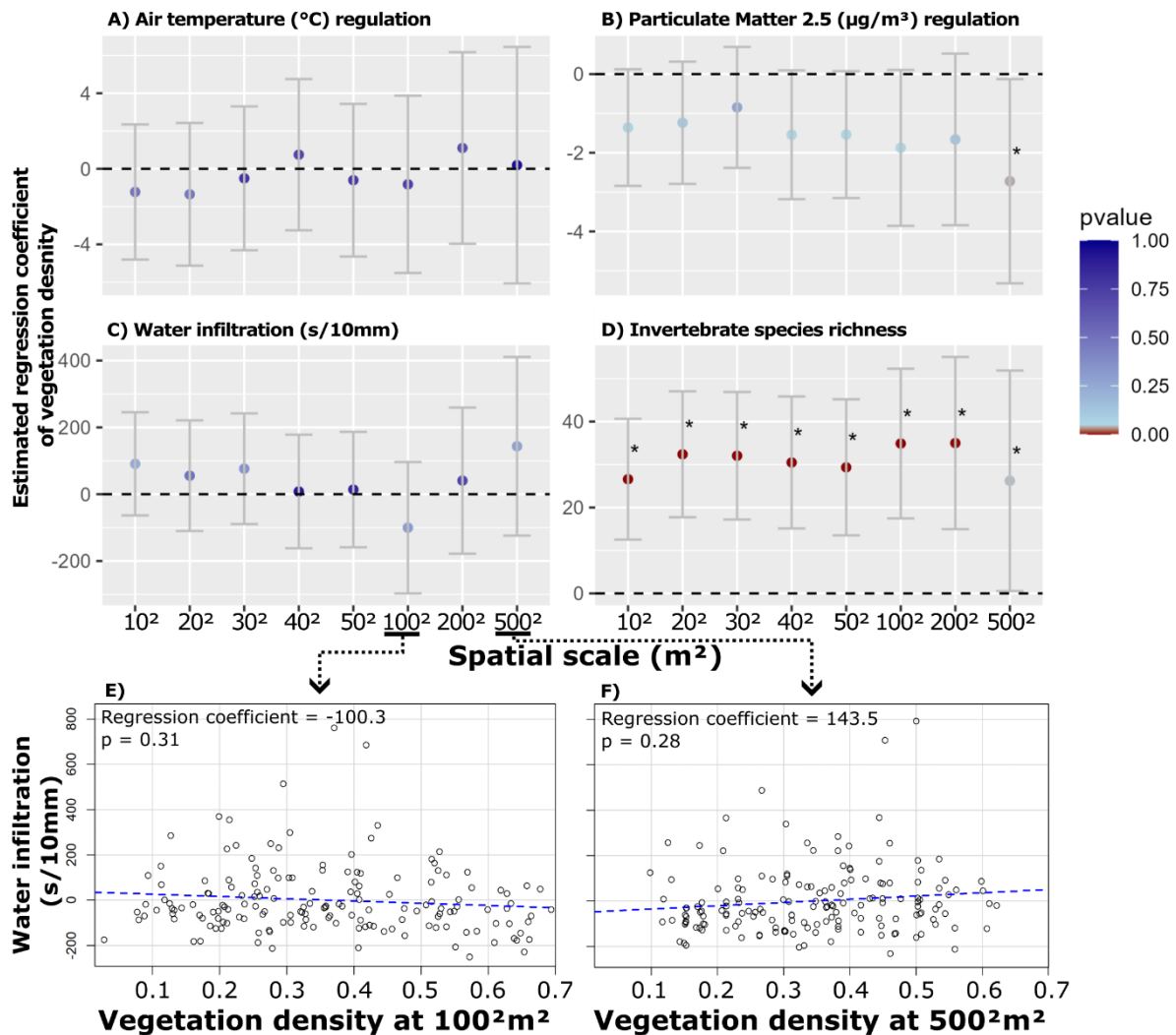


Figure 5.2. shows the estimated regression coefficients of increasing vegetation density on ES and biodiversity modelled across spatial scales (A-D). The dots, in panel A-D, indicate the estimated regression coefficients accompanied by the error bars. An asterisk indicates a statistically significant relationship with the ES or invertebrate species richness assessed at $p < 0.05$. The partial residual plots (E,F) show two examples of how the estimates in panels A-D have been derived. In particular, they indicate both a positive relationship at 100²m² (E) and negative relationship 500²m² (F) for water infiltration.

The proportion of shorter vegetation (<1m) to taller vegetation (>1m) showed mixed relationships with ES and biodiversity (Fig. 5.3). A higher proportion of tall vegetation showed positive relationships with air temperature regulation —indicated by negative regression coefficients— compared to short vegetation, and this relationship was more pronounced at large spatial scales of analysis (Supplementary sheet 5.2). Air pollution regulation showed negative relationships with higher proportions of tall vegetation —indicated by positive regression coefficients— and these relationships

were more pronounced when considering a large spatial scale (Supplementary sheet 5.2). Interestingly, only at the medium spatial scales of analysis (40^2 – 100^2 m²), a higher proportion of tall vegetation showed significant negative relationships with soil invertebrates species richness. Only water infiltration rate showed no significant relationships with a higher proportions of tall vegetation. Even so, the estimated regression coefficients were more pronounced with large spatial scale of analysis (Supplementary sheet 5.2). These results indicate that tall vegetation, compared to short vegetation, is particularly helpful for regulating temperature. In contrast, when considering the medium scale to larger spatial scale, increasing the proportion of taller vegetation in GI seems to negatively impact biodiversity and air pollution regulation.

Changes to the urban LULC showed one statistically significant difference among ES and invertebrate species richness. Water infiltration rate from natural lands was significantly higher than in park sites at a 500^2 m² ($p = 0.03$, Supplementary sheet 5.3).

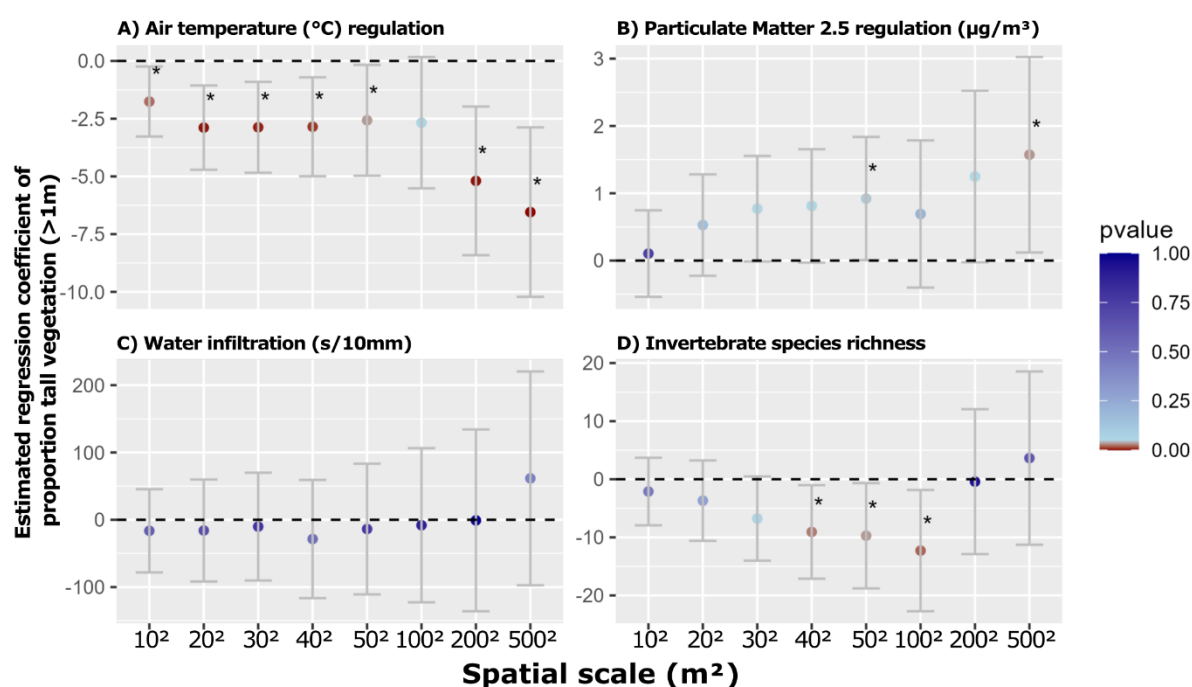


Figure 5.3. shows the estimated regression coefficients of a higher proportion vegetation above 1 meter in GI on functions, modelled across spatial scales (A-D). The dots indicate the estimated regression coefficients accompanied by the error bars. An asterisk indicates a statistically significant regression coefficient with the biodiversity or ES assessed at $p < 0.05$. Examples of how these estimates were derived are shown in figure 5.2 (E,F).

5.3.3 Importance of GI features for ES and biodiversity.

To assess the importance of different GI features, we calculated their contribution to the explanatory power of the models. At best, the explanatory power of all the features combined for either ES or biodiversity has a low combined explanatory power of just 15% (invertebrate species richness 100x100m; Fig. 5.4). These results indicate that much of the variation of ES and invertebrate species richness remains unexplained by our indicators on vegetation and included covariates.

Comparing GI features, vegetation density is the most important predictor for invertebrate species richness and air pollution regulation models. The proportion of tall vegetation (i.e. vegetation height in Fig. 5.4) is only the most important predictor in the air temperature regulation models, while contributing close to zero to air pollution regulation, water infiltration and invertebrate species richness. In contrast, LULC shows a comparatively high contribution across water infiltration, air quality regulation, and invertebrate species richness. For the water infiltration models, the included soil covariates were the most important predictors for explaining water infiltration rates, instead of GI features. These comparisons show that different GI and environmental features are important for explaining the individual patterns of biodiversity and ES.

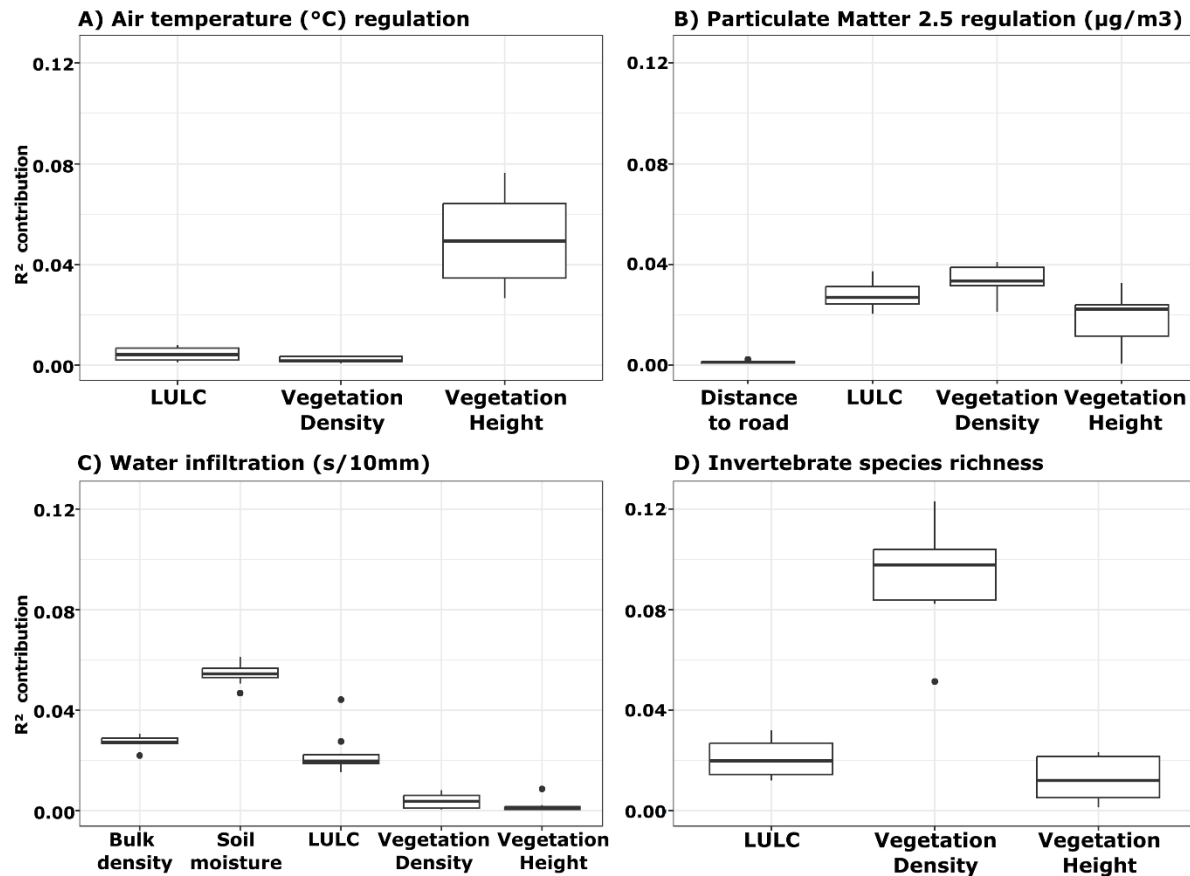


Figure 5.4. The contribution of the predictors to explaining the variance in ES and invertebrate species richness models. LULC is land use land cover. Vegetation height is the proportion of tall vegetation (>1m).

5.4 Discussion

The multiple functions of over 160 urban GI sites did not show evidence for the existence of either synergies and trade-offs for multiple ES and enhancement of invertebrate species richness. This can be explained by different features of GI being important for different ES and biodiversity patterns. For instance, GI with more tall vegetation (>1m, i.e. trees and shrubs) provides different benefits compared to GI with more short vegetation (<1m). These results are important as they contrast the current model-driven paradigm that broadly assumes synergies among ES and biodiversity (Haase et al., 2012; Karimi et al., 2021; Veerkamp et al., 2024), while they also provide the first evidence from a substantial number of urban field-sites covering biodiversity and ES.

We stress that synergies and trade-offs are unlikely to be an inherent property of GI, and that a more nuanced approach that individually assesses the contribution of each GI feature is needed to understand what drives ES and biodiversity. To explain our results, we argue that GI-ES relationships found previously are correlative in nature and mostly relate to the presence of GI instead of its features. To better understand GI multifunctionality, we argue that local features of GI, and other environmental variables, are more important for explaining the patterns of multifunctionality of urban GI-systems than just GI presence.

Our results show that different GI features play varying roles for different ES and invertebrate species richness. Understanding the dynamics that result in individual ES and support biodiversity is important as the multifunctional GI concept is increasingly prominent in research and policy that aims to support climate resilience and liveability of cities (Hansen et al., 2019; Pierce et al., 2024). Below, we suggest several potentially causal mechanisms to explain the different ES and biodiversity effects from GI features.

Results on air pollution regulation show that a high vegetation density is associated with increasing levels of air pollution regulation and that of tall vegetation is linked with decreasing air pollution regulation, as also presented in previous research (Abhijith et al., 2017; Janhäll, 2015; Setälä et al., 2013). While this seems conflicting, our results indicate that vegetation that is both dense *and* tall still results in a net positive for air pollution regulation. We highlight several potentially causal drivers that help to explain air pollution regulation capacity. First, there are likely less polluting vehicles in environments with large areas of abundant vegetation, lowering the amount of pollutants compared to more built-up, traffic heavy areas (Tomson et al., 2021). Second, the increase in area of dense foliage allows for higher retention of pollutants as there is more leaf surface to capture air pollutants (Janhäll, 2015). The reduced efficacy of air pollution regulation by taller vegetation is most likely caused by the obstruction of airflow. This phenomena is associated to urban canyons —streets with tall buildings at each side— where trees have been shown to increase air pollution regardless of wind direction (Abhijith et al., 2017; Jeanjean et al., 2017).

Our results show increased air temperature regulation from taller vegetation compared to short vegetation, but also that increased foliage density does not increase temperature regulation. Both observations likely result from a combined effect of increased evapotranspiration, albedo and the provision of shade. Taller vegetation provides shade, lowering air temperatures. At the same time, the capacity for evapotranspiration may have been especially low for short vegetation due to limited water availability in the soil (13% soil moisture) and high relative air humidity (Peng et al., 2019; Supplementary table 5.1). Compared to short vegetation, tall vegetation tends to have substantially deeper root structures which allow these plants to utilise water for evapotranspiration from deeper in the soil (Cascone et al., 2019; Chen et al., 2022). Furthermore, the higher drought resistance of tall vegetation compared to short vegetation, may result in greater leaf retention during dry periods,

further lowering temperatures by increased capacity for evapotranspiration and albedo-effect (reflecting sunlight).

Our analysis suggests that water infiltration rates are independent of the presence or type of GI and the soil invertebrate species composition. This suggests that other factors are more meaningful to water infiltration than properties of GI and the biota living in soils. This contradicts previous literature, which suggests that GI, through vegetation, increases infiltration rates by changing soil properties through mechanisms such as root growth, organic input and the creation of macropores (Berland et al., 2017). Instead, our results show that soil properties are more important predictors for water infiltration rate. However, much of the variation remains to be explained.

Our results on invertebrate species richness are in line with the ecological theory that increasing available habitat leads to increased biodiversity (Beninde et al., 2015; Lapoint et al., 2015). To our surprise, the results also show that at the medium spatial scale of analysis short vegetation tends to have more invertebrate species than tall vegetation ($40^2\text{m}^2 - 100^2\text{m}^2$). This difference is not significant at either the small scale or large spatial scale, suggesting an ecological effect dictated by the GI composition at the medium spatial scale. One explanation for this trend may be that areas with taller vegetation have lower plant species richness compared to areas with shorter vegetation, as taller vegetation may reflect more managed systems compared to spontaneous short vegetation (Aguilera et al., 2019; Ordóñez Barona et al., 2024). Alternatively, tall vegetation ecosystems simply may have lower soil invertebrate richness at base level and it may be more informative to assess composition and diversity indices (Kotze and Samways, 2001). These puzzling results warrant more research investigating invertebrate species richness across different spatial scales of analysis and urban GI compositions.

Our results give reason to seriously question the hypothesis that ES and biodiversity have synergies or trade-offs in urban GI. Urban GI assessed by commonly used remote sensing indicators mix a wide variety of potentially causal drivers. Hence, it seems logical that they perform poorly when explaining ES and biodiversity patterns. This finding deviates from the widespread idea that specific GI types, for example, trees are by default the key providers of multiple ES and biodiversity (Escobedo et al., 2019; Stroud et al., 2022). Similarly, our findings also deviate from the paradigm in the literature that argues that urban GI inherently is multifunctional (Korkou et al., 2023).

The paradigm-contrasting results have potentially substantial implications on our understanding of urban ecology, mapping of ES and policies that are based on both. In particular, ES models used for mapping spatial patterns of the benefits provided by GI in cities need to be seriously reconsidered when implying multifunctionality, synergies or trade-offs. LULC and vegetation indices are frequently core variables in such models and analyses (Paulin et al., 2020; Baró et al., 2016; Hamel et al., 2021; Lourdes et al., 2022). The low variable importance of estimated benefits from vegetation imply that in practice the urban challenges are influenced little by GI features. This implies that ES mapping tools based on general vegetation indices, such as vegetation density, height and LULC, should be cautious about estimated benefits as the uncertainties in these benefits are quite large (Willcock et al., 2020). In short, the reliability of future ES models, implying GI multifunctionality, will largely depend on inclusion of causal drivers and their validation through in-field empirical studies. This is occasionally done for single ES of biodiversity benefits (Bosch et al., n.d.), but such validation is lacking for assessment of multiple GI benefits.

To better understand the variety of processes within GI and within urban environments that affect different ES and biodiversity, we urgently need more empirical field studies assessing GI multifunctionality. This needs to be repeated in similar contexts to our study, but also broadened to a

range of other urban contexts (Zhang and MaxKenzie, 2024). The urgency for such studies is high, as ES and biodiversity are increasingly being considered in urban decision-making contexts (Cortinovis and Geneletti, 2018; Longato et al., 2021). Key predictors to be investigated are I) the attributes of GI and its link to ecosystem function and services, II) presence of built infrastructure and its composition and lay-out, and how such infrastructure drives micro-climate dynamics, III) the soil that GI is embedded in, and finally, IV) the temporal dynamics of climate regarding heat and precipitation.

Optimising the spatial lay-out and design of GI in cities is key to create liveable cities (Haase et al., 2014; Beninde et al., 2015; Hansen et al., 2019; Konijnendijk, 2023; van Oorschot et al., 2024). We provide three general guidelines based on three features of GI that urban landscape planners can work with to meet ES demands (Cortinovis and Geneletti, 2018). First, the density of GI consistently positively affects the functions included and therefore we advise urban planners to incorporate GI as much as possible to improve, albeit on a correlative basis, overall biodiversity and ES provision. We advise to implement taller vegetation where temperature reductions are more in demand and shade is absent. Second, shorter vegetation can be implemented at locations where air pollutant removal is more in demand. Implementing a variety of GI types, with different heights, will result to a more diverse set of ES provided. Third, across spatial scales of analysis the strongest effects for air temperature and pollution regulation are present at the largest scale of analysis, while biodiversity and water infiltration are impacted regardless of spatial scale. Therefore, we advise to also consider GI features of the neighbourhood scale to impact local ES provision. These guidelines align with other existing strategies, such as the 3-30-300 rule, that provide targets to improve and strategically plan urban nature at multiple scales simultaneously to improve health and well-being (Konijnendijk, 2023).

In conclusion, the results and analysis from our field study reject the hypothesis that GI is an inherently multifunctional nature-based solution to multiple urgent urban environmental issues. Instead, our findings underscore the complexity of urban GI as a generator of multiple ES, including regulation of water, temperature and air pollution, and biodiversity support. In general, increasing GI shows no downsides and tends to improve biodiversity, regulate air temperature and quality, albeit correlatively. Different features of GI drive different aspects of biodiversity and ES. Our low model performance and low variable importance of GI features also indicate that tackling urban challenges effectively requires solutions beyond just increasing GI. Future research should focus on understanding the multiple functions of GI mechanistically by incorporating data on different GI features, spatial lay-out or material composition of grey infrastructure, soil properties and temporal dynamics of climate. For urban planners, we stress the need for nuanced urban planning that considers the variety of GI features. Actionable recommendations are: prioritize high vegetation density for overall benefits, strategically deploy tall vegetation for cooling effects, and utilize short vegetation for air pollution improvements. Additionally, considering features of GI across larger spatial extents is important for ES generation and biodiversity. When implemented correctly, GI does contribute to creating more sustainable and liveable cities.

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