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Research Paper

The direct and indirect effects of road verges and urban greening on butterflies in a tropical city-state

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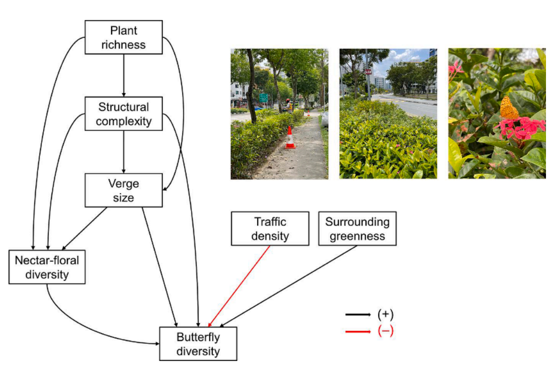
HIGHLIGHTS

- Butterflies benefit from urban road verges despite traffic disturbances.
- Road verge floral diversity and structural complexity increase butterfly diversity.
- Non-native plants benefit butterflies when native plants are lacking.
- Selective cutting regimes of urban road verges would benefit butterflies.
- The amount of urban green space at a landscape level is important for butterflies.

GRAPHICAL ABSTRACT



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ABSTRACT

Road verges have considerable potential to benefit wildlife, but in highly urbanised areas management often limits their value for biodiversity. Evaluating how the management of road verges affects wildlife, both directly and indirectly, provides opportunities to integrate biodiversity into urban planning, design, and management. We studied butterfly pollinators next to main roads across Singapore, a highly urbanised tropical city-state that envisions itself as 'A City in Nature'. Using structural equation models we quantified how road verge habitat quality (nectar-floral diversity, structural complexity, size, and plant richness) and surrounding landscapes (traffic density and greenness as a ratio of green to concreted areas) directly and indirectly affected butterflies. We found direct positive effects of nectar-floral diversity and structural complexity within road verges on butterfly diversity (abundance and richness). While road verge size and plant richness had no direct effects on butterfly diversity, both had indirect positive effects by increasing nectar-floral diversity and structural complexity. Greenness at a landscape ($\geq$ 500 m radius) rather than local ($\leq$ 250 m radius) scale positively

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affected butterfly diversity. Traffic density had a direct negative effect on butterfly diversity likely through increased mortality due to collisions. Our findings offer valuable insights for city planners and policymakers, and suggest that simple management decisions, such as improving resource quality within verges, can have positive benefits for biodiversity in highly urbanised areas. As cities around the world develop policy mechanisms to create greener environments, our results highlight opportunities to improve road verges to benefit butterflies, a commonly used flagship taxon for biodiversity.

1. Introduction

While urbanisation poses a significant threat to global biodiversity (Theodorou, 2022) cities offer opportunities to integrate green spaces (e.g., urban parks and gardens) that provide habitats for wildlife (Bowler et al., 2010; Jaung et al., 2020). Recent empirical studies have also shown that such green spaces improve human health and wellbeing (van den Bosch & Ode Sang, 2017). In an ideal world city planners may aim to support biodiversity though the preservation of large, undisturbed green spaces within urban cities (Beninde et al., 2015), e.g., preserving forest patches away from developed zones (Baldock et al., 2019; Koh & Sodhi, 2004). However, such strategies pose challenges when there is limited land available and the need for conserving land interacts with development goals (Haaland & van den Bosch, 2015). Small-scale green spaces, such as road verges (i.e., strips of vegetation alongside roads), may help to alleviate this issue by supporting biodiversity in urban areas (Horstmann et al., 2024; Veerkamp et al., 2021). The expansion of road networks is inevitable as landscapes become increasingly urbanised, providing kilometers of linear land that can be vegetated at low cost and contribute to the preservation of urban biodiversity (O'Sullivan et al., 2017).

Vegetated road verges are subject to frequent disturbances resulting in marginal ecological resources for biodiversity (Horstmann et al., 2024). Most are cut regularly to maintain their aesthetic appeal and prevent driver line-of-sight obstruction (Phillips et al., 2020). Surrounding urban green and grey spaces (i.e., impervious surfaces) also influence road verges (Collins et al., 2024; Cooper et al., 2024). Quantifying the habitat quality of verges and the landscape drivers of biodiversity provides opportunities to develop effective urban conservation strategies (Lepczyk et al., 2017; Marche et al., 2022). Unfortunately, studies on road verges in urbanised areas are limited (Battle et al., 2021; Veerkamp et al., 2021). Little is known about causal indirect impacts, as well as direct effects of road verges on biodiversity (Collins et al., 2024), particularly in tropical regions that are both rich in biodiversity and have a high likelihood of urban expansion (Collins et al., 2021; Haase et al., 2014; Veerkamp et al., 2021).

Singapore, a tropical developed Asian country, with a population of 5.9 million within its 734.3 km^2 land area (www.singstat.gov.sg/), has seen significant urban development leading to the clearance of nearly all primary forests (Chisholm et al., 2023; Tan et al., 2013). This has led to extinctions of both flora and fauna (Chisholm et al., 2023; Theng et al., 2020). Despite this, Singapore has recently adopted a vision to become 'A City in Nature' through integrating green spaces into urban planning, and now has around 50 % of its land area vegetated, comprising largely of urban parks and secondary forest patches (Gaw et al., 2019; Tan et al., 2013). These urban green spaces have been planned to enhance connectivity, increase biodiversity, and provide recreational spaces, with a network of green corridors ('Park Connectors' and 'Nature Ways') linking forest remnants and urban parks (Srikanth & Schroepfer, 2023). These efforts may have slowed extinction rates and facilitated the recovery of some species (Chisholm et al., 2023; Jain et al., 2018). Road verges in Singapore have a similar potential to contribute to landscape connectivity and biodiversity preservation (Corlett, 2013; Tan & Hamid, 2014). However, their ecological contributions, particularly for pollinators, remain unexplored.

Pollinators, including butterflies, are essential for maintaining ecosystems by facilitating plant reproduction, which underpins biodiversity, food security, and ecosystem services (Ollerton, 2017). While there are many types of insect pollinators, butterflies have been widely used as ecological indicators and flagship species that can promote public engagement in conservation (New, 1997). They contribute to pollination in both natural and urban environments, although their effectiveness varies across species and plant types (Jain et al., 2016). Despite urban fragmentation, butterflies have been shown to be highly adaptable to novel habitats such as road verges and green spaces (Phillips et al., 2020; Silva et al., 2023). If strategically managed, these areas could mitigate habitat loss and support pollinator conservation. In this study, we address the knowledge gap on the ecological potential of urban road verges and surrounding green spaces by focusing on butterfly communities in Singapore. Using causal inference methods, we tested the following hypotheses to assess how the design, planning, and management of road verges and surrounding green spaces can support butterfly communities (Fig. 1):

(H1). Nectar-floral diversity has a direct positive effect on butterflies within road verges, whereas overall plant richness has an indirect positive effect. Adult butterflies in urban areas tend to be generalists in flower selection for nectar, but specific to host plants for larvae (Baldock et al., 2019; Jain et al., 2016). Road verges, typically adorned with non-native flowering plants, provide nectar sources for adults. Floral diversity (e.g., of plants that flower) directly influences butterflies, while overall plant richness (independent of flowering) affects them indirectly by increasing nectar-floral diversity (Baldock et al., 2019; Horstmann et al., 2024; Wallisdevries et al., 2012).

(H2). The size and structural complexity of road verges have both direct and indirect positive effects on butterflies. The size (i.e., volume as a product of height, width, and length) and structural complexity (i.e., variation in vegetation heights) directly influence butterfly diversity by creating favourable microclimatic conditions, protection from traffic and predators. Structural complexity is also an indicator of management intensity, as vegetation is often cut to achieve uniformly flattened road verges (Aguilera et al., 2019; Phillips et al., 2019; Valtonen et al., 2006).

(H3). Traffic density has a direct negative effect on butterflies within road verges. Physical collisions, turbulence, and pollutants associated with traffic can disrupt butterflies' mobility, feeding, and reproductive behaviours, leading to direct negative effects on their populations (Horstmann et al., 2024; Phillips et al., 2019, 2020, 2021).

(H4). Urban greening has a direct, but scale-dependent, positive effect on butterflies within road verges. Vegetation surrounding road verges provides resources (e.g., larval host plants, nectar, and shelter) for butterflies (Baldock et al., 2019; Clark et al., 2007; Cooper et al., 2024; Koh & Sodhi, 2004). However, the magnitude of this effect may vary depending on the scale of urban greening initiatives (Chong et al., 2019).

2. Materials and methods

2.1. Study region and road verges selection

We employed a stratified random sampling design to identify a total of 101 road verges each separated by at least 500 m (Fig. 2). The verges were artificially created and planted mostly with shrubs and non-native plants (Appendix: Fig. A1). The verges were distributed across different quadrants (north, south, east, and west) of the city along roads with different speed limits (50 km/h N = 34; 60 km/h N = 37; and 70 km/h N = 70). Vegetated areas of road verges were a minimum of 30 m in length. All field surveys were conducted between June and August 2023, a period previously used in the same landscape to effectively sample butterflies, while minimising rainfall disruptions and logistical challenges (Jain et al., 2016). Our study region is influenced by a tropical monsoon climate with year-round high temperatures, high humidity, and abundant rainfall (www.weather.gov.sg).

2.2. Observed variables

To address our causal hypotheses (Fig. 1), we measured eight variables both within and outside of the road verges (Table 1).

2.2.1. Observed variables within the road verges

Butterfly abundance and richness: We sampled adult butterflies undertaking nectar-feeding activity (Appendix: Fig. A2) along a 30 m transect. We note that while a longer transect may have been preferable, the reality of urban planning meant that verges were often short, such that in this study the minimum verge length was 30 m. We walked transects at a rate of 2 m per minute (not inclusive of time identifying butterflies). All surveys were performed on sunny days with no rain and no strong wind (Beaufort scale < 5). As time of day may affect butterfly activity, each verge was visited twice at different times of the day (once in the morning, once in the afternoon) with this order randomised (similar to Priyadarshana et al., 2021). In total, we performed 202 transect walks (101 transects $\times$ 2). Morning and afternoon counts were pooled for each road verge. Species accumulation (or 'collector') and 'rarefaction' curves were used to confirm the adequacy of our sampling effort (Colwell & Coddington, 1994), with these curves approaching a plateau in the majority of cases (Appendix: Fig. A3). Butterfly identification was conducted using Khew (2015). All but two of those species considered by Khew (2015) to be associated with urban environments in Singapore were recorded (i.e., 24/26, see the results), further validating our sampling effort.

Verge size: Previous studies have often used road verge width as a measure of size (e.g., Horstmann et al., 2024; Saarinen et al., 2005). However, as road verges vary in both width and height, reflecting different cutting regimes (Appendix: Fig. A1), we measured road verge size as volume, i.e., width $\times$ height $\times$ length. However, volume and width were highly correlated (Pearson r = 0.88). Width and height were recorded at six randomly chosen points along the 30 m long fixed transect, and a mean taken.

Structural complexity: We computed this variable as the standard deviation of the vegetation height that was measured at the six randomly chosen points along the transect (see above). This considers the variances in cutting regimes and microclimatic conditions (Aguilera et al., 2019; Valtonen et al., 2006).

Nectar-floral diversity: Butterflies exhibit preferences for certain flower species (Baldock et al., 2019; Jain et al., 2016). We photographed all the flowering areas (both vertical and horizontal) within the sampled road verges and identified known butterfly nectar-feeding species. We used those photos in ImageJ software (imagej.net/ij/; version 1.54i) to measure the floral areas covered by each flowering plant species within the sampled road verges. Finally, we defined the nectar-floral diversity of each verge using the Shannon diversity index with $H' = -\sum_{i=1}^{n} pi \ln pi$,

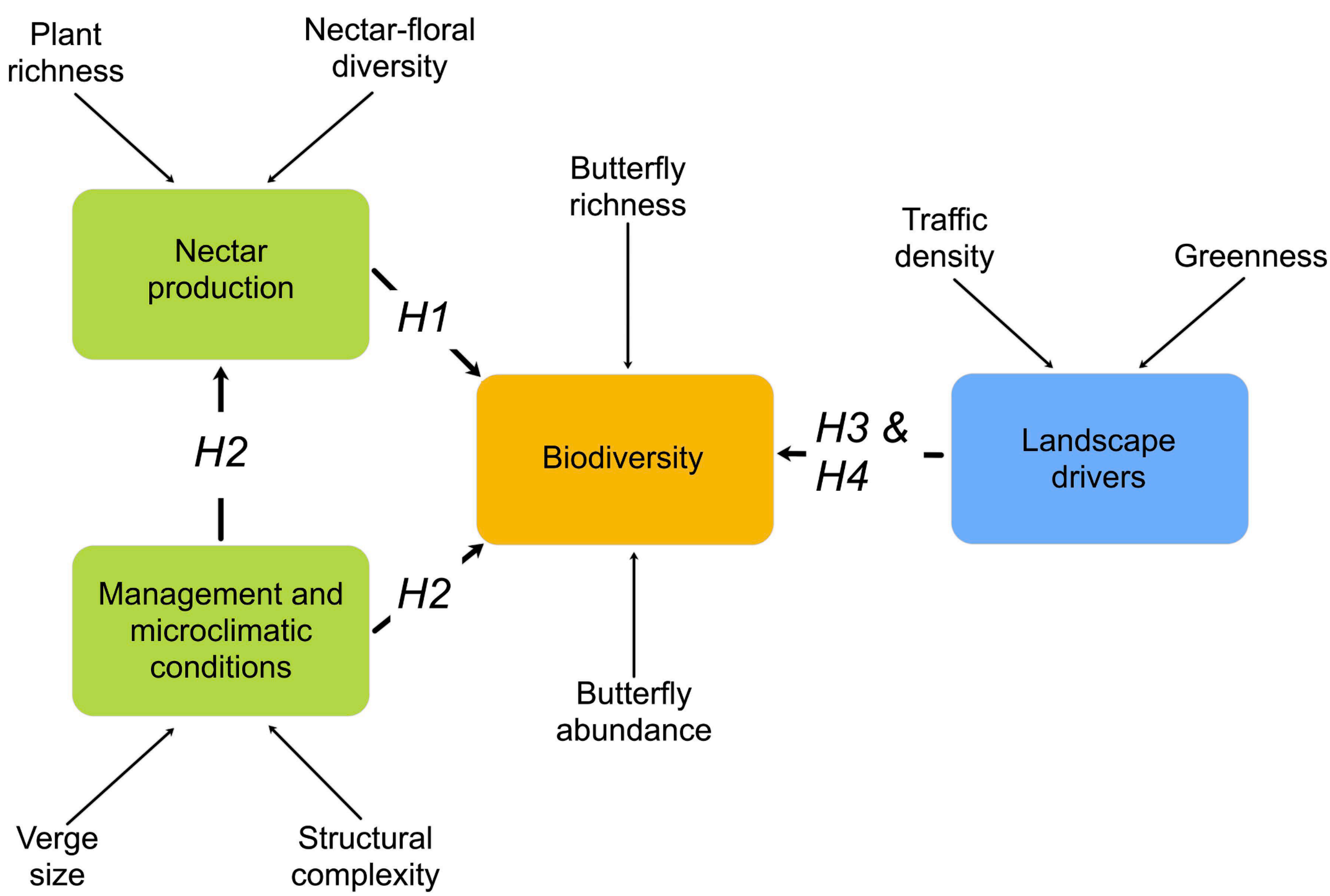

Fig. 1. A graphical representation illustrating the hypothesised causal processes in this study. The green box represents resource quality within road verges, and the blue box represents landscape drivers, with black arrows showing their effects on butterfly diversity (orange box). The observed variables used in the final SEMs are shown surrounding the respective coloured boxes. *H1–H4* denote the tested hypotheses, which are detailed in the introduction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

where *pi* is the proportion of each flowering plant species i in the total area (Shannon, 1948).

Plant richness: We measured this variable by counting the number of morphospecies of plants, excluding Poaceae grasses, within the sampled area of the road verges. This provides a measure of plant species richness, independent of whether they are flowering, and also an estimate of the richness of potential larval host plants. Plants with many horticultural varieties (e.g., *Bougainvillea*, *Hibiscus*, *Ixora*, and *Ruellia*) were treated as single species.

2.2.2. Observed variables outside of the road verges

Traffic density: Previous studies have measured traffic density by counting the vehicles passing the road verge within a fixed time period (Phillips et al., 2019). We used a similar methodology, counting vehicles within one minute, but weighted our counts by vehicle size classes defined to be either light (e.g., motorcycles and motor cars) or heavy (e.g., buses and trucks) vehicles. Counts were undertaken three times with a five-minute interval and conducted during the morning and afternoon butterfly surveys on two different days ($1 \times 3 \times 2 = 6$ min). We assigned a weight of 1 to light vehicles and 2 to heavy vehicles, before pooling all the counts.

Greenness: We computed this metric as the ratio of the area of green (i.e., numerator; any vegetation) to grey spaces (i.e., denominator; all impervious surfaces such as roads, buildings, and pavements), making it a relative measure. We used the most recent high-resolution map (0.30 m spatial resolution) created for our study region's (Singapore) terrestrial ecosystems by Gaw et al. (2019). Previous studies highlighted the importance of using a multiple scale approach when studying biodiversity (e.g., Priyadarshana et al., 2024). Therefore, we assessed greenness surrounding the road verges for six different spatial scales (i.e., local scales: 50, 100, and 250 m radii; and landscape scales: 500, 750, and 1000 m radii). This was done using QGIS (www.qgis.org/; version 3.32) and the 'landscapemetrics' package (Hesselbarth et al., 2019). These scales were defined as local and landscape based on previous

Table 1
The observed variables and their variations (±standard deviation).

Observed variables	Mean ± SD	Minimum	Maximum
Butterfly abundance (individuals)	13.10 ± 4.84	2	24
Butterfly richness (species)	7.37 ± 2.99	1	14
Verge size (m^3, width × height × length)	91.89 ± 30.75	16.72	167.23
Structural complexity (m, standard deviation of the vegetation height)	0.70 ± 0.35	0.11	1.51
Nectar-floral diversity (Shannon diversity index of the spatial extent of flowers in butterfly nectar plants)	2.10 ± 0.72	0.68	3.93
Plant richness (morphospecies)	17.60 ± 4.81	8	28
Traffic density (weighted number of vehicles)	190.36 ± 55.49	94	288
Greenness at 50 m radius (dimensionless ratio of green/grey cover)	0.89 ± 0.55	0.11	2.37
Greenness at 100 m radius (dimensionless ratio of green/grey cover)	0.81 ± 0.54	0.14	2.30
Greenness at 250 m radius (dimensionless ratio of green/grey cover)	0.78 ± 0.46	0.081	2.28
Greenness at 500 m radius (dimensionless ratio of green/grey cover)	0.68 ± 0.34	0.085	1.86
Greenness at 750 m radius (dimensionless ratio of green/grey cover)	0.72 ± 0.37	0.030	1.74
Greenness at 1000 m radius (dimensionless ratio of green/grey cover)	0.76 ± 0.42	0.026	2.42

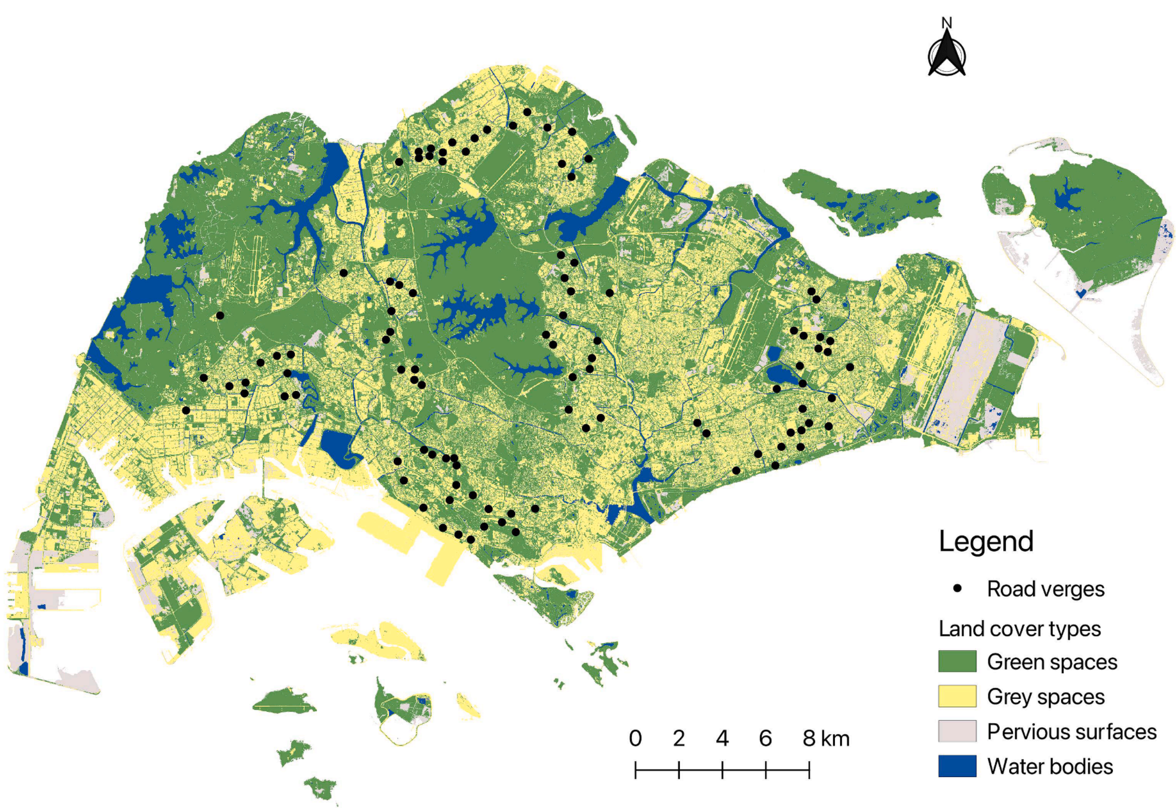

Fig. 2. Map of the road verges (N = 101) across Singapore included in this study. The land cover data was sourced from Gaw et al. (2019).

studies in modified landscapes, which reflect the typical foraging and dispersal distances for butterfly reproduction (Nowicki et al., 2014; Priyadarshana et al., 2024).

2.3. Statistical analysis

We used confirmatory path analyses to test our causal hypotheses (Shipley, 2009), in which the direction of causality among observed variables was hypothesised *a priori* based on our understanding of the study system and previous urban ecology studies.

2.3.1. Construction of a directed acyclic graph (DAG) and testing for the conditional independence claims in it through a theoretical simulation

Our causal hypotheses consider both direct and indirect effects of observed variables on butterflies within road verges (see *H1–H4* in the introduction), suggesting a complex network of interconnectedness among the observed variables. Certain variables serve as both causal and affected variables (Fig. 1; Appendix: Table A1). To inform this, we constructed a directed acyclic graph (DAG) that connects observed variables according to our causal hypotheses, allowing us to integrate all hypotheses into a single causal network (Fig. 1; Appendix: Table A1; Grace et al., 2012). This DAG illustrates the causal and conditional dependence, as well as causal and conditional independence among our observed variables (Appendix: Table A2).

To evaluate these claims of causal dependence and independence, we conducted 'd-separation' tests. This is a mathematical operation on a DAG to translate between the concepts of causal and statistical dependence or independence (Shipley, 2000, 2016). If the data are causally generated as in our proposed DAG, then all the 'd-separation' claims in it (Appendix: Table A2) should be reflected by equivalent conditional independent relationships in the statistical population of realised data (Shipley, 2000, 2016). This does not depend on the type of the probability distribution or whether the relationships are linear or nonlinear (Shipley, 2009, 2016). We employed a simulation to validate whether the predicted conditional independent relationships in our DAG could conform within the observed data (Shipley, 2016). We conducted 'd-separation' tests by simulating data for our observed variables from a normal distribution, assuming linearity and mutual independence of observations (Shipley, 2009, 2016). This process confirmed that our proposed DAG can be used to test our causal hypotheses as the Fisher's C statistic follows a Chi-square ($\chi 2$) distribution (for more details, see our annotated R scripts in Priyadarshana, 2025).

2.3.2. Fitting structural equation models to test the causal hypotheses

We fitted the above DAG with the observed variables using covariance-based Structural Equation Models (SEMs). The use of SEM offers several advantages over a univariate approach, enabling simultaneous evaluation of hypotheses that include direct and indirect effects (Grace, 2006). We built SEMs with Maximum Likelihood (ML) estimators using the 'sem' function in the 'lavaan' package (Rosseel, 2012) in the R statistical environment (www.r-project.org/; version 4.2.2). We used the 'Satorra-Bentler correction' to correct for non-normality and heteroscedasticity of the residuals. Our sampled road verges were located within six clusters (Fig. 2). To account for this we corrected our SEMs for this nested structure using the 'svydesign' function in the 'lavaan.survey' package (Oberski, 2014). Finally, we evaluated overall fit using $\chi 2$ statistics (see above) as a measure of the discrepancy between observed and model-implied covariance matrices (Shipley, 2016). We scaled all the path coefficients reported in the SEMs by means and standard deviations, allowing us to compare the strength of direct and indirect causal links. The strength of an indirect effect for an observed variable was calculated by multiplying the path coefficients associated with each indirect path and summing them together (Appendix: Table A1). The total effect of an observed variable was calculated by summing direct and indirect path coefficients. We also subtracted the non-causal spurious effects when assessing the indirect and total effects of floral diversity and road verge size on butterfly abundance and richness (Appendix: Table A1, for more details).

SEMs were fitted separately for each spatial scale (six scales; 50, 100, 250, 500, 750, and 1000 m radii, each with a different value for greenness), as well as for both butterfly abundance and species richness ($6 \times 2 = 12$ SEMs). This was done to identify the best scale that explains butterfly diversity by comparing AICc values of the models. We decided not to incorporate both abundance and species richness into a single model, as our causal hypotheses apply to each of these metrics individually. For simplicity, we show only the 500 m spatial scale for which the greenness data was most influential in the main text (as judged by the lowest AICc value; Appendix: Table A3).

2.3.3. Sensitivity analysis

Testing for the relative importance of the proportion and richness of nectar-flowering plants on butterflies.

The Shannon diversity index calculated for nectar-floral diversity effectively integrates both the proportion (evenness) and richness of flowering plants in a verge (see above). To determine how these two metrics independently influence butterfly diversity we fitted separate SEMs for each metric and compared their model fit against the SEMs for diversity using the AICc values (Appendix: Table A3).

Testing for potential causal heterogeneity in the structural equation models.

The sampled road verges were located across three different road types with speed limits of 50, 60, and 70 km/h. Traffic density, butterfly abundance and richness may vary across these road types (see *H3* in the introduction). To account for this, we compared the mean variances in traffic density and butterfly abundance and richness across these three road types using ANOVA tests. These tests identified that the mean traffic density, as well as the mean butterfly abundance and richness, varied between the three road types (see *H3* in the results). As such, the SEM path coefficients could significantly differ indicating potential causal heterogeneity in our SEMs. To test for this, we used the 'multi-group' SEM approach (Shipley, 2016). Firstly, we ran SEMs forcing each path coefficient to be equal across the three road types. We then ran SEMs allowing each path coefficient to vary across the road types. In all cases, SEMs accounted for non-normality, heteroscedasticity, and for the clustered placement. Finally, we conducted likelihood ratio tests to compare these models. We applied this procedure for all models, for each spatial scale, and for both butterfly abundance and species richness.

3. Results

In total, we recorded 1320 nectar-feeding events from 56 butterfly species (Appendix: Table A4) on 96 floral species (Appendix: Table A5). All butterflies were commonly found species belonging to five families (Appendix: Table A4): Nymphalidae (21), Lycaenidae (11), Hesperiidae (10), Pieridae (9), and Papilionidae (5). Among the nectar-producing flora, there were only six native plant species with all the others (90) being non-natives (Appendix: Table A5). The sampled road verges had an average width of 2.62 m (standard deviation = 0.91 m; minimum = 0.78 m; and maximum = 4.46 m) and an average height of 1.17 m (standard deviation = 0.48 m; minimum = 0.64 m; and maximum = 1.71 m). Variation among the observed variables is summarised in Table 1. Nectar-feeding butterfly abundance and richness in our dataset were strongly correlated (Pearson r = 0.95), leading to qualitatively similar SEM results for both biodiversity measures.

(H1). Nectar-floral diversity has a direct positive effect on butterflies within road verges, whereas overall plant richness has an indirect positive effect. We found evidence supporting this hypothesis, as nectar-floral diversity within the road verges showed a direct positive effect on butterfly abundance and species richness (Fig. 3, for 500 m scale; Appendix: Figs. A4-A8, for other five scales; Appendix: Tables A6-A11, for all six scales). We observed similar results when fitting the models separately

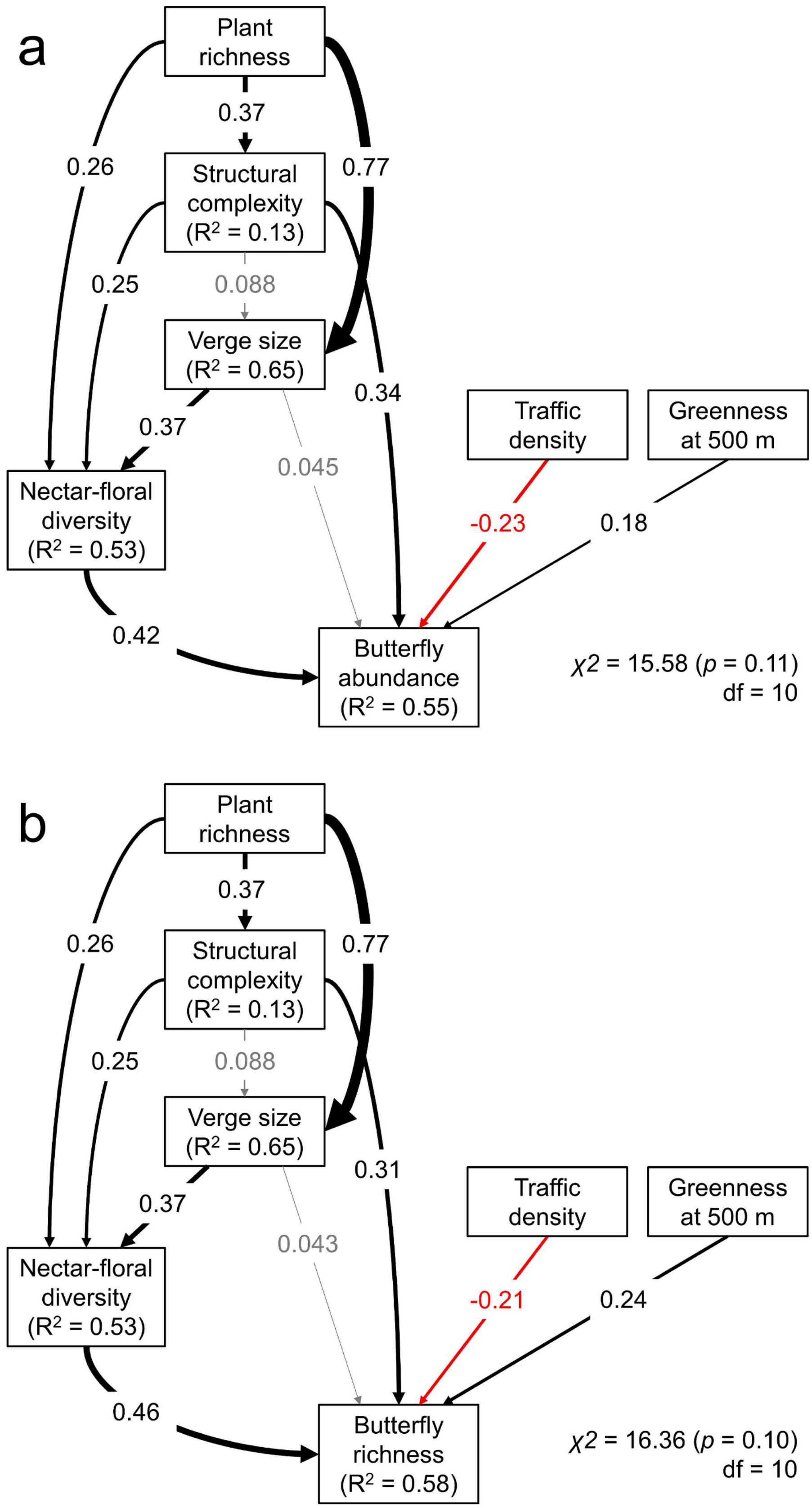

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Fig. 3. Path diagrams illustrating direct and indirect causal links between observed variables at the 500 m scale for butterfly **(a)** abundance and **(b)** richness. Standardised direct effect sizes are indicated along the arrows, representing the direction of causal links and proportional to the standardised effect sizes. Black arrows indicate significantly positive effects, red arrows indicate significantly negative effects, and lightly shaded arrows indicate non-significant effects (alpha level of 0.05). R^2 = the proportion of variance in the affected variable that is explained by the causal variables. $\chi 2$ = Chi-square. df = Degree of freedom. For detailed statistics, including indirect and total effects between observed variables, see Appendix: Tables A9.1–2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

using the proportion (evenness) and richness of nectar-producing plants, but these models did not explain variation in butterfly diversity as effectively as those incorporating the nectar-floral diversity metric (Appendix: Table A3). Plant richness within the road verges had a positive indirect effect on butterfly abundance and species richness by increasing nectar-floral diversity, structural complexity, and the size of the road verges (Fig. 3; Appendix: Figs. A4-A8; Appendix: Tables A6-A11). Interestingly, the direct effect of floral diversity, and the indirect effect of plant diversity, on butterflies were comparable in strength (Fig. 3; Appendix: Figs. A4-A8; Appendix: Tables A6-A11).

(H2). The size and structural complexity of road verges have both direct and indirect positive effects on butterflies. Contrary to our hypothesis, we did not observe a significant direct positive effect of road verge size on butterfly abundance and richness. However, it had an indirect positive effect on both butterfly abundance and richness, mediated through changes mostly in nectar-floral diversity (Fig. 3; Appendix: Figs. A4-A8; Appendix: Tables A6-A11). As we hypothesised, the structural heterogeneity within the road verges had both a direct and indirect positive effects on butterfly abundance and richness (Fig. 3; Appendix: Figs. A4-A8; Appendix: Tables A6-A11). This indirect effect was mainly mediated through increases in the nectar-floral diversity, but was weaker than its direct effect on butterflies.

(H3). Traffic density has a direct negative effect on butterflies within road verges. This hypothesis was supported by our SEM results. We observed a direct negative effect of traffic density on both butterfly abundance and species richness (Fig. 3; Appendix: Figs. A4-A8; Appendix: Tables A6-A11). Our comparison tests of the mean traffic density and the mean butterfly abundance and richness across different road types (50, 60, and 70 km/h) confirmed this hypothesis. We found higher traffic density on roads with higher maximum speed limits, and both butterfly abundance and richness decreased with higher speed limits (Appendix: Fig. A9). However, butterfly abundance and richness were not significantly different between roads that had 60 and 70 km/h speed limits. Furthermore, there was no statistically significant causal heterogeneity associated with the three road types as judged by *p*-values of the likelihood ratio tests (Appendix: Table A12).

(H4). Urban greening has a direct, but scale-dependent, positive effect on butterflies within road verges. Consistent with our hypothesis, increasing the area of green spaces surrounding the road verges (i.e., ratio of green/grey cover) had a direct positive effect on butterfly abundance and species richness (Fig. 3; Appendix: Figs. A4-A8; Appendix: Tables A6-A11). However, this effect was scale-dependent and was only statistically significant at the landscape (500, 750, and 1000 m radii) and not at the local scales (at 50, 100, and 250 m radii).

4. Discussion

While urban green spaces offer potential refuges for wildlife, the ecological resources of these areas, and in particular that of road verges, remain understudied (Veerkamp et al., 2021). Our results provide insights into the complex relationships among local habitat and landscape features on butterfly diversity in highly urbanised areas. We showed direct positive effects of floral diversity and structural complexity within road verges, and surrounding green spaces on butterfly diversity, but negative effects of traffic density. The size and plant richness of road verges also had a positive but indirect effect on butterflies, mediated through the effect of these variables on nectar-floral diversity. We provide strong evidence for the first time that road verges in tropical cities can support urban butterflies, even when planted with non-native species.

4.1. Nectar-floral diversity within road verges directly influences butterfly diversity

As we hypothesised, nectar-floral diversity increased butterfly abundance and richness. This was not surprising given that our analysis focused on nectar-feeding butterflies. Nectar availability is one of the most important factors influencing the presence of butterflies in many habitat types, including road verges, urban parks, and gardens (Baldock et al., 2019; Horstmann et al., 2024; Saarinen et al., 2005; Wallisdevries et al., 2012). In addition, previous studies have also shown that butterflies are generalists nectar-feeders, particularly in modified landscapes, allowing them to utilise many plant species (Baldock et al., 2019; Jain et al., 2016; Pla-Narbona et al., 2022). It was, however, remarkable to find that even these small-scale artificially planted road verges have the potential to support butterfly communities (see Battle et al., 2021). Our results showed that nectar-floral diversity increased as more plant species were planted within the road verges, so that plant richness indirectly increased the butterfly diversity. Higher plant/floral diversity creates more diverse nectar sources, which are crucial for pollinating insects to support their physical body condition, flight activity, reproductive success, and survival rates (Gavini et al., 2021; Lebeau et al., 2016). However, it is important to note that this relationship between plant richness and nectar-floral diversity could be mediated through other unmeasured variables, such as plant age, disturbance history, and hydrological conditions within the road verges.

Almost all the flowers utilised by the adult butterflies in our study were non-native species. A previous study conducted in Singapore also reported that butterflies in urban parks preferred non-native flowers more than native flowers (Jain et al., 2016). Green spaces in urban areas are often planted with non-native flowering plant species that flower more consistently than seasonally flowering native species. While this is largely for aesthetic reasons it also provides more consistent nectar resources for butterflies. Previous studies have also suggested that such non-native species, especially when planted near forest areas, could create 'ecological traps' for forest-dependent butterflies, attracting them to leave forest habitats with the greater nectar availability (Schlaepfer et al., 2002). However, in our study road verges were located in highly urbanised areas that do not have forest areas nearby. Moreover, we did not observe any forest-dependent butterflies nectar-feeding within our sampled road verges. Similarly, Vanderstock et al. (2022) also found no evidence of spillover of flower-visiting insects between gardens and forest fragments in urban areas. Previous studies have highlighted the importance of planting native over non-native species to support biodiversity in urban areas (Baldock et al., 2019; Berthon et al., 2021; Chong et al., 2014; Phillips et al., 2020). This may be particularly important for larval stages that depend on native plants for food. However, harsh conditions such as increased soil temperatures, compaction, pollution, and nutrient imbalances near concrete and asphalt roads often make it difficult to grow native plant species along road verges (Calfapietra et al., 2015). Our results highlight the importance of non-native species within road verges for urban butterflies. However, the focus on adult butterflies may have obscured a reduced role for road verges dominated by non-native plants for larval stages. Ideally, a mixture of both native and non-native plants would provide even greater benefits for urban insect pollinators.

4.2. Higher variability in vegetation height of road verges directly influences butterfly diversity

Our results supported this hypothesis confirming a positive effect of structural complexity (i.e., variation in vegetation height) within road verges on butterfly abundance and richness, both directly and indirectly. Higher variability in vegetation height changes the shape of road verges, potentially creating more favourable conditions for butterflies than uniform, flat vegetation. The greater variation in vegetation height within road verges may also indicate lower management intensity (Marche et al., 2022; Phillips et al., 2019), as it suggests that some areas are left uncut or have regrown after the previous cutting. Together these effects may directly influence butterfly diversity (Horstmann et al., 2024; Munguira & Thomas, 1992; O'Sullivan et al., 2017; Valtonen et al., 2006). For example, these practices could create different microclimatic conditions (e.g., insulation, temperature, humidity, and light intensity) across road verges that butterflies may prefer (He et al., 2022). Similar results have also been found for butterflies when crops with varying height are grown in farmlands (Priyadarshana et al., 2021). Greater height variability might also offer protection from traffic and predators. For instance, taller vegetation may act as a physical barrier, mitigating the impact of the turbulence from passing vehicles and providing cover from predators such as birds (Phillips et al., 2021; Saarinen et al., 2005).

The indirect effect of verge vegetation height is mainly mediated through nectar-floral diversity. We often observed that regrown areas had more flowers compared to uniformly flat road verges. Additionally, our results suggested that higher variation in vegetation height occurred when more plant species were grown within the road verges, which also indirectly influenced butterfly diversity. This could be due to the diverse environmental conditions created by variation in plant growth rates and differences in cutting regimes for different plant species.

4.3. Road verge size indirectly influences butterfly diversity

Contrary to our hypothesis, we did not find a direct positive effect of road verge size (i.e., its volume) on butterfly diversity. Instead, our causal path analysis revealed an indirect positive effect of road verge size on butterfly diversity, primarily mediated through changes in nectar-floral diversity. Previous studies have shown positive correlations between the size of road verges (but often measured by verge width) and insect diversity (Horstmann et al., 2024; Phillips et al., 2020 and references cited within). These studies have attributed such positive correlations to favorable biotic (e.g., nectar abundance and diversity) and abiotic (e.g., insulation, temperature, humidity, and light intensity) factors associated with increased verge size, though they were unable to disentangle the effects of each factor. Our results, however, provide deeper insights into how verge size influences butterfly diversity. We found that this is driven primarily through increasing nectar-floral diversity. Moreover, we found no support for the hypothesis that structural complexity of the verges increases road verge size. This finding is important when considering the management of road verges. For example, increasing the size of road verges is not always feasible for city planners to implement, due to the limited land area and requirements for other uses, e.g., pedestrian walkways. However, our results suggest that smaller road verges can still effectively support butterfly diversity by enhancing nectar-floral diversity, thus partially compensating for their limited size. Our results further suggest that the size (i.e., volume) of road verges can be increased by planting more species, particularly tall and fast-growing plants, which also enhances nectar-floral diversity and supports greater butterfly diversity. Therefore, maintaining patches of taller and uncut vegetation could be crucial to support butterflies (Horstmann et al., 2024; Marche et al., 2022; Phillips et al., 2019; Valtonen et al., 2006), especially within narrow road verges, and could reduce the maintenance costs to local authorities. However, taller vegetation may need to be avoided in areas where clear sightlines are essential for driver safety, such as at traffic merge points.

4.4. Traffic density directly reduces butterfly diversity

Our causal path analyses showed a direct negative effect of traffic density on butterfly diversity within road verges, regardless of the maximum speed limits of 50, 60, or 70 km/h. Additionally, our comparison tests across these road types showed that both butterfly abundance and richness decline as the speed limits increased. Traffic density could disrupt butterflies utilising the road verges through a number of mechanisms outside of simple physical collisions that kill flying adults. For instance, turbulence from passing vehicles can significantly disrupt butterfly nectar feeding and make it harder for them to fly across the roads (Horstmann et al., 2024; Phillips et al., 2019, 2020, 2021). Road verges are also regularly exposed to various forms of traffic pollution, such as light, noise, exhaust fumes, and heavy metals, which also can directly or indirectly affect both plants and butterflies (Calfapietra et al., 2015; Moroń et al., 2012; Phillips et al., 2019, 2020, 2021). For example, Girling et al. (2013) demonstrated that exposure to diesel exhaust alters the chemical composition of floral scents, and thus affects insect pollinators' ability to locate flowers for foraging.

4.5. Landscape-scale green spaces, but not local-scale ones, directly influences butterfly diversity

As we hypothesised, surrounding urban green spaces directly influenced the butterflies utilising road verges. However, this effect was scale-dependent: landscape-scale (500, 750, and 1000 m radii) greenness had a statistically significant impact, but local-scale (50, 100, and 250 m radii) greenness did not. These green spaces can offer a variety of nectar resources and larval host plants for butterflies, and help regulate microclimatic conditions (e.g., insulation, temperature, humidity, and light intensity) (Baldock et al., 2019; Clark et al., 2007; Cooper et al., 2024; Jain et al., 2016; Koh & Sodhi, 2004). Interestingly, we rarely observed egg-laying and basking butterflies within road verges, possibly due to the poor representation of native plants. It is likely that the butterflies we observed in the road verges utilise specific plants within the surrounding vegetation, rather than plants within the road verges, as their larval host plants (Clark et al., 2007; Koh & Sodhi, 2004). They may also find relatively undisturbed areas within the surrounding green spaces for resting and basking. This scale-dependent effect could be caused by the greater availability of relatively undisturbed resources at the landscape-scale compared to the local-scale (Aguilera et al., 2019; Clark et al., 2007; Nowicki et al., 2014), especially considering the closeness of the verges to main roads. For example, patches of natural vegetation are more likely to be present at the landscape-scale than at the local-scale. A previous study conducted within the same landscape has also shown that natural vegetation is more important than cultivated vegetation for butterflies (Chong et al., 2014). These results particularly highlight the importance of considering spatial scales in urban planning and management efforts aimed at supporting biodiversity. For example, studying the landscape-scale characteristics that support biodiversity and integrating them into local-scale initiatives, while ensuring connectivity of vegetation across each scale, could provide greater benefits for urban biodiversity.

5. Conclusions and policy implications

As urbanisation continues to grow, incorporating biodiversity-friendly practices into urban planning and management strategies will be crucial for the sustainable coexistence between humans and wildlife. We provide evidence that road verges next to main roads can benefit butterflies, an often used taxa for monitoring urban biodiversity. These findings have specific implications for designing, planning, and management of road verges and urban wildlife conservation strategies.

First, we demonstrate that small structural adjustments within road verges, such as enhancing floral diversity and maintaining varied vegetation heights, can significantly benefit insect pollinators like butterflies without having to increase verge width. Planting a mix of both native and non-native flowering plants that bloom at different times of the year may be particularly valuable for butterflies by increasing floral diversity, providing a continuous nectar supply for adults, and providing native host plants for larvae (Berthon et al., 2021). Importantly, we showed that for foraging adults, increased floral diversity in non-native plants can deliver many benefits to urban butterflies even in the absence of native plants. Maintaining varied vegetation heights within road verges may also enhance nectar-floral diversity, create favourable microhabitats for invertebrate pollinators, and provide protection from disturbances such as traffic turbulence and predators. Selective cutting regimes that take advantage of a more rotational management approach that allow verges to grow taller and flower would provide greater benefits to these taxa (Wintergerst et al., 2021). This may be especially important for narrow road verges where widening them is not an option due to limited available space. Second, incorporating green spaces into urban landscapes at various spatial scales and increasing the connectivity between them must also be considered to facilitate the persistence and movement of insect pollinators. These managed urban green spaces can provide essential ecosystem services, such as mitigating the urban heat island effect (Bowler et al., 2010), supporting residents' mental health (van den Bosch & Ode Sang, 2017), and increasing the value of residential real estate (Teo et al., 2023). Third, careful consideration of traffic management measures is crucial to minimise disturbances and support urban biodiversity. However, reducing speed limits to benefit biodiversity may not be feasible given the need for transportation efficiency. Promoting awareness among citizens about these factors affecting biodiversity may at least go some way toward benefiting biodiversity. Educating people that slower traffic lanes, particularly in residential areas where they also reduce pedestrian risks, combined with less-cut and more flower rich verges, which are more cost-effective to manage, will result in higher biodiversity could reshape the traditional perception of an ideal city as purely efficient and manicured. Ultimately, collaborative creation of urban green spaces that accounts for the competing interests of citizens, community stakeholders, scientists, and policymakers may be crucial in leading to more resilient and ecologically sustainable cities (Pickett et al., 2022).

CRediT authorship contribution statement

Tharaka S. Priyadarshana: Writing – review & editing, Writing – original draft, Visualisation, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualisation. **Ben A. Woodcock:** Writing – review & editing, Validation, Methodology, Conceptualisation. **Anuj Jain:** Writing – review & editing, Validation, Conceptualisation. **Carlos Martínez-Núñez:** Writing – review & editing, Validation, Conceptualisation. **Eben Goodale:** Writing – review & editing, Validation, Conceptualisation. **Emilio Pagani-Núñez:** Writing – review & editing, Validation, Conceptualisation. **Friederike Gebert:** Writing – review & editing, Validation. **Janice S.H. Lee:** Writing – review & editing, Validation. **Eleanor M. Slade:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualisation.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2025.105335.

Data availability

All the data and annotated source codes to reproduce our results are publicly available via the Digital Repository of Nanyang Technological University (DR-NTU), at https://doi.org/10.21979/N9/ZRDFUN (Priyadarshana, 2025).

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