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Global wetland biodiversity declines and compositional shifts under urbanization

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Abstract

Urbanization is rapidly transforming wetlands worldwide, threatening biodiversity. The lack of a global synthesis of wetland biodiversity responses to urbanization hinders biodiversity-informed urban planning. We conduct a global meta-analysis, quantifying wetland biodiversity responses to urbanization (343 comparisons of urbanized and non-urbanized reference sites from 124 studies). Wetland biodiversity loss is substantial – with urbanization causing local loss of one in three taxa and reducing Shannon diversity by ~25%. Declines were pervasive across spatial scales, national wealth indicators and the intactness of reference locations, but greatest for river and amphibian communities. Urbanization significantly altered species composition, especially for tropical rainforest and fish communities, but did not consistently drive biotic homogenization. Evidence was concentrated in temperate and high-income regions, highlighting critical knowledge gaps in biodiverse tropical and low-income regions. These findings reveal context-dependent biodiversity responses to urbanization, identifying habitat and taxa with the greatest sensitivity to urban development, informing wetland conservation worldwide.

Introduction

Urbanization affects biodiversity through direct and indirect pathways by altering land use, human activities, resource consumption, and pollution[1], with urban expansion particularly concentrated along coastlines, lakes, and major river systems[2]. As a result, wetland ecosystems are at the frontiers of urban growth, facing substantial pressure that drives complex changes in biodiversity[3,4]. The biodiversity changes underscore the urgency of aligning urban planning with the objectives of the Ramsar Convention, the Kunming–Montreal Global Biodiversity Framework and United Nations Sustainable Development Goals[5–7]. Although previous global and regional syntheses have examined the effects of urbanization on biodiversity across terrestrial and aquatic ecosystems[8–10], existing studies have often focused on specific taxa, ecosystem types (typically terrestrial) or geographic regions[11–16]. Consequently, a consensus on the general patterns of wetland biodiversity responses to urbanization is lacking at the global scale, and comparative understanding across wetland types, biological groups and geographic contexts remains limited.

Current evidence shows that urbanization can lead to the proliferation of generalist and disturbance-tolerant species and the decline of sensitive taxa, thereby reshaping species composition and altering community similarity[14,17–20]. While some studies have reported substantial biodiversity losses and increasing biotic homogenization in urbanized wetlands[21–23], others have documented enhanced species richness and biotic differentiation along urban gradients[24–26]. This marked heterogeneity in responses indicates that the consequences of urbanization for wetland biodiversity are highly context-dependent.

This heterogeneity in response can arise from numerous factors, including focal taxonomic group, habitat type, spatial scale, climatic conditions, and socioeconomic status[8,27–29]. First, biodiversity responses to urbanization may vary among biological groups because species differ in their ecological requirements and tolerances to habitat alteration[10,15]. Previous studies have reported heterogeneous responses across vertebrates, invertebrates, plants, and microorganisms, indicating that the effects of urbanization are often heterogeneous rather than consistent within broad taxonomic groups[10,15]. Second, wetland type may influence biodiversity responses because wetland habitats vary in the extent to which urbanization alters their physical and hydrological characteristics of wetlands[30,31]. Riverine wetlands, for example, are often strongly modified by channelization, altered flow regimes, and pollutant transport associated with urban development, which can drive substantial declines in species richness and shifts in community composition[32]. In contrast, inland vegetated wetlands, such as peatlands, may experience more limited urban impacts depending on surrounding land use and connectivity[21]. Third, spatial scale critically alters the detected signal, fine-scale studies often capture differentiation due to local disturbance filters, whereas broad-scale analyses tend to reveal regional homogenization driven by the widespread dominance of generalist species[33]. Fourth, climatic conditions may modulate the sensitivity of biodiversity in wetlands to urbanization because baseline hydrological conditions and environmental constraints differ among climate zones, arid-region wetlands may experience amplified water stress and salinization[34], whereas tropical wetlands face synergistic pressures from land use and climate warming because many tropical species already exist near their upper thermal tolerance limits[35,36]. Finally, socioeconomic context may modulate the vulnerability of wetlands to urbanization. At the country level, wetlands in upper-middle-income countries may be more vulnerable to biodiversity loss under urbanization because environmental regulation and restoration capacity often lag behind the pace of urban expansion[37], whereas wetlands in high-income group countries may experience relatively weaker biodiversity responses under comparable levels of urbanization due to stronger protection, pollution control, and restoration measures[38], although the strength and effectiveness of such policies can vary over time and among jurisdictions. These five factors can be viewed as potential moderators underlying the heterogeneity observed in wetland biodiversity responses to urbanization globally. Examining whether biodiversity responses differ significantly across ecological and socio-environmental contexts is essential for understanding the context dependency of urbanization impacts and for identifying which wetland systems and biological groups are most vulnerable to urbanization.

Our critical knowledge gaps on response of wetland biodiversity under urbanization result from two persistent limitations in the current evidence base. First, most studies conducted at local or regional scales focus on specific wetland types or biological groups, limiting the identification of general, cross-system patterns[11–16]. In addition, substantial variation in study design (for example the geographical extent of studies and the type of reference sites selected to compare with urban locations), biodiversity metrics, and proxies used to characterize urbanization further complicates cross-study comparisons[11–16]. Together, these limitations impede our ability to determine whether urbanization drives consistent global patterns of wetland biodiversity change or whether responses are fundamentally contingent on biological group,

wetland type, spatial scale, climate zone and country-level socioeconomic contexts. This uncertainty restricts the development of effective, generalizable conservation strategies that support global biodiversity and sustainability targets. A comprehensive global synthesis that quantitatively integrates both alpha- and beta-diversity dimensions across moderating factors is therefore an urgent prerequisite for evidence-based policy and management aimed at safeguarding wetland biodiversity under urbanization.

Here we present the first global quantitative synthesis of urbanization impacts on wetland biodiversity and examine how biodiversity responses vary across ecological, geographical and socioeconomic contexts. We synthesized data from 124 studies employing different urbanization frameworks, including urbanization-gradient designs and direct urban-reference comparisons. To standardize comparisons among studies, we contrasted the two extreme ends of urbanization within each study, representing the highest and lowest levels of urban influence and yielding 343 comparisons worldwide. Reference sites therefore represented the least urbanized and least human-impacted wetlands available within each study rather than necessarily pristine systems, and we thus accounted for variation in reference site condition. Using log-response ratios (LRRs) as effect sizes, and multilevel random-effects meta-analytic models, we quantified urbanization effects across four dimensions of wetland biodiversity: taxonomic richness, Shannon diversity, biotic homogenization and shifts in species composition. We further tested whether biodiversity responses varied across biological groups, wetland types, spatial scales (the maximum geographic extent of a study, measured as the greatest distance between any urbanization and reference sampling sites), Köppen climate zones, World Bank's income groups and reference site types. Our results are robust to publication bias (Supplementary Information Section 3) and reveal widespread declines in taxonomic richness and Shannon diversity and strong shifts in species composition, but no consistent evidence of biotic homogenization, while highlighting substantial variation across biological groups, wetland types and Köppen climate zones.

Results

Global patterns of studies on wetland biodiversity under urbanization

A total of 343 urbanization–reference comparisons were included in the meta-analysis, encompassing nine biological groups and six wetland types (Fig. 1a). Most comparisons focused on macroinvertebrates (n = 141), followed by fish (n = 56) and bacteria (n = 40; Fig. 1b). The identified studies were primarily conducted in river ecosystems (Fig. 1c), which accounted for 69% of the identified effect size records. Most comparisons were conducted at 10–50 km spatial scale (n = 149; Fig. 1d). Based on World Bank income groups, most comparisons derived from high- and upper-middle-income groups, whereas low- and lower-middle-income groups were underrepresented (Fig. 1e). Studies covered all Köppen climate zones (main classes) but were predominantly conducted in two Köppen zone classes, temperate and cold, with relatively few comparisons from tropical, arid and polar regions (although the limited number of studies from polar regions is unsurprising given the rarity of urban areas in this climatic zone; Fig. 1f). Studies had four reference site types: natural vegetation with minimal human impact, semi-natural vegetation with moderate impact, intensively managed non-urban landscapes (e.g. agricultural land), peri-urban. These comparisons provide a global overview of urbanization effects on wetland biodiversity across multiple contexts.

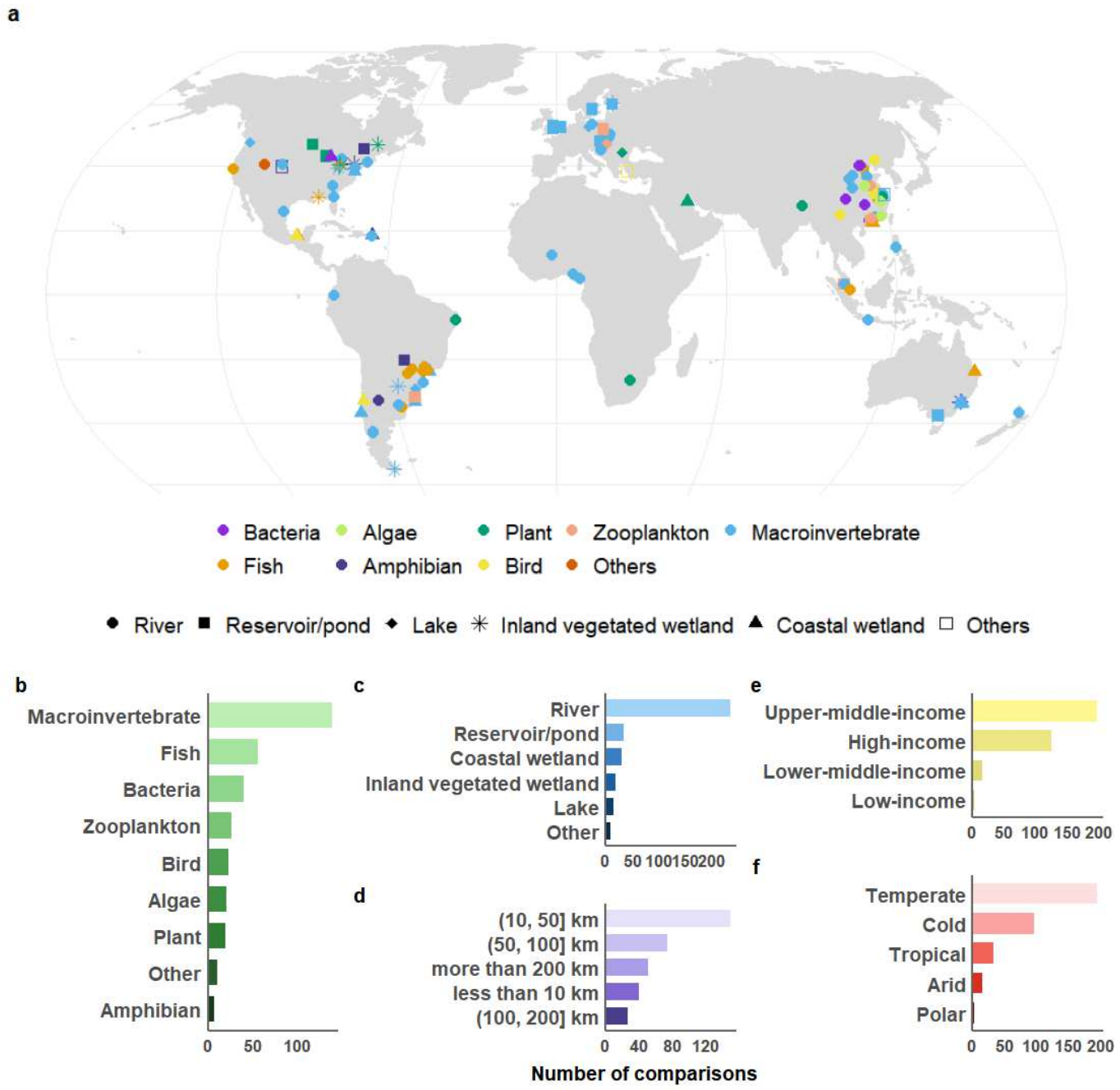


Fig. 1 **Distributions of identified records across wetland types, biological groups, spatial scales, World Bank's income groups and Köppen climate zones. a**, Geographic distributions of identified records classified by biological groups and wetland types. **b-f**, The number of comparisons across biological groups (**b**), wetland types (**c**), spatial scales (**d**), World Bank's income groups (**e**), and Köppen climate zones (five main classes; **f**).

Urbanization drives widespread declines in wetland taxonomic richness and Shannon diversity

We assess the generality and heterogeneity of urbanization effects on taxonomic richness and Shannon diversity across wetlands worldwide. The overall LRR taxonomic richness was significantly negative (LRR = -0.340, 95% confidence interval (CI): -0.491 to -0.309; Fig. 2a), indicating an overall mean decline of approximately 33% under urbanization, with most individual effect sizes distributed below zero (Fig. S5a). The magnitude of taxonomic richness decline differed significantly among biological groups (χ^2 = 25.909, P = 0.001; Table S2). Significant reductions were detected across all biological groups (Fig. 2a). Amphibians

exhibited the strongest decline, with taxonomic richness reduced by 46% (LRR = −0.620, 95% CI: −0.839 to −0.401; Fig. 2a), followed by fish, bacteria, plants, birds, macroinvertebrates, zooplankton and algae (Fig. 2a). Urbanization effects on taxonomic richness also varied among wetland types (χ^2 = 19.218, P = 0.004; Table S2). Significant richness declines were observed in rivers and reservoir/pond ecosystems, whereas other wetland types showed no significant reductions (Fig. 2a). By contrast, taxonomic richness responses did not differ significantly across spatial scales, income groups, Köppen climate zones or reference site types (Table S2).

Consistent with taxonomic richness responses, Shannon diversity declined by approximately 25% under urbanization (LRR = -0.286, 95% CI: -0.382 to -0.190; Fig. 2b), with most individual effect sizes again distributed below zero (Fig. S5b). As observed for taxonomic richness, the magnitude of Shannon diversity decline differed significantly among biological groups (χ^2 = 22.116, P = 0.003; Table S2) and wetland types (χ^2 = 20.919, P = 0.0008; Table S2). Significant reductions were detected in plants, zooplankton, fish, macroinvertebrates and algae (but note insufficient species composition data were available to test amphibian responses; Fig. 2b). Across wetland ecosystems, Shannon diversity declined significantly in rivers (LRR = -0.375, 95% CI: -0.488 to -0.263; Fig. 2b) under urbanization, whereas other wetland types showed no significant reductions (Fig. 2b). No significant differences in LRR Shannon diversity were detected among spatial scales, income groups, Köppen climate zones or reference site types (Table S2).

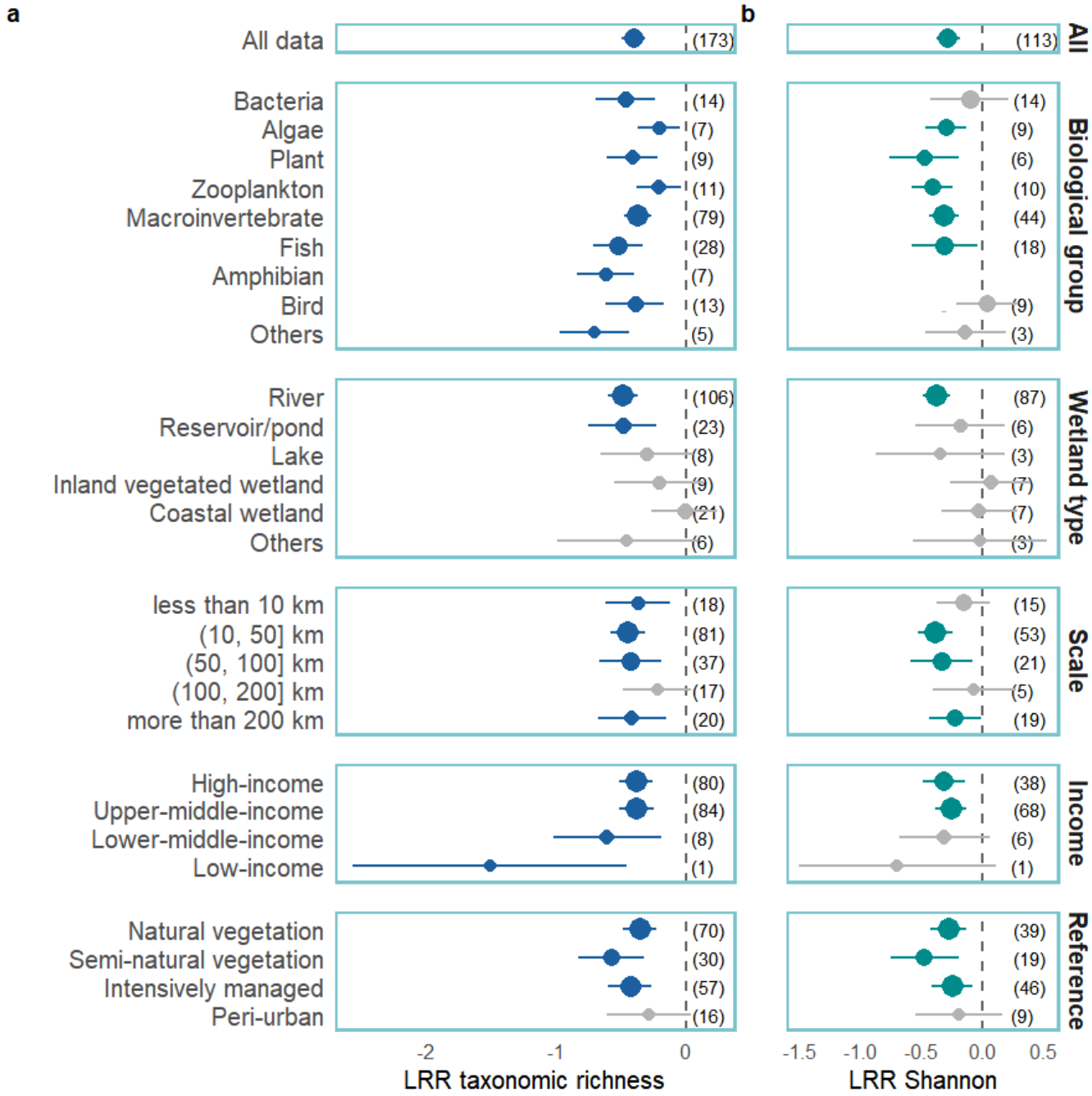


Fig. 2 **Impacts of urbanization on taxonomic richness and Shannon diversity across biological groups, wetland types, spatial scales, World Bank's income groups, and reference site types. a**, log-response ratio of taxonomic richness (LRR taxonomic richness). **b**, log-response ratio of Shannon diversity (LRR Shannon). The global response (all data) is shown in the first row of each panel and is separated by factors in the following rows. The numbers in parentheses inside the box indicate the number of comparisons. For each category, the dot represents the marginal mean computed from the model; dot size is proportional to the number of comparisons included. The error bar shows the 95% confidence interval.

Urbanization shifts wetland species composition without consistent biotic homogenization

We next assessed whether urbanization restructures wetland communities by examining species compositional shifts and biotic homogenization, following the approach proposed by Keck and colleagues[39]. Species composition shift was measured using the LRR shift, estimated as the log-response ratio of the mean distance separating urbanized and reference communities and the mean within-group

distance of urbanized and reference communities in PCoA and NMDS ordination space. Positive LRR shift values indicate that differences between urbanized and reference communities exceed natural within-group variation, reflecting significant species compositional turnover under urbanization. Biotic homogenization was quantified using LRR homogeneity, calculated as the log-transformed ratio of the mean distance in urbanized communities and the mean distance in reference communities in PCoA or NMDS ordination space. Negative LRR homogeneity values indicate biotic homogenization, whereas positive values indicate biotic differentiation.

The overall LRR shift was significantly positive (LRR = 0.514, 95% CI: 0.381 to 0.646; Fig. 3b), indicating that urbanization strongly altered species composition within wetland communities. Most effect sizes were distributed above zero (Fig. S5d), demonstrating widespread species compositional turnover associated with urbanization. The magnitude of compositional shift differed significantly among biological groups (χ^2 = 39.970, P < 0.0001). Fish communities exhibited the strongest compositional shifts (LRR = 0.767, 95% CI: 0.431 to 1.102; Fig. 3b), followed by macroinvertebrates, plants, zooplankton, bacteria and algae (Fig. 3b). Species composition shifts also varied significantly among Köppen climate zones (χ^2 = 24.301, P = 0.003). Significant shifts were detected in Af (Tropical, rainforest), Cfa (Temperate, no dry season, hot summer), Cwa (Temperate, dry winter, hot summer), Cwb (Temperate, dry winter, warm summer), Dfa (Cold, no dry season, hot summer), Dfb (Cold, no dry season, warm summer) and Dwa (Cold, dry winter, hot summer) climate zones, whereas other studied climate zones showed no significant compositional change (Fig. S7). No significant differences in LRR shift were detected among wetland types, spatial scales, income groups or reference site types (Table S2).

By contrast, the overall LRR homogeneity was not significant (LRR = 0.155, 95% CI: -0.044 to 0.355; Fig. 3a), indicating no consistent evidence for either biotic homogenization or differentiation across wetland communities globally. Effect sizes were broadly distributed around zero (Fig. S5c), suggesting substantial variability in community responses among studies. However, responses differed significantly among biological groups (χ^2 = 54.280, P < 0.0001; Table S2). Macroinvertebrate communities showed significantly positive LRR homogeneity values (LRR = 0.473, 95% CI: 0.219 to 0.727; Fig. 3a), indicating community differentiation under urbanization. In contrast, other biological groups showed no significant evidence of either homogenization or differentiation (Fig. 3a). Although bird communities exhibited negative LRR homogeneity values, the analysis was based on a single comparison (n = 1), preventing robust inference regarding homogenization patterns in birds (Fig. 3a). No significant differences in LRR homogeneity were detected among wetland types, spatial scales, income groups, Köppen climate zones or reference site types (Table S2).

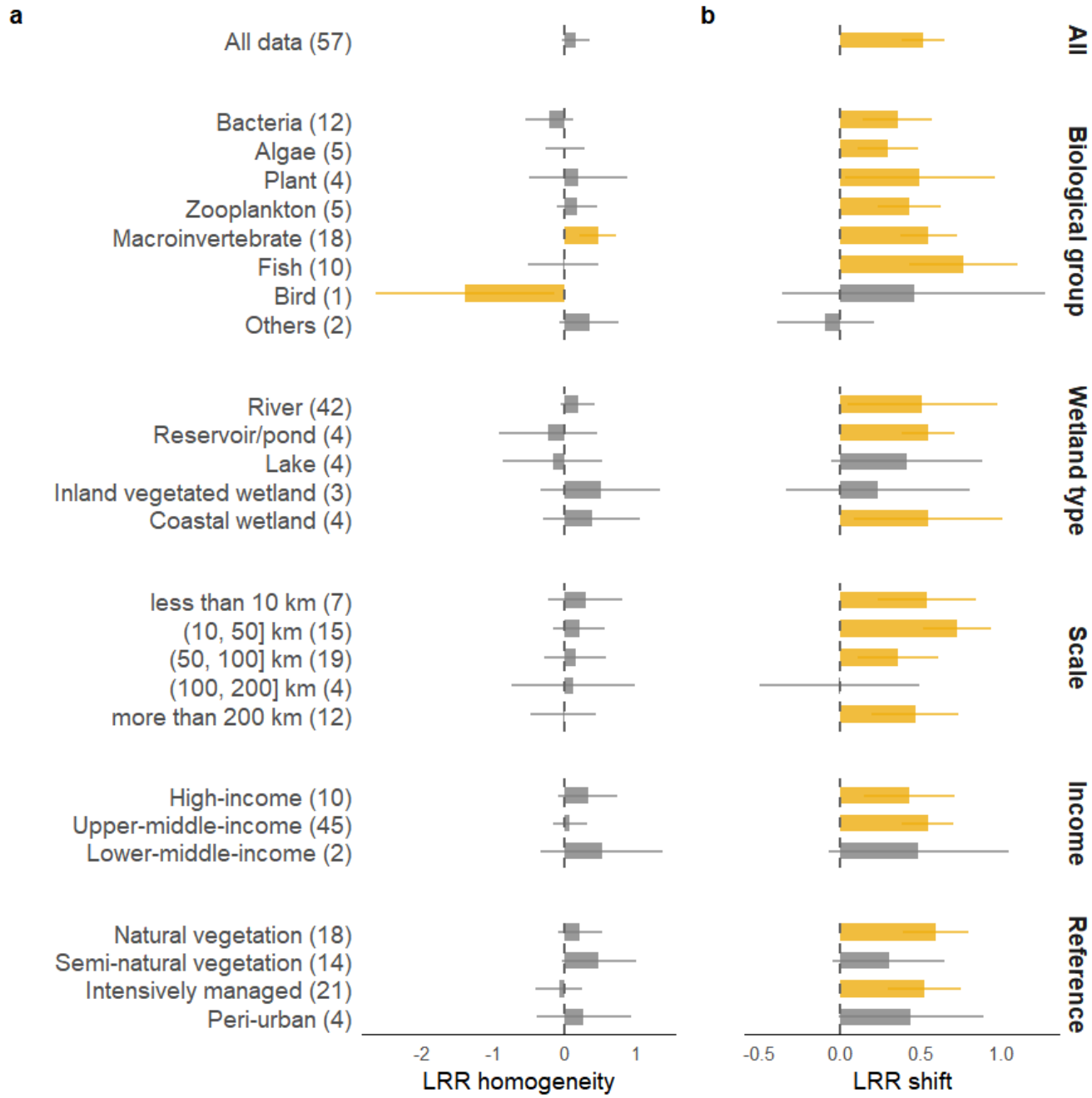


Fig. 3 **Impacts of urbanization on homogeneity and species composition shift across biological groups, wetland types and spatial scales, World Bank's income groups, and reference site types. a**, log-response ratio of homogeneity (LRR homogeneity). **b**, log-response ratio of species composition shift (LRR shift). The global response (all data) is shown in the first row of each panel and is separated by factors in the following rows. The numbers in parentheses on y-axis indicate the number of comparisons. For each category the column represents the marginal mean computed from the model. The error bar shows the 95% confidence interval.

Discussion

Drawing on a global meta-analysis of 343 urbanization–reference comparisons from 124 studies, we show that urbanization markedly reduces taxonomic richness (with on average one in three taxa becoming locally extinct) and Shannon diversity (declining by approximately 25%) and reshapes species composition across diverse wetland ecosystems worldwide (Fig. 2; Fig. 3). However, despite widespread community reorganization, we found no consistent evidence that urbanization drives global biotic homogenization or differentiation in wetland communities (Fig. 3). This deviates from the widely held expectation that

urbanization promotes biotic homogenization across ecosystems[40]. Our findings further demonstrate that wetland biodiversity responses to urbanization vary significantly among biological groups, wetland types and Köppen climate zones (Table S2), suggesting that the ecological consequences of urban expansion are strongly context dependent, with some habitat types and species groups being particularly sensitive and thus in need of greater protection.

Our results reveal that urbanization consistently shifted wetland species composition without producing a corresponding global pattern of biotic homogenization (Fig. 3), and neither compositional turnover nor homogenization responses varied systematically across spatial scales (Table S2). These findings suggest that species turnover under urbanization does not necessarily lead to increasing similarity among wetland communities. While urbanization has traditionally been viewed as a major driver of biotic homogenization[40], recent conceptual developments argue that this expectation may have been overstated and that urban ecosystems frequently generate biotic heterogeneity through metacommunity processes, environmental filtering and diverse management practices[41]. Our findings are consistent with this emerging framework. Contrary to predictions that community re-organization may be strongly scale dependent[33,39], we found no evidence that either compositional shifts or biotic homogenization responses varied systematically across the spatial scales considered in our analysis, suggesting that the processes restructuring wetland communities under urbanization may operate consistently from local to regional extents.

We found that the magnitude of biodiversity responses to urbanization differed substantially among biological groups and wetland types (Table S2), highlighting that urbanization does not affect wetland biodiversity uniformly across ecological contexts. Amphibians exhibited the strongest declines in taxonomic richness (Fig. 2a), likely reflecting their dependence on both aquatic and terrestrial habitats and sensitivity to urban-associated stressors, including habitat fragmentation, disease, invasive fish and water-quality degradation[42–44]. Fish communities showed the largest compositional shifts under urbanization (Fig. 3b), likely driven by the combined effects of biological invasions, hydrological alteration, and declining water quality, which favor tolerant and non-native species over sensitive native taxa[20,45]. Notably, macroinvertebrates are the only biological group exhibiting clear patterns of community differentiation (Fig. 3a), although the underlying mechanisms remain insufficiently understood. Together, these patterns highlight that urbanization does not affect biodiversity uniformly but instead interacts with ecological traits of species to produce taxon-specific outcomes. Similarly, the particularly strong biodiversity declines observed in river ecosystems may be associated with their linear structure and high hydrological connectivity which expose rivers to cumulative upstream disturbances, including pollution, flow alteration, and propagule influx from non-native species[20]. In contrast, lakes, coastal wetlands, and inland vegetated wetlands, show weaker or less consistent responses, potentially due to greater hydrological stability, resilience, or spatial separation from urban expansion fronts[2,30,46].

We further show that the magnitude of species compositional shifts differed significantly among Köppen climate zones (Table S2), with tropical rainforest (Af) regions exhibiting the strongest turnover (Fig. 3b). This pattern may reflect the combined effects of rapid urban expansion and the sensitivity of tropical biota to habitat modification[47], suggesting that urbanization could have especially important conservation consequences in tropical wetlands. Urbanization effects were similar regardless of whether reference wetlands represented relatively pristine ecosystems or the least urbanized sites available within modified landscapes (Table S2). This finding suggests that the observed biodiversity responses are not driven solely by contrasts with exceptionally intact reference systems but instead emerge across a broad gradient of urban influence. Despite variation in effect sizes among taxa, wetland types and climatic regions,

significant declines in taxonomic richness and Shannon diversity together with widespread compositional shifts were broadly consistent across spatial scales, income groups and reference categories, indicating that urbanization impacts on wetland biodiversity are pervasive across diverse environmental and socioeconomic contexts.

Our findings have important implications for urban planning, wetland management and biodiversity conservation under accelerating global urbanization. As urban expansion increasingly concentrates around rivers, lakes, and coastal zones, the ecological integrity of wetlands will become increasingly critical for sustaining biodiversity, climate resilience, water security, and human well-being in rapidly urbanizing regions[2]. The strong taxon- and wetland-specific responses identified here indicate that conservation and urban planning strategies should be context dependent rather than uniform. In particular, the pronounced declines observed in amphibians suggest the need to prioritize habitat protection, pollution control, and the enhancement of connected blue–green infrastructure within urban landscapes[48]. Riverine wetlands located in urban corridors may require stronger controls on hydrological alteration and pollution, given their high exposure to urban runoff and flow modification[31,49].

Several limitations of our study highlight important priorities for future research. Comparisons of low-income and tropical regions remained comparatively limited, reflecting geographical imbalances in the available literature. In addition, our analyses focused primarily on taxonomic and compositional dimensions of biodiversity. Although a growing body of research has examined functional and phylogenetic responses to urbanization, comprehensive global syntheses remain limited, particularly for wetland ecosystems. Furthermore, although species composition shifts were widespread, the available data was insufficient to consistently distinguish the relative contributions of native and non-native species to community reorganization across studies. Many studies did not provide complete species inventories or openly accessible community-level datasets, limiting our ability to evaluate whether compositional changes were primarily driven by biological invasions, native species declines or both. Addressing these limitations will require expanded long-term monitoring in underrepresented regions, the incorporation of multidimensional biodiversity metrics, and greater adoption of standardized open-data practices.

In conclusion, this study provides the first global quantitative synthesis of the impacts of urbanization on multiple dimensions of wetland biodiversity and evaluates variation in responses across taxa, wetland types, climatic regions and socioeconomic contexts. We show that urbanization is associated with the local loss of approximately one-third of wetland taxa and a quarter reduction in Shannon diversity. Urban development also drives substantial shifts in species composition, however, despite this compositional turnover, we found no evidence for the widely held assumption that urbanization inevitably promotes biotic homogenization. Biodiversity responses were highly context dependent, with rivers, tropical rainforest wetlands, and amphibian and fish communities showing particular sensitivity to urban impacts. Our findings provide new insights into how urban development reshapes ecological communities worldwide and identify vulnerable taxa, ecosystems and regions that may require targeted conservation efforts under continued urban expansion. Given the accelerating growth of cities and the increasing pressures imposed by climate change, closer integration between urban biodiversity research, wetland conservation and urban planning will be essential for reducing biodiversity loss and promoting more sustainable and resilient cities.

Methods

Literature search and screening

We conducted a systematic literature review to collect evidence from peer-reviewed studies documenting the responses of wetland biodiversity to urbanization following the PRISMA guidelines (Fig. S1). The initial search was conducted on 14 February 2025 on Web of Science (Science Citation Index Expanded database in the Web of Science Core Collection) using a set of terms related to urbanization and wetlands (Table S1). This search returned 13,536 articles. An updated search was performed on 9 December 2025 using the same databases and search terms. The searches yielded 16,989 articles published in English. Four studies were removed after checking for duplicates and seven studies were removed due to an inability to access the full text.

The remaining articles were refined using a two-step procedure. First, titles and abstracts of these articles were screened to exclude irrelevant studies that did not investigate the responses of wetland biodiversity to urbanization. Abstract screening was conducted in R version 4.4.1[50] using the GPT-4o model accessed via the OpenAI API. The model strictly followed the criteria and produced binary predictions (i.e., "relevant" or "excluded"; Supplementary Information Section 1). To evaluate model performance, a random subset of 1,067 articles was manually labeled as "relevant" or "excluded" following the same criteria provided to the model. The manual labels were then compared with the model's predictions for the same articles, and a confusion matrix was constructed to assess classification accuracy (Supplementary Information Section 2). The confusion matrix yielded the following results: true positives (TP) = 70, false negatives (FN) = 2, false positives (FP) = 29, and true negatives (TN) = 966. The model achieved an accuracy of 0.97, a precision of 0.71, a recall of 0.97, and an F1-score of 0.82, indicating high sensitivity and overall predictive reliability (Supplementary Information Section 2). This step reduced the candidate pool of relevant studies to 1,249 articles.

In the second step, we manually went through the full text of the remaining 1,249 studies to determine their eligibility for inclusion in the meta-analysis. Studies were included only when the urbanization treatment represented clearly urban environments located within cities or metropolitan areas. Studies focusing exclusively on small rural settlements, villages, or low-density residential developments that did not meet the definition of urban land use were excluded. An article was included in the meta-analysis when it reported the response of taxonomic richness or Shannon diversity, including sample size, mean, and standard deviation, to urbanization, or it contained a plot displaying the projection of biological communities in the first two dimensions of a Principal Coordinates Analysis (PCoA) or Non-metric Multidimensional Scaling (NMDS) based on a species dissimilarity matrix. Taxonomic richness, which weights all taxa equally, and the Shannon diversity index, which integrates both richness and evenness[51], are both widely used and consistently available metrics in wetland studies, and were therefore selected as the primary biodiversity indicators. Data from PCoA/NMDS plots were extracted to assess the magnitude and direction of community responses to urbanization. As these ordinations are derived from pairwise beta-diversity matrices, the method reflects standard indices[52], and more commonly reported than explicit beta-diversity indices[53]. In total, 124 studies were eligible for the meta-analysis.

Data Extraction

For each study included in the meta-analysis, we extracted comparisons contrasting biodiversity metrics between reference and urbanized sites. For studies based on urbanization gradients, only the two extreme ends of the gradient, representing the lowest and highest levels of urbanization, were extracted as reference and urbanization sites, respectively. To standardize comparisons across studies with heterogeneous definitions of urbanization, we adopted a within-study contrast approach. Based on the authors' original classification or reported urbanization metrics (e.g., population density[54], impervious surface[55], composite indices[56] or categorical designations such as urban, peri-urban, and rural[15]), the group

representing the highest level of urbanization was defined as the "urbanization site," whereas the group with the lowest level of urbanization and anthropogenic disturbance was defined as the "reference site." Each site was required to include at least two independent sampling locations. This approach ensured comparability by consistently capturing the strongest contrast in urbanization intensity within each study, regardless of how urbanization was originally measured. Reference site were further classified into four categories according to their degree of anthropogenic disturbance and urbanization intensity: (1) natural vegetation with minimal human impact, including relatively pristine habitats; (2) semi-natural vegetation with human disturbance, including habitats dominated by natural vegetation but exposed to low-intensity human activities; (3) intensively managed non-urban landscapes, including highly modified agricultural lands and pastures; (4) peri-urban habitats, located at the urban fringe with relatively low urbanization intensity. Classification of reference systems was based on habitat descriptions, land-use characteristics, and urbanization metrics reported in the original studies. Multiple records were extracted when studies reported results for different taxonomic groups, wetland types and seasons. When multiple definitions of the same community were provided (e.g., including or excluding non-native species), we consistently prioritized the most complete definition.

For each record, we extracted bibliographic information (title and publication year) and geographical context. The coordinates were directly extracted from the text or determined using Google Maps based on the description of investigated sites. Each site was assigned to a country and categorized into its income group based on the World Bank's classifications for the study year[57] and a Köppen climate zone[58]. Wetlands were classified into six categories, including river, reservoir/pond, lake, inland vegetated wetland, coastal wetland, and others, while organisms were grouped into nine biological categories, including bacteria, algae, plant, zooplankton, macroinvertebrate, fish, amphibian, bird, and others. Spatial scale was recorded based on the maximum distance between the most distant reference and urbanization sampling sites within each study, which served as a proxy for the degree of spatial aggregation or dispersion of communities and reflected the geographical extent of the study. Spatial scale was categorized into five non-overlapping distance classes (less than 10 km apart, 10-50 km apart, 50-100 km apart, 100-200 km apart, and more than 200 km apart).

To quantify biodiversity responses to urbanization, we extracted mean values, sample size and standard deviation for all-species taxonomic richness and Shannon index in both the reference and urbanization groups. When statistics were only available in graphical form, values were digitized using WebPlotDigitizer v5.2. When mean values and standard deviations were not directly available, they were estimated using established statistical methods. Specifically, means were estimated from reported medians and interquartile ranges using the approach described by Luo et al.[59], and standard deviations were estimated following the methods proposed by Wan et al.[60] . When standard errors were reported, standard deviations were calculated using the corresponding sample sizes. For each PCoA and NMDS ordination plots, we extracted the coordinates of all points belonging to urbanization and reference groups using WebPlotDigitizer v5.2. These coordinates were subsequently used to compute effect sizes describing shifts in species composition. In total, 343 independent comparisons were extracted, including 173 for taxonomic richness, 113 for Shannon diversity, and 57 for species composition.

Effect Size Calculation

To quantify biodiversity responses to urbanization, we applied the log response ratio (LRR) as a scale-free and symmetric measure of proportional change. Within the R 4.4.1[50] environment using the *metafor* package[61], we calculated four effect sizes (LRR taxonomic richness, LRR Shannon, LRR homogeneity, and

LRR shift) via the *escalc()* function (measure = "ROM"). LRR taxonomic richness and LRR Shannon were computed as:

$$LRR\ taxonomic\ richness = ln(\overline{T_U}/\overline{T_R}) \quad (1)$$

$$LRR\ Shannon = ln(\overline{H_U}/\overline{H_R}) \quad (2)$$

$\overline{T_U}$ and $\overline{T_R}$ are mean taxonomic richness in urbanization and reference communities, and $\overline{H_U}$ and $\overline{H_R}$ represent the corresponding means for Shannon diversity. The negative values indicate a reduction in diversity under urbanization, while positive values indicate an increase. Sampling variances for LRR taxonomic richness, equation (3), and LRR Shannon, equation (4), were computed as:

$$v_T = \frac{s_U^2}{n_U \overline{T}_U^2} + \frac{s_R^2}{n_R \overline{T}_R^2} \quad (3)$$

$$v_H = \frac{s_U^2}{n_U \overline{H}_U^2} + \frac{s_R^2}{n_R \overline{H}_R^2} \quad (4)$$

where n_U and n_R are the sample sizes of the variable in urbanization and reference communities, respectively; s_U and s_R are the standard deviations of the variable in urbanization and reference communities, respectively. For species composition, we reconstructed a pairwise Euclidean distance matrix among communities using the ordination coordinates extracted from PCoA and NMDS plots following the approach proposed by Keck and colleagues[39]. From this matrix, we derived two complementary effect size metrics to characterize changes in community structure under urbanization. The first quantifies variation in community similarity, expressed as the log response ratio of the mean distance in urbanization communities $\overline{D_U}$ and the mean distance in reference communities $\overline{D_R}$, equation (5). The negative values of LRR homogeneity indicate increased community similarity (i.e., homogenization) under urbanization, whereas positive values indicate increased dissimilarity (i.e., differentiation).

$$LRR\ homogeneity = ln(\overline{D_U}/\overline{D_R}) \quad (5)$$

The second metric captures the shift in species composition (LRR shift), estimated as the log response ratio of the mean distance between urbanization and reference communities $\overline{D_B}$ and the mean distance in urbanization and reference communities $\overline{D_W}$, equation (6). Positive values of LRR shift indicate greater divergence between urbanization and reference communities, reflecting compositional change.

$$LRR\ shift = ln(\overline{D_B}/\overline{D_W}) \quad (6)$$

Sampling variances for both LRR homogeneity and LRR shift were calculated using the same log response ratio framework, based on the means, standard deviations, and sample sizes of the corresponding distance measures.

$$v_{homogeneity} = \frac{s_U^2}{n_U \overline{D}_U^2} + \frac{s_R^2}{n_R \overline{D}_R^2} \quad (7)$$

$$v_{shift} = \frac{s_B^2}{n_B \overline{D}_B^2} + \frac{s_W^2}{n_W \overline{D}_W^2} \quad (8)$$

n_U and n_R are the numbers of pairwise distances used to calculate $\overline{D_U}$ and $\overline{D_R}$, respectively, s_U and s_R are their corresponding standard deviations. n_B and s_B denote the sample size and standard deviation of $\overline{D_B}$. n_W and s_W were derived from pooled within-group distances across urbanization and reference communities. Given that these two effect sizes depend on the distances between communities in the analyses and that these distances can be altered by the inclusion of more groups or treatments in the plots, it has been demonstrated that LRR homogeneity and LRR shift are generally robust to the inclusion of more groups in the PCoA and NMDS graphs from which they are derived[39].

Statistical Analysis

To estimate the overall magnitude of biodiversity change under urbanization, we fitted separate multilevel random-effects models for each effect size using the *metafor* package[61]. To account for non-independence among effect sizes extracted from the same study, we included a nested random-effects structure with plot identity nested within study identity as random intercepts (~1|Study_ID/Plot_ID). Models were fitted using *rma.mv()* function in *metafor*[61]. Each LRR was weighed by the sampling variances. Multilevel random-effects models revealed substantial heterogeneity in the effects of urbanization on wetland taxonomic richness, Shannon diversity, homogeneity and species composition shift (LRR taxonomic richness: Q = 2132.838, df = 170, p < 0.0001; LRR Shannon diversity: Q = 907.044, df = 111, p < 0.0001; LRR homogeneity: Q = 1898.644, df = 56, p < 0.0001; LRR shift: Q = 1751.7180, df = 56, p < 0.0001), indicating considerable variability in biodiversity responses across studies and systems. To evaluate potential sources of heterogeneity, we fitted multilevel mixed-effects models including six moderators: biological groups, wetland types, spatial scales, World Bank's income groups, Köppen climate zone. All moderators were included simultaneously as fixed effects, while retaining the same nested random-effects structure. Moderator significance was assessed using Type II Wald χ^2 tests, which evaluate each moderator while holding all others constant. To obtain effect size estimates for each level of the moderators, we fitted five additional mixed models for each effect size, each including only one moderator at a time plus the same nested random effect. From each model we computed estimated marginal means and their 95% CIs, respectively, for each level of the included factor. We also examined publication bias for LRR taxonomic richness, LRR Shannon diversity, LRR homogeneity and LRR shift. (Supplementary Information Section 3).

Data Availability

The dataset supporting the findings of this study has been deposited in the Zenodo 10.5281/zenodo.20710039. World Bank income group classifications were obtained from the World Bank Country and Lending Groups[57]. Köppen–Geiger climate classifications were derived from the high-resolution (1 km) Köppen–Geiger climate maps available through Figshare[58].

Code Availability

The code that supports the findings of this study is available at: https://github.com/xinruiweng/meta-urbanization-wetland-biodiversity

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Competing Interest

The authors declare no competing interests.

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