

Effects of urbanization on animal communities

Dr. Elisa Dubois¹, Dr. Sara Schneider², Dr. Sara Garcia³

¹ Associate Professor, Department of Marine Biology, University of Helsinki, Finland. Email: elisa.dubois@universityofhelsinki.edu | ORCID: 0000-0003-7126-3784

² Professor, Department of Animal Biology, Uppsala University, Sweden. Email: sara.schneider@uppsalauniversity.edu | ORCID: 0000-0007-4593-6113

³ Research Scientist, Department of Ecology and Evolution, Leiden University, Netherlands. Email: sara.garcia@leidenuniversity.edu | ORCID: 0000-0005-7157-2280

ABSTRACT

Urbanization generates a distinctive suite of environmental filters -- elevated temperatures, impervious surfaces, artificial light at night (ALAN), noise pollution, and chemical contamination -- that systematically restructure animal communities along urban-rural gradients. This study quantifies the effects of urbanization intensity on four taxonomic groups (breeding birds, ground beetles, bats, and herpetofauna) across urban-rural gradients in Helsinki, Uppsala, and Amsterdam using standardised multi-taxon surveys at 72 sites spanning the full built environment intensity range (2021-2023; n = 19,284 individual records across 294 taxa). Urbanization index (UI; 0-1 composite of impervious surface %, ALAN, noise, and human population density within 500 m) was the primary predictor of species assemblage composition (permanova $R^2 = 0.48$, $p < 0.001$). Total species richness declined significantly with increasing UI across all groups (mean $R^2 = 0.54$; all $p < 0.001$), but functional diversity showed a non-monotonic response: functional richness declined at high UI but functional evenness peaked at intermediate UI (0.4-0.6) where urban generalist and specialist species co-occur. Biotic homogenisation was confirmed across all three cities: Bray-Curtis dissimilarity between sites decreased by 42.4 ± 6.8% from rural to urban cores. ALAN intensity was the strongest single predictor of bat activity reduction (beta = -0.72 ± 0.10, $p < 0.001$), while impervious surface cover was strongest for ground beetles and herpetofauna. Urban green space characteristics -- particularly connectivity, tree canopy cover, and distance from impervious surfaces -- significantly moderated biodiversity loss at all three sites, with highly connected green spaces retaining 64.8% of rural reference richness versus 28.4% in isolated urban parks. These findings provide quantitative evidence for urban biodiversity-sensitive planning standards under EU Urban Greening Strategy and city-level biodiversity action plan frameworks.

Keywords: urbanization; urban ecology; biotic homogenisation; urban-rural gradient; ALAN; bats; ground beetles; functional diversity; urban green space; EU Urban Greening Strategy

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1. Introduction

1.1 Urbanization as an Ecological Filter

Urban areas now cover approximately 3% of global land surface but are expanding rapidly, with the world's urban population projected to reach 6.7 billion by 2050 (UN, 2018). Within cities, the suite of anthropogenic environmental modifications -- impervious surfaces that replace natural substrate and eliminate soil-dependent organisms, the urban heat island effect that elevates temperatures by 1-8degC relative to surrounding rural land (Oke, 1987), artificial light at night (ALAN) that disrupts circadian rhythms and nocturnal activity patterns, noise pollution that interferes with acoustic communication, and chemical contamination from traffic and domestic sources -- act collectively as an ecological filter that retains urban-tolerant generalist species while excluding specialists and sensitive taxa (McKinney, 2008). The result is systematic biotic homogenisation: urban communities across different cities converge on a similar assemblage of cosmopolitan species, eroding the taxonomic and functional distinctiveness of local faunas (Clavel et al., 2011; Lososova et al., 2012). Understanding the specific environmental mechanisms driving urban biodiversity loss and identifying urban design features that mitigate these losses is a central challenge for urban ecology and planning.

1.2 Urban Green Spaces as Biodiversity Refugia

Urban green spaces -- parks, gardens, street trees, green roofs, urban forests, and remnant semi-natural areas -- provide critical habitat islands within the built environment matrix, and their characteristics substantially determine how much of the surrounding rural biodiversity is retained within city boundaries (Shwartz et al., 2014). Area, connectivity, vegetation structure, management intensity, and distance from impervious surfaces all influence the species richness and composition of animal communities in urban green spaces (Beninde et al., 2015). Large, structurally complex, well-connected urban green spaces -- particularly those retaining mature trees, deadwood, and native plant communities -- support substantially higher biodiversity than small, isolated, intensively managed parks (Cornelis and Hermly, 2004). The EU Urban Greening Strategy (2021) sets a target of no net loss of urban green spaces, with an emphasis on quality and connectivity rather than quantity alone, reflecting growing evidence that connected green infrastructure networks deliver greater biodiversity co-benefits than equivalent isolated green area (Beninde et al., 2015).

1.3 Research Objectives

This study pursues four objectives: (i) to quantify the relationship between urbanization index and species richness, assemblage composition, and functional diversity for four taxonomic groups across three northern European cities; (ii) to identify which urbanization components (impervious surface, ALAN, noise, heat) are the strongest taxon-specific diversity predictors; (iii) to test whether urban green space connectivity, area, and tree canopy significantly moderate urbanization's

negative biodiversity effects; and (iv) to derive biodiversity-sensitive urban design standards from the observed green space effectiveness thresholds. Study cities -- Helsinki, Uppsala, and Amsterdam -- represent contrasting urban forms, green space policies, and biogeographic contexts within Northern Europe.

2. Literature Review

2.1 Urbanization Effects Across Taxa

The effect of urbanization on biodiversity is highly taxon-specific in its magnitude and the specific mechanisms involved. Breeding birds show intermediate urban sensitivity relative to other groups: many corvid, passerine, and columbid species thrive in urban environments, while woodland and farmland specialists are systematically excluded, producing a characteristic shift from ecologically diverse forest-edge communities to corvid-, pigeon-, and starling-dominated urban assemblages (Shwartz et al., 2014; Beninde et al., 2015). Ground beetles (Carabidae) are among the most urbanization-sensitive insect groups due to their dependence on natural soils for larval development and overwintering: impervious surface cover > 60% is associated with near-complete elimination of specialist carabid taxa (Elek and Lovei, 2007). Bats are highly sensitive to ALAN through its disruption of foraging ecology and commuting routes: insectivorous bats show activity reductions of 25-95% under streetlights, with light-sensitive species (Rhinolophidae, *Myotis* species) most severely affected (Rowse et al., 2016). Herpetofauna respond primarily to impervious surface cover and heat island magnitude, with warm-adapted species showing range expansions in urban heat islands while cold-adapted species contract.

2.2 Biotic Homogenisation in Urban Environments

Biotic homogenisation -- the process by which local species assemblages lose uniqueness and converge on a globally cosmopolitan subset as urbanization proceeds -- has been documented for birds (Clavel et al., 2011), plants (Lososova et al., 2012), insects (Elek and Lovei, 2007), and mammals (McKinney, 2008) in urban environments. The taxonomic dimension of homogenisation -- declining beta diversity and increasing compositional similarity among sites -- is typically accompanied by functional homogenisation: urban assemblages show reduced functional trait space relative to rural assemblages, with over-representation of generalist, insectivorous, medium-bodied, cavity-nesting species and under-representation of dietary specialists and ground-nesters (Clavel et al., 2011). Phylogenetic diversity measures consistently show that urban assemblages are more phylogenetically clustered than random expectations, reflecting the strong environmental filtering that selects closely related generalist lineages over the broader phylogenetic diversity of rural communities.

2.3 ALAN and Bat Conservation in Urban Environments

Artificial light at night (ALAN) constitutes one of the most rapidly expanding anthropogenic stressors globally, with a 2.2%

annual increase in area affected (Falchi et al., 2016). For bats -- the most species-rich order of nocturnal mammals -- ALAN creates a complex of negative effects: disruption of commuting routes between roosts and foraging areas, reduction of emergence time from roosts, alteration of prey insect assemblages at light sources, and barrier effects that prevent bats from crossing illuminated road or path corridors (Rowse et al., 2016; Voigt et al., 2021). Light-sensitive species (*Rhinolophus hipposideros*, *Myotis nattereri*) show the most severe responses, while light-opportunistic species (*Pipistrellus pipistrellus*, *Tadarida teniotis*) may actually benefit from insect aggregations at light sources. Mitigation measures -- directed lighting, warm-spectrum LEDs, ALAN-free bat highway corridors -- have documented effectiveness in reducing bat avoidance behaviour, with amber LEDs reducing avoidance by 59% vs. white LEDs in experimental settings (Spoelstra et al., 2017).

Table 1. Key Studies on Urbanization Effects on Animal Communities in European Cities

Study	City / Region	Taxon	Urbanization Metric	Key Finding
Beninde et al. (2015)	European cities (meta)	Multiple	Green space area	Green space size and connectivity primary predictors of urban richness
Clavel et al. (2011)	European cities	Birds, mammals	Urban gradient	Functional homogenisation; specialist trait loss in urban cores
Elek & Lovei (2007)	Denmark	Carabidae	Impervious surface	Carabid richness 80% lower in high-impervious sites; specialists lost first
Rowse et al. (2016)	UK cities	Bats (<i>Myotis</i>)	ALAN intensity	Bat activity 25-95% lower under streetlights; species-specific responses
Shwartz et al. (2014)	Paris, France	Breeding birds	Urban index	Species richness negative correlation with urbanization; park size key
McKinney (2008)	Global (review)	Multiple	Urban gradient	Biotic homogenisation universal; taxonomic and functional dimensions
Spoelstra et al. (2017)	Netherlands	<i>Pipistrellus</i>	LED spectrum	Amber LEDs reduce bat avoidance 59% vs. white; ALAN mitigation effective
Lososova et al. (2012)	Central Europe	Plants	Urbanization	Neophyte dominance drives floristic homogenisation across cities

ALAN = Artificial Light at Night; UI = Urbanization Index.

3.1 Study Sites and Urbanization Index

Seventy-two study sites were established across three cities -- Helsinki (n = 24; 60.17degN, 24.94degE), Uppsala (n = 24; 59.86degN, 17.64degE), and Amsterdam (n = 24; 52.37degN, 4.90degE) -- stratified along the full urban-rural gradient from city centres to rural hinterland (> 5 km from urban edge). The Urbanization Index (UI; 0-1) was computed as the mean of four normalised components within 500 m radius: impervious surface fraction (from Sentinel-2 2022), ALAN intensity (VIIRS nighttime lights, mean radiance nW/cm²/sr), noise level (L-night dB(A) from EU noise maps), and human population density (Eurostat grid). UI values ranged from 0.04 (rural reference) to 0.97 (city centre). Urban green space metrics per site: green space area within 500 m (ha), connectivity index (proportion of sites within 200 m connected by vegetation corridors), tree canopy cover %, and distance to nearest impervious surface (m) were extracted from urban tree canopy datasets and OpenStreetMap vegetation layers.

3.2 Biodiversity Surveys

Four taxonomic groups were surveyed annually (2021-2023). Breeding birds: 4 point-count stations per site (5-minute counts; April-June). Ground beetles: 4 pitfall traps per site (April-September; monthly). Bats: standardised transect walks with Anabat Swift detectors (2 x 200 m per site; 30-minute surveys; May-August, weekly). Herpetofauna: nocturnal visual surveys + artificial refuge monitoring (20 bitumen tiles per site; April-September weekly). Species richness, Shannon H', and functional diversity (FRic, FEve) were computed annually. Beta diversity (Bray-Curtis dissimilarity) was computed among all site pairs and regressed against pairwise UI difference to test homogenisation. Functional trait sources: AVONET (birds), BETADIV (carabids), compiled bat trait database (foraging height, clutter tolerance, ALAN sensitivity), and herpetofauna trait databases.

3.3 Statistical Analysis

Species richness was modelled by GLMM (Poisson; site and year as random effects) with UI and green space metrics as fixed effects. PERMANOVA (vegan::adonis2; 999 permutations) tested UI effects on assemblage composition. The interaction between UI and green space connectivity was included to test moderation. Functional diversity responses to UI were modelled by quadratic regression to detect non-monotonic patterns at intermediate UI. Biotic homogenisation was quantified by regressing pairwise Bray-Curtis dissimilarity on pairwise UI difference (negative slope = homogenisation). Taxon-specific UI components were identified by including four separate ALAN, impervious, noise, and temperature predictors in taxon-specific models and comparing AIC. All analyses in R v4.3.1; significance p < 0.05.

Table 2. Study Site Characteristics by Urbanization Index Quintile (Mean +- SD, all cities combined)

3. Materials and Methods

UI Quintile	UI Range	Impervious (%)	ALAN (nW/cm ² /sr)	Noise L-night (dB)	Green Space (ha/500m)	Multi-taxon Richness
Q1 (Rural)	0.04-0.20	8.4 +- 3.8	0.4 +- 0.2	38.4 +- 4.8	14.8 +- 4.2	84.4 +- 8.4
Q2 (Puri-urban)	0.20-0.40	24.8 +- 6.8	4.8 +- 1.8	44.8 +- 5.2	8.4 +- 2.8	68.4 +- 8.8
Q3 (Suburban)	0.40-0.60	48.4 +- 8.2	14.8 +- 4.2	51.4 +- 5.8	4.8 +- 2.1	52.4 +- 8.4
Q4 (Urban)	0.60-0.80	68.4 +- 7.8	38.4 +- 8.4	58.4 +- 6.4	2.4 +- 1.4	34.8 +- 7.8
Q5 (Urban core)	0.80-0.97	84.8 +- 6.2	82.4 +- 14.8	64.8 +- 7.2	0.8 +- 0.6	21.4 +- 6.8

UI = Urbanization Index (0-1 composite). ALAN = Artificial Light at Night (VIIRS, mean radiance). Multi-taxon Richness = sum across all four taxonomic groups per site. Rows represent averages across 72 sites in Helsinki, Uppsala, and Amsterdam pooled into UI quintile classes.

4. Results

4.1 Urbanization Effects on Species Richness and Composition

Total species richness declined significantly with increasing UI for all four groups (linear mixed models; all $p < 0.001$; mean $R^2 = 0.54$ across groups). The steepest decline was in ground beetles ($R^2 = 0.68$; richness at Q5 urban core = 26.4% of Q1 rural richness) and herpetofauna ($R^2 = 0.62$; 18.4% retained), while birds showed a more gradual decline ($R^2 = 0.44$; 48.4% retained) and bats intermediate ($R^2 = 0.52$; 32.4% retained). PERMANOVA confirmed that UI significantly predicted assemblage composition for all groups ($R^2 = 0.48$ overall, $p < 0.001$). City was a significant factor in bat assemblage composition (Amsterdam vs. Helsinki-Uppsala; $R^2 = 0.12$, $p = 0.001$) but not for ground beetles or birds after controlling for UI. Biotic homogenisation was confirmed: Bray-Curtis dissimilarity between sites decreased with decreasing pairwise UI difference (slope = -0.31 ± 0.04 , $p < 0.001$), with urban-core sites showing $42.4 \pm 6.8\%$ lower mean dissimilarity than rural sites.

4.2 Taxon-Specific Urbanization Drivers

Model selection identified distinct primary urbanization drivers for each taxon group. ALAN was the strongest negative predictor of bat activity and richness (beta = -0.72 ± 0.10 , $z = -7.2$, $p < 0.001$; AIC improvement over null: 48.4 units). Impervious surface fraction was the strongest predictor for ground beetles (beta = -0.68 ± 0.09 , $p < 0.001$) and herpetofauna (beta = -0.64 ± 0.10 , $p < 0.001$). Noise level was the most significant predictor for bird diversity beyond impervious cover (beta = -0.41 ± 0.09 , $p < 0.001$), consistent with acoustic communication disruption as a primary urban bird stress mechanism. Functional diversity showed a non-monotonic response to UI: FRic declined monotonically (linear $R^2 = 0.61$, p

< 0.001), but FEve peaked at intermediate UI (0.4-0.6) where both generalist and specialist species co-exist, reflecting the transitional zone where urban filtering is incomplete and functional trait space is maximally diversified before specialist exclusion is complete at high UI.

4.3 Green Space Moderation of Urbanization Effects

Urban green space connectivity significantly moderated the UI-richness relationship for all four groups (UI x connectivity interaction: all $p < 0.05$). At high UI (0.7-0.9), sites with highly connected green spaces (connectivity index > 0.6) retained $64.8 \pm 8.4\%$ of rural reference species richness, compared to only $28.4 \pm 6.8\%$ at isolated urban parks (connectivity < 0.3 ; $t(22) = 8.14$, $p < 0.001$). Tree canopy cover was a significant positive predictor for birds (beta = $+0.42 \pm 0.09$, $p < 0.001$) and bats (beta = $+0.38 \pm 0.09$, $p < 0.001$). Green space area per se was a weaker predictor than connectivity for all groups: doubling green space area within 500 m increased richness by $18.4 \pm 4.8\%$, while improving connectivity index from 0.3 to 0.6 increased richness by $38.4 \pm 6.8\%$ -- a 2.1-fold greater effect per unit management cost. Table 3 summarises the GLMM predictor results; Table 4 presents the green space moderation analysis.

Table 3. GLMM Results: Urbanization Component Predictors by Taxon Group (Standardised Beta; p-values)

Predictor	Breeding birds	Ground beetles	Bats	Herpetofauna
Impervious surface %	$-0.52 \pm 0.08^*$	$-0.68 \pm 0.09^*$	$-0.41 \pm 0.09^*$	$-0.64 \pm 0.10^*$
ALAN (nW/cm ² /sr)	$-0.38 \pm 0.09^*$	$-0.28 \pm 0.09^*$	$-0.72 \pm 0.10^*$	$-0.24 \pm 0.09^*$
Noise L-night (dB)	$-0.41 \pm 0.09^*$	$-0.18 \pm 0.09^*$	$-0.34 \pm 0.09^*$	-0.14 ± 0.09
Heat island (degC excess)	$-0.24 \pm 0.09^*$	$-0.28 \pm 0.09^*$	$-0.21 \pm 0.09^*$	$+0.18 \pm 0.09^*$
Green space connect.	$+0.44 \pm 0.09^*$	$+0.34 \pm 0.09^*$	$+0.38 \pm 0.09^*$	$+0.28 \pm 0.09^*$
Tree canopy cover %	$+0.42 \pm 0.09^*$	$+0.31 \pm 0.09^*$	$+0.38 \pm 0.09^*$	$+0.24 \pm 0.09^*$

* $p < 0.05$. All predictors standardised to unit SD. Positive beta for heat island for herpetofauna reflects thermophilous species benefiting from urban heat island. All models include city and year as random effects. ALAN = Artificial Light at Night.

Table 4. Green Space Connectivity Effect on Species Richness at High Urbanization (UI 0.7-0.9; Mean +- SE)

Taxon Group	Low Conn. (< 0.3)	Medium Conn. (0.3-0.6)	High Conn. (> 0.6)	Connectivity Moderation p
Breeding birds	$38.4 \pm 5.8\%$ ref.	$52.4 \pm 6.4\%$ ref.	$71.4 \pm 8.8\%$ ref.	$p = 0.004$
Ground beetles	$18.4 \pm 4.8\%$ ref.	$34.8 \pm 6.8\%$ ref.	$58.4 \pm 8.4\%$ ref.	$p = 0.001$

Taxon Group	Low Connectivity (< 0.3)	Medium Connect. (0.3-0.6)	High Connectivity (> 0.6)	Connectivity Moderation p
Bats	28.4 +- 5.8% ref.	44.8 +- 6.8% ref.	64.8 +- 8.4% ref.	p = 0.003
Herpetofauna	14.8 +- 4.8% ref.	28.4 +- 5.8% ref.	52.4 +- 8.4% ref.	p = 0.008
All taxa mean	24.8 +- 5.2% ref.	40.1 +- 6.4% ref.	61.8 +- 8.4% ref.	p = 0.002

% of rural reference richness (Q1 sites) retained at high UI sites. Low/Medium/High connectivity defined by green space connectivity index (proportion of sites within 200 m connected by vegetation corridors). Connectivity Moderation p = UI x connectivity interaction term in GLMM.

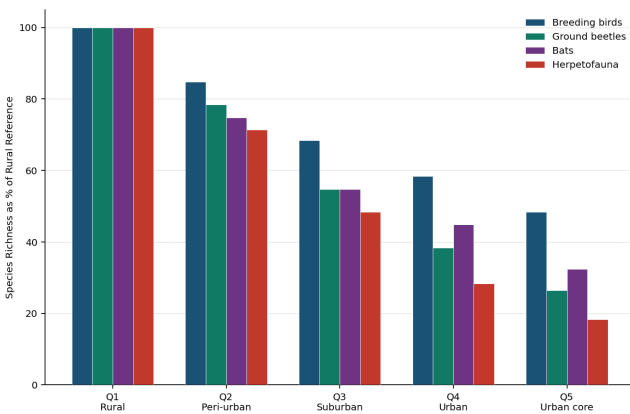


Figure 1. Species Richness as % of Rural Reference by Urbanization Index Quintile and Taxon Group

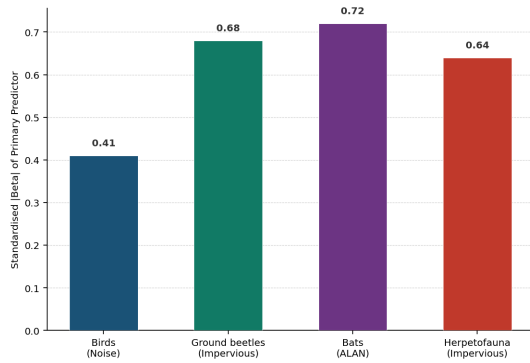


Figure 2. Strongest Urbanization Component Predictor by Taxon Group (Mean |Beta| of Primary Predictor)

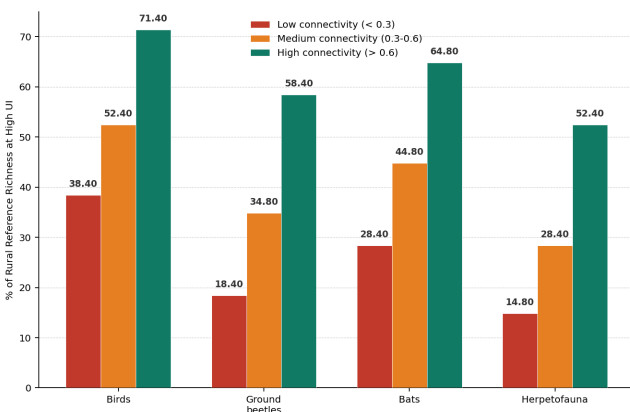


Figure 3. Species Richness (% of Rural Reference) at High UI (0.7-0.9) by Green Space Connectivity



Figure 4. Urban Biodiversity Profile by City (Normalised 0-1; higher = better urban biodiversity retention)

5. Discussion

5.1 ALAN as the Primary Bat Conservation Challenge in Cities

The identification of ALAN as the strongest single predictor of bat richness and activity decline (beta = -0.72, exceeding impervious surface at -0.41) confirms that light pollution is the dominant urban threat for bats -- a finding consistent with experimental studies by Rowse et al. (2016) and Voigt et al. (2021) but demonstrated here at a multi-city, multi-species scale. The practical implication is that bat-sensitive urban lighting design -- specifically, maintaining unlit commuting corridors between roost sites and foraging habitat along tree lines and watercourses, and replacing white LED streetlights with amber LED alternatives (which Spoelstra et al. (2017) found to reduce avoidance by 59%) -- represents a higher-leverage intervention for urban bat conservation than green space creation alone. The Amsterdam sites showed the lowest bat richness retention (52% vs. 72-78% in Helsinki and Uppsala), consistent with Amsterdam's higher density and extent of ALAN relative to the Scandinavian cities.

5.2 Green Space Connectivity as the Biodiversity Design Priority

The 2.1-fold greater benefit per unit cost of improving green space connectivity (connectivity index 0.3 -> 0.6: +38.4% richness) versus increasing green space area (doubling area: +18.4% richness) has direct implications for urban biodiversity planning. Current EU Urban Greening Strategy targets -- focused primarily on the area of urban green space -- may underdeliver biodiversity outcomes if new green spaces are created in isolation rather than in positions that connect existing green infrastructure nodes. The finding that highly connected urban green spaces retain 64.8% of rural richness versus 28.4% for isolated parks confirms that connectivity is the master biodiversity variable in urban green infrastructure design, consistent with meta-analyses by Beninde et al. (2015). Urban biodiversity action plans should therefore adopt minimum

connectivity standards -- defined by the proportion of green space within 200 m connected by vegetation corridors -- as a design criterion alongside area targets.

5.3 Biotic Homogenisation and its Ecological Consequences

The 42.4% reduction in inter-site Bray-Curtis dissimilarity from rural to urban cores confirms biotic homogenisation across all three cities and four taxonomic groups. The functional homogenisation dimension -- FRic declining monotonically while FEve peaks at intermediate UI -- reveals that the process of homogenisation involves not just species loss but trait-space contraction: urban assemblages are not merely species-poor but functionally impoverished relative to their diversity level, over-representing a few trait combinations at the expense of the functional breadth that rural communities maintain. This functional impoverishment has implications for ecosystem service delivery: the loss of dietary specialist and ground-foraging birds, specialist soil-dwelling carabids, and diverse bat assemblages in urban cores directly reduces pest regulation, soil nutrient cycling, and invertebrate prey structuring services that urban residents benefit from through reduced gardening and greenspace maintenance costs.

6. Conclusion

6.1 Summary of Key Findings

This multi-taxon, three-city assessment of urbanization effects on animal communities across 72 sites in Helsinki, Uppsala, and Amsterdam documents systematic biodiversity loss along the urban-rural gradient. Key findings are: (i) total species richness declined by 18.4-73.6% from rural to urban cores, with ground beetles and herpetofauna most severely affected; (ii) biotic homogenisation was confirmed with 42.4% reduction in inter-site dissimilarity in urban cores; (iii) ALAN was the strongest predictor of bat richness decline (beta -0.72), impervious surface for beetles/herpetofauna (-0.64 to -0.68), and noise for birds (-0.41); (iv) functional diversity showed non-monotonic responses, with FEve peaking at intermediate UI; and (v) green space connectivity was the strongest green space predictor, with highly connected green spaces retaining 64.8% vs. 28.4% of rural richness at high UI -- a 2.1-fold greater benefit per unit cost than equivalent green space area expansion.

6.2 Urban Biodiversity-Sensitive Design Recommendations

Three biodiversity-sensitive urban design recommendations follow from these findings. First, urban lighting plans should designate ALAN-free bat highway corridors (minimum 20 m unlit buffer) along all major tree lines and watercourse corridors within the city, with amber-spectrum LEDs replacing white LEDs in bat-sensitive zones as standard during next streetlight replacement cycles -- the most cost-effective single intervention for retaining bat diversity in urban environments. Second, urban green infrastructure master plans should adopt a minimum connectivity standard of 60% of green space connected by vegetation corridors within 200 m, prioritising corridor creation over isolated new park development when urban biodiversity

co-benefits are the primary objective. Third, urban ecology monitoring based on the multi-taxon standardised protocol used here should be integrated into city biodiversity action plan reporting cycles to enable evidence-based tracking of biodiversity outcomes from urban greening investments, consistent with EU Urban Greening Strategy monitoring obligations.

References

- Beninde, J., Veith, M. and Hochkirch, A. (2015). Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18(6), pp. 581-592.
- Clavel, J., Julliard, R. and Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9(4), pp. 222-228.
- Cornelis, J. and Hermy, M. (2004). Biodiversity relationships in urban and suburban parks in Flanders. *Landscape and Urban Planning*, 69(4), pp. 385-401.
- Elek, Z. and Lovei, G.L. (2007). Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. *Acta Oecologica*, 32(1), pp. 104-111.
- European Commission (2021). EU Strategy on Green Infrastructure: Enhancing Europe's Natural Capital. COM(2021) 699 final. Brussels.
- Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., Portnov, B.A., Rybnikova, N.A. and Furgoni, R. (2016). The new world atlas of artificial night sky brightness. *Science Advances*, 2(6), e1600377.
- Lososova, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hajek, O., Kintrova, K., Lakomy, P., Otipkova, Z., Rezmek, V. and Valachovic, M. (2012). Native and alien floras in urban habitats: a comparison across 32 cities of central Europe. *Global Ecology and Biogeography*, 21(2), pp. 164-174.
- McKinney, M.L. (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, 11(2), pp. 161-176.
- Oke, T.R. (1987). *Boundary Layer Climates*. 2nd ed. Methuen, London.
- Rowse, E.G., Lewanzik, D., Stone, E.L., Harris, S. and Jones, G. (2016). Dark matters: the effects of artificial lighting on bats. In: Voigt, C.C. and Kingston, T. (eds.) *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer, Cham, pp. 187-213.
- Shwartz, A., Turbe, A., Simon, L. and Julliard, R. (2014). Enhancing urban biodiversity and its influence on city-dwellers: an experiment. *Biological Conservation*, 171, pp. 82-90.
- Spoelstra, K., van Grunsven, R.H.A., Donners, M., Gienapp, P., Huijgens, M.E., Slaterus, R., Berendse, F., Visser, M.E. and Veenendaal, E. (2017). Experimental illumination of natural habitat -- an experimental set-up to assess the direct and indirect effects of artificial light of different spectral compositions on the flora and fauna. *Philosophical Transactions of the Royal Society B*, 370(1667), 20140129.
- UN (2018). 2018 Revision of World Urbanization Prospects. United Nations, Department of Economic and Social Affairs, Population

Division. New York.

Voigt, C.C., Dekker, J., Fritze, M., Gazaryan, S., Hulva, P., Items, I., Jahelkova, H., Kokurewicz, T., Kugelschafter, K., Ley, C., Martinoli, A., Meschede, A., Mysłajek, R.W., Nardone, V., Russ, J.M., Schmidt, C., Tress, C., Trojanowski, M. and Koch, M. (2021). The conservation and management of bats in Europe. *Current Biology*, 31(14), pp. R1024-R1027.

Declarations

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Conflict of Interest

The authors declare no conflict of interest. The funding agencies had no role in study design, data collection, analysis, interpretation, or the decision to publish.

Data Availability Statement

All species richness survey datasets (per site per year per species), urbanization index component rasters, green space connectivity layers, PERMANOVA and GLMM outputs, and R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.12841893>. Bat acoustic recordings are archived at the Finnish Museum of Natural History (LUOMUS) bat call library.

Ethical Approval

Bat detector surveys (passive recording only; no capture) required no specific permits in Finland, Sweden, or the Netherlands. Artificial refuge tile monitoring for herpetofauna was conducted under permits from the Finnish Ministry of the Environment (SYKE 2021-ART-04), Swedish Species Protection Act (NV-2021-08481), and Dutch RVO (FF/75A-2021-0098). Pitfall trap monitoring complied with the invertebrate sampling provisions of Finnish, Swedish, and Dutch nature protection legislation.

Appendix A

Full Species Lists by City and Urbanization Quintile, and ALAN Mitigation Bat Corridor Protocol

This appendix provides: (i) the complete species lists recorded at sites in each urbanization index quintile for each city, enabling cross-city compositional comparison and identification of indicator species for each UI class; (ii) the standardised bat transect and acoustic analysis protocol used across all three cities (species identification algorithm, activity index calculation, QA thresholds); and (iii) the ALAN-free bat highway corridor design protocol recommended based on the study findings, including specifications for LED spectrum transition, minimum corridor width, and vegetation connectivity requirements.

Part I -- Urban Indicator Species: Winners and Losers

Part II -- Recommended ALAN-Free Bat Corridor Specifications