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The urban tree of life: synthesizing relationships between body size and urban affinity

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This study provides an **important** assessment of how body size influences the occurrence of macro-organisms in urban areas across the globe. Size in most plants, but only some animal families, was positively associated with urban affinity. The data set is impressive and the strength of evidence **solid**.

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Abstract

Urbanization is a major global driver of biodiversity change, with species responses to urban settings ranging from avoidance to exploitation. To better understand these responses, we conducted a global analysis of urban relative affinity inferred from occurrence data across more than 30,000 animal and plant species. Our synthesis showed a consistent pattern across taxa and biogeographic regions: many species are urban avoiders, while few thrive as urban exploiters—a pattern we coin “Species Urbanness Distribution”. We then assessed whether body size, an integrative ecological trait fundamental to space use, mobility, metabolism, and environmental sensitivity, showed consistent associations with urban affinity among species and across 371 taxonomic families. Analyses were conducted at the interspecific level and focused primarily on variation among taxonomic families (with an accompanying application to view results available here: *https://globalecologyresearchgroup.github.io/body_size_results_visualization/*). Larger body sizes were generally associated with greater urban affinity in plants compared to animals, though these size-affinity relationships showed considerable variability among families. Our findings highlight the heterogeneous relationship between body size and urban affinity across the tree of life, underscoring the importance of tailored strategies to support urban biodiversity. This research advances ecological understanding of urban filtering and provides a framework for guiding biodiversity-sensitive urban planning amid accelerating global urbanization.

Main

Cities represent novel anthropogenic environments, leading to significant mismatches with the evolutionary history of most organisms[1]. As urban areas are set to expand two- to sixfold over the 21st century[2], urbanization poses a substantial and accelerating threat to global biodiversity[3]. Yet species vary widely in their responses: some are completely extirpated (‘urban avoiders’), others persist through behavioral or ecological acclimation (‘urban adapters’) and/or rapid adaptive evolution to cities[4,5], and some even thrive in urban environments[6] (‘urban exploiters’). Quantifying these divergent responses is key for understanding how urbanization will continue to shape global biodiversity and urban ecosystem functioning (e.g., reshaping of food webs[7,8]). However, urban ecology has typically relied on small-scale studies, often focused on relatively few species and/or particular taxonomic groups such as birds[9] or mammals[10]. Thus, whether general patterns of urban preference or avoidance emerge across species within and across regional pools remains untested.

Species likely do not respond randomly to urbanization as traits may modulate species’ responses. Trait-based approaches are powerful for identifying generalizable patterns across diverse taxa, particularly at broad spatial and phylogenetic scales[11]. Although many traits (e.g., diet, reproductive strategy, dispersal ability) may influence species-specific responses to urbanization, body size stands out as both the most widely measured and most taxonomically integrative. It is a key trait of any organism, relating to space use, life-history, and metabolic rate across the tree of life[12,13,14], making it a plausible direct or indirect predictor of species’ responses to key stressor gradients in urban landscapes, including resource fragmentation, heat stress from urban heat islands, and anthropogenic disturbance (Fig. 1).

Body size correlates with urban mobility, but in complex ways[15]. For instance, while higher mobility allows some animal species to better cope with the fragmented nature of urban habitat resources, reduced mobility might be advantageous for exploiting localized resources and avoiding risks associated with the urban matrix[16,17]. In plants, body size—often indexed by height—correlates with competitive ability, light acquisition, and reproductive strategy, with larger species generally having greater resource needs but potentially higher resilience to urban stressors[18]. Notably, the urban heat island effect may drive shifts to smaller-bodied animal species due to elevated metabolic costs[14,15], echoing similar patterns observed under global warming[19,20]. However, these shifts toward smaller size can be overruled by requirements for increased urban mobility in taxa where mobility increases with body size[15]. Overall, despite body size’s fundamental role in modulating species responses to their environment, a systematic, cross-taxon assessment of how urbanization filters body size distributions is lacking.

Here, we present a global synthesis of urban affinity across more than 30,000 animal and plant species, using occurrence records from the Global Biodiversity Information Facility (GBIF) and remotely sensed night-time light intensity as a proxy for urbanization. We define a continuous metric of regional urban affinity calculated as the realized spatially-explicit urban affinity per species in each subrealm. This metric measuring a species’ relative affinity to urban areas, with negative values indicating avoidance and positive values indicating preference[21]. To account for regional variation in both species pools and in species’ urban affinity across their range[22,23], we calculated urban affinity within 52 geographic subrealms (Fig. S1), representing broadly coherent species pools and ecological contexts. Our dataset spans 47 taxonomic classes—from flowering plants (8,980 species) to insects (8,674 species) to mammals (648 species)—and represents a uniquely taxonomically broad assessment. We first introduce the concept of “Species Urbanness Distribution” (SUD) to characterize the composition of a regional community in terms of its species’ urban affinities. We then use Bayesian hierarchical modeling to test whether body size predicts urban affinity across 17,722 species from 371 families, across multiple subrealms. These analyses allow us to quantify both consistency and heterogeneity of body size effects on urban affinity across multiple taxonomic levels, and across regions. This synthesis addresses two core questions: (1) What is the shape of species’ urban affinity distributions within regional communities? (2) Does body size consistently correlate with species’ urban affinities across

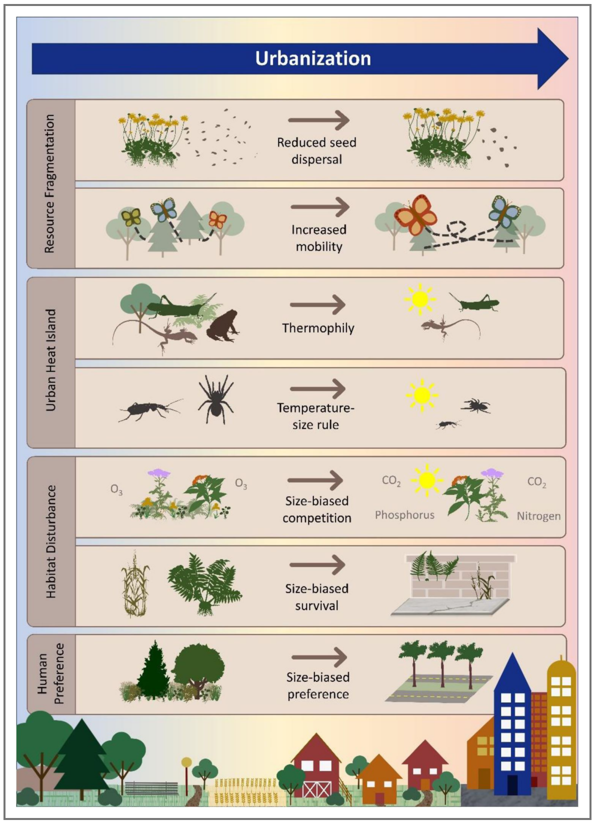

Fig. 1. Conceptual framework illustrating hypothesized mechanisms linking urban affinity to interspecific body-size shifts.

These include dispersal and mobility constraints under habitat fragmentation[44,45], thermophily and the temperature–size rule driven by the urban heat island effect[15,30], size-biased competition and survival[94,95], and size-biased human preferences[64]. Urban fragmentation of habitat resources can select for increased mobility (e.g., larger butterflies) or reduced mobility (e.g., larger seeds) depending on isolation severity. Elevated urban temperatures favor thermophily, which often negatively correlates with size as it affects the heat balance via thermal inertia. Similarly, these higher temperatures generally favor smaller-bodied adult ectotherms because they accelerate development and reduce time available for growth (i.e., temperature-size rule). In plants, the increased CO_2 and nutrient availability associated with anthropogenic environments—due to heating- and traffic-related CO2 emissions and eutrophication—provides a competitive advantage to larger plant species, and human preferences too may favor larger species (e.g., tree-lined streets), whereas smaller species may be advantaged in colonizing built infrastructure.

taxonomic groups and biogeographic contexts? Our aim is to identify broad, cross-taxonomic patterns in species' urban affinity at a global scale, rather than to resolve the specific causal mechanisms driving urban success or failure within individual taxa or cities.

Results and Discussion

Species Urbanness Distributions (SUDs)

We identified a consistent pattern in the extent to which regional communities—defined as all species within a given biogeographic subrealm—consist of urban avoiders and exploiters. We term this the Species Urbanness Distribution (SUD), which captures the full distribution of urban affinity values across species in a community. SUDs exhibited a characteristic shape: a pronounced peak at negative values and a long right-skewed tail toward high positive values, indicating that most species are 'urban avoiders', while only a few are 'urban exploiters'. These patterns in central tendency were broadly consistent across subrealms and taxonomic levels, although distributional shapes varied among higher taxonomic groups (Fig. 2). Conceptually, SUDs parallel the well-known Species Abundance Distributions[24] (SADs), which describe the general law of communities being composed of many rare and few common species[24,25]. Similarly, much like the skewed distributions observed in SADs[24,26], the skewed shape of SUDs indicates that while many species exhibit some degree of urban affinity, a relatively small subset of species attain high levels of urban affinity and dominate urban environments. While previous studies have reported a similar pattern at smaller spatial scales[27], our synthesis demonstrates this applies across the globe and taxa. To evaluate this more formally, we compared distributions across subrealms for groups with the largest sample sizes and found that while distributional shapes varied among higher taxa, median values and overall spread were broadly similar within comparable taxonomic levels (Figs. S2–S4).

The skewed shape of SUDs suggests that traits enabling species to tolerate urban environments are unevenly expressed, given that only a handful of species show extreme urban affinity values, but our results suggest this is geographically widespread across taxa. These traits may be partly found in human-commensal species, which are found globally and often include invasive non-native species[28]. Such traits "pre-adapted" to urban conditions allow for some species to not only persist but thrive in urban environments where most species cannot. Framing these patterns through the lens of exaptation may be particularly useful, as traits that evolved under non-urban selective pressures may incidentally confer advantages in urban environments without having arisen in response to urbanization per se (sensu Lambert et al.[4]). We therefore speculate that the skewed shape of SUDs may reflect the uneven distribution of exaptive traits across species pools, rather than widespread adaptive evolution to urban conditions.

Consistent with this interpretation, if exaptive traits that facilitate urban persistence are unevenly distributed across species pools, most species would be expected to exhibit avoidance rather than affinity toward urban environments. Indeed, we found that the median urban affinity is most often below one, indicating widespread avoidance among species (Fig. 2, S5). This is expected, given that urbanization typically involves severe loss and fragmentation of habitat resources for most organisms[1], which negatively impacts numerous taxa, including birds[29], beetles[30], and moths[31]. Additionally, the urban heat island—typical of most cities[32]—imposes thermal stress, especially during extreme heat events[33], which may drive community shifts toward heat-tolerant species, as observed in ants[34], bees[35], and plants[36]. Yet, urban environments also frequently contain green infrastructure and remnants of natural habitats that can act as sanctuaries for rare and endangered species[37], and cities can harbor a large part of the regional diversity[38]. But these green infrastructure spaces are often also dominated by widespread generalist species. The multitude of environmental stressors, combined with competition dynamics between urban-tolerant and intolerant species, likely influence the shape of SUDs (Fig. 2). Future ecological research should aim to disentangle these contrasting drivers across taxa and regions to better understand the ecological filters at play.

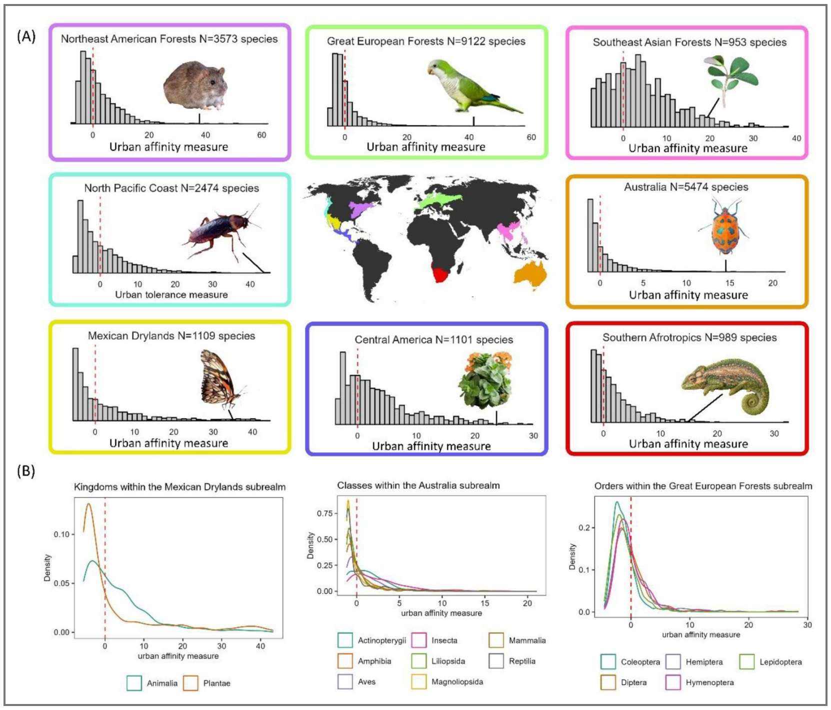

Fig. 2. **Species urbanness distributions (SUDs) exemplified for eight subrealms.**

Plotted are all species per subrealm (**A**), with the images highlighting an example 'hyper-exploiter' species from each of these subrealms (i.e., with a high urban affinity score). The x-axis shows the urban affinity measure whereas the y-axis is the number of species within that bin. There were consistent patterns for kingdoms, classes, and orders (**B**) as shown by similar central tendencies despite variation in distributional shape. The vertical dashed line represents where species are neutral towards urbanization. Photos acquired from iNaturalist CC BY-NC and background was removed by authors: Brown rat (© Ouwesok), Monk parakeet (© Juan Emilio), Cape dwarf chameleon (© Berkeley Lumb), American cockroach (© Len Worthington), Flaming kay (© Lyubo Gadzhev), Juno silverspot (© Rigoberto Ramírez Cortés), Hibiscus harlequin bug (© Sam Fraser-Smith), and Mascarene island leaf-flower (© Douglas Goldman).

The relationship between body size and urban affinity

To test whether there is a consistent pattern of body size filtering associated with urban affinity across the tree of life, we integrated our species-level urban affinity values with body size measures collated from the literature. We performed this analysis for 17,722 species spanning both plants (i.e., plant height) and animals (e.g., body length, mass, wingspan). We first evaluated the overall relationship between body size and urban affinity across all taxa, fitting two models (see Methods for details). We found that the effect of body size on urban affinity is stronger in plants than in animals (0.64 vs. 0.21), although uncertainty was substantial in both groups, with zero-overlapping 95% credible intervals (plants: -0.68 to 1.84; animals: -0.25 to 0.66). Variation in urban affinity was most pronounced at the family level (sd = 2.43), followed by class and order level (sd = 2.34 and 1.75, respectively). Similarly, the effect of body size varied most among families (sd = 1.24), compared to orders (sd = 0.73) and classes (sd = 0.27), suggesting that body size predicts urban affinity most consistently within the finer family-level taxonomic scale, rather than at higher scales where other factors may obscure relationships. Based on these patterns, we focused subsequent analyses at the family level, fitting Bayesian models for families with data on at least ten species to independently explore the relationships between urban affinity and body size. Because body size covaries with multiple ecological traits (e.g., dispersal ability and metabolic rate), we focused on family-level analyses to capture shared ecological strategies while still allowing sufficient variation among species to detect trait–environment relationships[39].

Across 371 families (93 plant and 278 animal families), we found no universal relationship between body size and urban affinity; instead, patterns were heterogeneous (Fig. 3). Using 80%, 90%, and 95% credible intervals to infer weak, moderate, and strong effects, respectively, we found evidence of body size filtering in 83 families (29 strong, 19 moderate, and 35 weak). These included 48 animal families (17% of animal families) and 35 plant families (38% of plant families), indicating that for most families, body size does not consistently predict urban affinity. Nonetheless, among plant families, the effect of body size on urban affinity was predominantly (N=77; 83%) positive, with 23 families showing strong or moderate effects. In contrast, animal families (N=278) exhibited more variable responses: 58% showed positive effects and 42% negative, with only a subset showing strong or moderate effects (positive: 18 families; negative: 6 families). Notable families with the strongest positive associations included Salicaceae (willows) and Columbidae (doves and pigeons), where larger species are more urban-tolerant. In contrast, Dipsadidae (snakes) and Accipitridae (birds of prey) showed the strongest negative associations. Further discussion of notable order-level effects is provided in the Supporting Information. While the overall patterns for family-level effects are visible in Fig. 3, we also developed an interactive online visualization of family-level effect sizes, available *here*.

The variability in both the direction and strength of urban body size filtering across taxa likely reflects the diversity of urban stressors and the contrasting taxon-specific pathways through which body size mediates sensitivity to them. In raptors, for example, the negative association between body size and urban affinity—consistent with previous findings[40,41]—likely stems from large species' need for extensive hunting territories, whose availability and access are constrained by urbanization-driven habitat loss and fragmentation. Similarly, the strong negative effect observed in Coleoptera supports the hypothesis that the urban heat island drives shifts to smaller body sizes in urban-tolerant ectotherms, consistent with Atkinson's temperature-size rule[42]. Larger beetles may also be more vulnerable to urban disturbance due to lower reproductive output and reduced dispersal capacity[43]. In contrast, urban communities of Lepidoptera (moths and butterflies) typically shift toward larger—and hence more mobile—species than rural communities[15], likely because greater mobility facilitates persistence in typically fragmented urban landscapes[44].

Our results are broadly consistent with prior taxon-specific trait-based studies (e.g., Hahs et al.[17]), but also highlight that relationships between body size and urbanization vary across taxa and analytical frameworks. For example, global syntheses and regional studies have reported positive, negative, or null size–urbanization relationships depending on clade and spatial scale. A recent global analysis that compiled empirical occurrence data for multiple terrestrial faunal taxa across

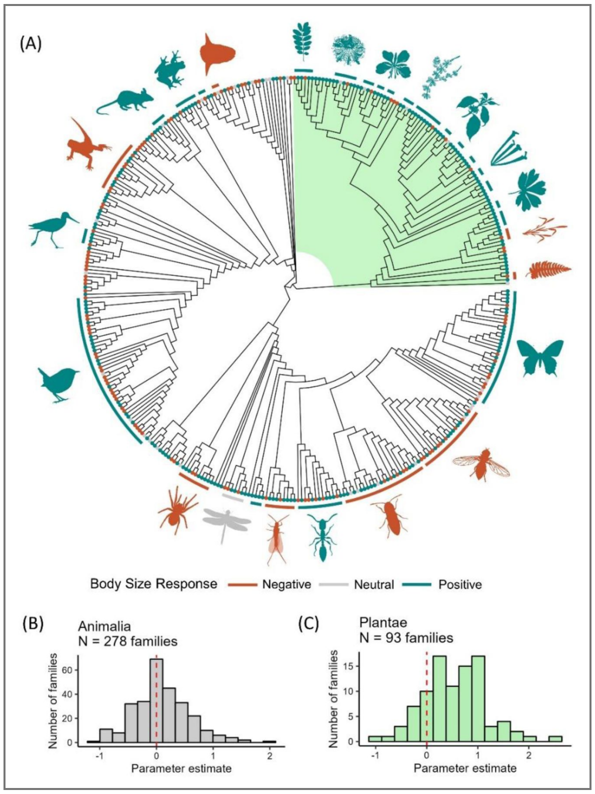

Fig. 3. **Effect sizes between body size and urban affinity across the tree of life and individual effect sizes for animals and plants families.**

(**A**) Effect sizes of the relationship between body size and urban affinity for the 371 families included in our analysis, plotted along a phylogenetic tree of life (see Methods); Plantae are highlighted and shaded in green. Colors indicate the direction of the effect: orange indicates negative, petrol indicates positive, grey indicates neutral (i.e. any effect sizes between -0.05 and 0.05). (**B**) and (**C**) histograms of individual effect sizes for each family, for animals (B) and plants (C). Orders are shown along the outside edge of the phylogenetic tree, each with a bar and icon, for any order with more than 3 families. An interactive version for full exploration of our results at both family and order level is available *here*.

cities worldwide reported broadly similar body-size responses to urbanization[17]. For four of the five groups that overlap with our analysis—amphibians, bats, bees, and birds—the direction of the body-size relationship with urbanization was consistent between studies. The only exception was carabid beetles, which tended to be smaller-bodied in highly urbanized environments in that analysis, whereas we detected no significant size effect for this family. Studies on birds, for example, have found mixed results, including positive associations to urbanization in some regional assemblages[45], no global relationship in others[46] or an overall negative relationship globally[23], and negative relationships in particular clades such as raptors[40]. Such discrepancies likely arise because different studies quantify urbanization differently, focus on different spatial grains, or analyze different components of species responses (e.g., presence–absence, abundance, or occurrence distributions). Additionally, a study on multiple taxa including butterflies and moths found a positive relationship in butterfly and moth community-weighed mean body size with increases in urbanization level, similar to our findings[31]. Researchers have also found that smaller-bodied dung-associated beetles potentially benefit from urban environments, which is similar to the negative association we found between urbanization and body size in beetles[47]. Our approach complements these studies by estimating occurrence-based urban associations across thousands of taxa simultaneously, allowing comparison of how consistently body size predicts urban affinity across taxonomic groupings rather than within a single lineage. In this sense, variation among published results does not contradict our findings but instead reinforces the conclusion that body size is a context-dependent filter whose direction and strength depend on ecological setting, taxonomic scope, and the urbanization metric used.

Order-level analyses (see Supplementary Text and our interactive figure *here*) offer further insight into the mechanisms shaping body size responses to urbanization. In plants, we consistently observed a positive association between body size and urban affinity, except for grasses and ferns. Taller species may gain a competitive edge in urban settings[48], by exploiting higher temperatures, increased CO_2 and nitrogen availability[49], and typically reduced O_3 concentration[50]. In contrast, smaller species of grasses and ferns were favored by urbanization in our study, likely stemming from high disturbance regimes in urban grasslands and ruderal environments. Among ectotherm animals—including Diptera, Coleoptera, Hemiptera, and Squamata—the general expectation is a shift toward smaller species, consistent with metabolic constraints imposed by the urban heat island (Fig. 1, Fig. 3). However, exceptions occur when urban fragmentation requires greater mobility, favoring larger and more mobile species[15]. Urban spiders also exhibit body size reductions, driven by both elevated temperatures and reduced prey size[51]. For endotherms such as rodents and birds, we typically anticipate a shift toward larger species because of increased habitat fragmentation, especially when body size correlates positively with mobility. While this pattern held for most bird families, notable exceptions—like Piciformes and Accipitridae—demonstrate negative associations, possibly due to constraints related to large home range requirements and prey size[52,53]. Future research should further explore such trophic consequences of urban size filtering, as these effects can either align across trophic levels or become mismatched. For instance, urban environments may favor larger predators—such as insectivorous birds and mammals—while simultaneously selecting for smaller insect prey species. Such mismatches can lead to nutritional stress, reduced reproductive success, and ultimately a more severe homogenization of urban predator guilds[54,55]. Another ecological consequence of size mismatches may occur when urban pollinator assemblages become disproportionally large or small relative to the floral traits of native plants, potentially reducing pollination efficienc[56]—although rapid evolutionary shifts in floral morphology could help mitigate these effects[57]. Because our synthesis is correlative and macroecological in nature, the mechanisms discussed above are best viewed as hypotheses that can be evaluated through future work combining experimental, trait-based, and longitudinal data.

Ultimately, the heterogeneous and sometimes weak relationships between body size and urban affinity suggests that body size alone cannot explain the emergence of extreme urban exploiters and the skewed shape of SUDs. Focusing on body size as a focal trait necessarily represents a simplification of the multidimensional processes underlying species' responses to urbanization, driven in part by data availability when conducting a taxonomically-broad synthesis. Instead, urban affinity likely depends on multivariate trait combinations[17,58] that vary among taxa[59] and ecological contexts[60]. Traits that are likely to correlate with urban affinity include dispersal capacity, behavioral flexibility, diet breadth, reproductive strategy, thermoregulatory ability, and, in plants, life history traits such as growth form, clonality, phenology, and seed size. The diversity of trait pathways through which species may persist or thrive in urban environments is consistent with the pronounced taxonomic heterogeneity we observe and helps explain why body size alone does not yield a universal pattern.

Current limitations and future directions

Our analysis, which incorporates over 17,000 species, represents the most extensive assessment to date of how body size relates to urban affinity across the tree of life. Such scale was enabled by the growing mobilization of biodiversity data through GBIF, particularly from citizen science platforms like iNaturalist[61]. Still, our analysis largely focused on common species, as we applied a cutoff of at least 100 observations per species per subrealm. As a result, rare or less frequently observed species are underrepresented, and their responses to urbanization remain an important avenue for future study. This is especially important given the growing recognition of cities as sanctuaries for various species[37]. Nevertheless, our findings highlight the relevance of common species to understanding macro-ecological patterns (sensu[62]). We focused here on broad-scale patterns, but future work should further explore the context-dependency of body size filtering—for instance, how it varies with city size, urban green infrastructure configuration, regional climate, and human cultural preferences. For example, one possible explanation for the observed trend of larger, urban-tolerant plants may lie in the widespread use of non-native woody ornamentals, such as alien trees and tall shrubs, which reflect human aesthetic preferences[63,64]—suggesting human preferences are an additional filter on plant size. These human-driven preferences may also influence detectability and recording effort, as larger and more conspicuous plant species are more likely to be planted, maintained, and documented in urban environments, and thus be available in GBIF for our analyses. However, we suggest that this is not purely a sampling artifact, but such processes likely interact with ecological filtering to shape the realized size structure of urban plant communities. Similarly, human–wildlife conflict and active management of large-bodied animals in cities may influence which species persist in urban environments, potentially constraining the upper end of the body size distribution. Taken together, these examples illustrate the importance of considering the socio-ecological context of urban species assemblages[65]. In parallel, while our study examined interspecific variation, growing evidence also points to important intraspecific responses, where body size shifts within species can modulate urban affinity[31,66,67].

One important limitation of our synthesis is the heterogeneity in how body size is measured across taxa, including differences among mean, maximum, and sex-specific estimates. While our analytical framework explicitly accounts for this variation through transformation, scaling, and hierarchical modeling with random intercepts (see Methods), residual measurement noise may still obscure weak size–urban affinity relationships. This challenge is inherent to large-scale trait syntheses that integrate data from disparate sources, and highlights the need for continued efforts to standardize trait databases and expand the availability of harmonized organismal trait data across the tree of life. Nevertheless, the urban affinity scores presented here will form a valuable foundation for future research and local-scale planning efforts, in particular those that use citizen science to track restoration progress. For example, these affinity scores could inform urban greenspace surveys aimed at calculating integrity indices—providing a repeatable, quantitative tool to assess and monitor the long-term success of urban ecological restoration by measuring the ‘urbanness’ of local species communities in urban greenspace[45]. In this context, incorporating taxon-specific body size-urban affinity relationships can enhance conservation outcomes by tailoring strategies to the size dynamics of assemblages. For instance, in assemblages where larger species are disproportionally filtered out (i.e., a negative size-affinity link), efforts should focus on increasing the size and quality of habitat patches and mitigating the urban heat island.

Conversely, in assemblages where smaller, less-mobile species are more vulnerable, improving functional connectivity between habitat patches should be prioritized[68]. For butterflies in particular, Pla-Narbona *et al.*[68] advocate for such context-specific management strategies—balancing habitat patch quality and connectivity—to promote more diverse urban butterfly communities.

Conclusions

Our global analysis of over 30,000 species provides new insight into how diverse taxa respond to urbanization, revealing a consistent skew in urban affinity—characterized by many urban avoiders and few exploiters—across biogeographic regions and taxonomic groups. We introduce the concept of Species Urbanness Distributions (SUDs) as a novel framework to quantify and compare the impact of urbanization on species communities. Much like Species Abundance Distributions (SADs) are essential for ecology and biodiversity research, SUDs offer a generalizable lens through which the community structure and ecological resilience of urban biotas can be assessed. Understanding the processes that generate SUDs, and understanding the ecological impacts of differently shaped SUDs, represent key avenues for future research.

Although body size emerged as a predictor of urban affinity, we found not only substantial heterogeneity across families and orders, but also that body size filtering alone is unlikely to explain the consistently skewed SUD shape. Taken together, these patterns suggest that urban affinity likely emerges from multiple trait combinations rather than a single, universally advantageous trait, and that strong affinity to urban environments is not uniformly expressed across taxa, despite occurring broadly across regions. Nevertheless, trait-based approaches—especially those integrating multiple functional traits—hold strong potential for uncovering the processes driving the diversity of species' urban responses and for interpreting the shape and skew of SUDs. Moreover, trait-based predictions of species' vulnerability could be used to formulate effective strategies to promote biodiversity in urban environments[17]. Our synthesis complements taxon-specific, presence–absence trait studies by identifying broad, cross-taxonomic patterns that can motivate and contextualize more mechanistic analyses[17,23].

Looking ahead, the continued growth of citizen science data platforms, such as iNaturalist, will play an increasingly critical role in tracking and understanding the mechanisms driving biodiversity responses to urbanization. These data streams will enable broader quantification of species' urban affinity, including rare and currently underrepresented taxa. Combined with trait-based modeling, this growing dataset could be leveraged to identify urban-vulnerable species and hence guide urban habitat restoration initiatives. In this way, SUDs and trait-informed predictions offer powerful tools for more effective urban strategies to conserve biodiversity on an increasingly urban planet.

Methods

Our methodological approach can be broken down into three key steps: (1) quantifying species-specific urban affinity scores, stratified by subrealm (i.e., biogeographic region); (2) collating measures of body size for as many species as possible for which we were able to quantify urban affinity; and (3) quantifying the relationship between urban affinity and body size at various taxonomic levels.

Quantifying urban affinity

Our aim was to derive a continuous, occurrence-based metric that describes how species are distributed along an urbanization gradient within a given biogeographic region. To do this, we followed a three-step procedure (sensu Callaghan et al.[21,69,70]). First, we quantified the level of urbanization associated with individual species' occurrence locations (i.e., coordinates) using remotely sensed night-time lights. Second, we summarized these values at the species level within each subrealm to obtain a species-specific regional urban score. Third, we expressed each species' urban score relative to the regional background of urbanization level to obtain a subrealm-specific measure of urban affinity, which reflects whether a species tends to occur in more or less urbanized environments than is typical for that region. In the following paragraphs, we walk through each of these steps in detail, including the assumptions, limitations, and intended interpretation of the resulting metrics.

Assigning urbanization level to species' occurrences

We downloaded occurrence data from the Global Biodiversity Information Facility (hereafter GBIF) (*https://doi.org/10.15468/dl.4dcbgt*) on February 4th, 2021, including ~1.4 billion biodiversity records from >24,000 datasets. GBIF data were filtered to only include observations that were recorded as species, and an additional step was taken to ensure that the listed genus in GBIF matched the genus of the species name, ensuring validity of the taxonomic nomenclature of GBIF. Due to uncertainty in matching observations with remotely-sensed products, any GBIF observation with a coordinate uncertainty > 1 km was removed. This filtering step removed individual observations with high spatial uncertainty, rather than excluding entire datasets or survey types. We only included species from a taxonomic Class (i.e., the rank between Phylum and Order) that had at least 10 species reported to GBIF, focusing on the most common classes for downstream analyses.

We then overlaid GBIF species occurrence observations with a remotely-sensed layer representing a continuous proxy of urbanization—Visible Infrared Imaging Radiometer Suite (VIIRS) night-time light[71]. We used this proxy as it is a continuous measure of urbanization commonly used to represent urban extent[72,73,74]. Previous work has shown that VIIRS night-time lights is negatively correlated with greenness measured through the Enhanced Vegetation Index (EVI) and positively correlated with human population density[69,71]. Although night-time light intensity can vary among cities with similar impervious surface due to differences in land use, infrastructure, and cultural lighting practices, at broad spatial scales it functions as an integrative proxy of urbanization[75,76,77,78,79,80], with localized heterogeneity contributing primarily to additional variance rather than systematic bias. We used Google Earth Engine[81] for our geospatial processing and data were obtained for the VIIRS Stray Light Corrected Nighttime Day/Night Band Composites product, representing monthly composites, (i.e., this dataset in Google Earth Engine: *NOAA/VIIRS/DNB/MONTHLY_V1/VCMSLCFG*) with a native resolution of ~500 m^2. We took the median of all monthly composites for each pixel (i.e., a single grid cell of the nighttime lights raster representing a fixed ground area) to calculate a pixel-level urbanization value, measured in average radiance, using imagery from January 2015 to January 2021. GBIF data were filtered from January 1st, 2010 to February 4th, 2021. We acknowledge that these two temporal scales do not precisely match, but because urban conversion at the landscape/regional scale happens relatively slowly, we assume that the level of urbanization between 2015 and 2021 accurately captures the relative differences between regions with low and high urban land cover.

To avoid computational overload, we used geohash encoding to assign every record in GBIF to a "pixel" representing the VIIRS average radiance based on its geographic coordinates. We used geohash7 encoding to divide the geographic area into grid cells (referred to as blocks), each representing an approximate spatial area of 150 m^2. The VIIRS night-time lights data, with a native resolution of ~500 m^2, was then matched to these blocks by assigning each geohash7 block the average VIIRS radiance value that intersects it. We do not assume positional accuracy at the scale of the geohash blocks, but geohash encoding was used solely for computational indexing, while the effective spatial resolution of the urbanization metric is that of the VIIRS data (~500 m). This approach allows us to avoid unnecessary redundancy in the data while maintaining the original VIIRS resolution.

Accounting for geographic context through subrealm stratification

To account for geographic heterogeneity in both species' distributions and the baseline levels of urbanization, we stratified our analyses by global biogeographic subrealms (N=52; Fig. S1). Subrealms represent an intermediate hierarchical level within the One Earth[82] (*https://www.oneearth.org/bioregions/*) bioregionalization framework, grouping the 185 terrestrial bioregions into broader units that reflect shared species pools and ecological contexts while maintaining meaningful regional structure. This scale represents a practical compromise between analyzing data at the finer bioregion level (which would result in many regions with insufficient observations for robust analysis) and broader classifications such as continents or the 14 biogeographic realms, which aggregate ecologically distinct regions and species pools. This regionalization has been widely used in macroecological and biogeographic research to contextualize species–environment relationships because subrealms capture meaningful gradients in biotic assemblages that are not accounted for by climatic classifications alone[83,84].

This stratification allows species' associations with urban environments to be interpreted relative to the environments available within the regions they occupy. This is important, as previous work has shown that species' responses to urbanization are constrained by biogeographic context, because regional species pools reflect shared evolutionary, ecological, and historical filters[23]. Previous work has also shown that urban associations among species are context-dependent, and interpreting species' responses without accounting for regional baselines conflates availability of urban environments with species' affinity to them. This distinction is critical because identical levels of urbanization (e.g., VIIRS radiance) can have different ecological meanings across regions with different species pools and land-use histories. It avoids conflating species' urban affinity with global differences in urban availability.

Calculating urban affinity

After each GBIF occurrence record was assigned a VIIRS radiance value, as described above, we summarized these values at the species level within each subrealm. Specifically, for each species *s* within each subrealm *r*, we calculated the mean VIIRS radiance across all occurrence locations of that species in that subrealm. We refer to this quantity as the subrealm-specific urban score ($U_{s,r}$). Formally, the urban score for species *s* in subrealm *r* is defined as:

$$U_{s,r} = \frac{1}{n_{s,r}} \sum_{i=1}^{n_{s,r}} L_i$$

where $n_{s,r}$ is the number of GBIF occurrence records for species *s* within subrealm *r*, and L_i is the VIIRS night-time lights radiance value associated with occurrence i. The urban score is therefore an absolute descriptive summary of the urbanization levels associated with a species' occurrence locations within a given subrealm. Higher urban scores indicate that a species tends to be observed in more highly urbanized (i.e., more brightly lit) environments, whereas lower values indicate occurrence in less urbanized environments. These urban scores serve as the intermediate step in our workflow and form the basis for the subsequent calculation of urban affinity.

To express species' urban associations relative to the regional context in which they occur, we converted species-specific urban scores into a subrealm-specific measure of urban affinity. This step accounts for differences in baseline urbanization among regions and ensures that species are evaluated relative to the environments available within their biogeographic context. Within each subrealm r, we defined urban affinity for species s as: $A_{s,r} = U_{s,r} - \text{mean}(U_r)$, where $U_{s,r}$ is the species-specific urban score calculated for species *s* within subrealm *r*, and $mean(U_r)$is the mean VIIRS radiance across all occurrence records of all species in that subrealm. This transformation centers species' urban scores on the regional background level of urbanization.

Urban affinity values therefore describe whether a species tends to occur in environments that are more urbanized or less urbanized than is typical for that region (Fig. S6). Species with negative values occur disproportionately in less urbanized environments (urban avoiders), whereas species with positive values occur disproportionately in more urbanized environments (urban exploiters). By default, these values are relative measures, interpretable only within subrealms, and are not intended to represent absolute or globally comparable levels of urbanization. Importantly, this metric quantifies a species' realized spatial association with urban environments relative to the regional background based on occurrence data. This framing is consistent with previous macroecological studies that infer species' environmental affinities from spatial distributions rather than performance metrics (e.g.[21,85]). Consistent with this interpretation, previous work has also shown that measures of urban affinity (sometimes referred to as tolerance) calculated from VIIRS night-time lights are strongly correlated with analogous metrics using alternative proxies of urbanization such as human population density and the global human modification index[45].

We applied the above procedure to any species that had at least 100 observations in a subrealm. Previous work has shown that this cutoff approximates the variability of a species' response to urbanization and ensures that enough of a species urban habitat use has been captured[21,86]. After this filtering we were left with a total of 56,181 data points—i.e., unique urban affinity measures of a species in a subrealm—for potential inclusion in our analyses. These records represented 30,373 species that had at least one urban affinity measure, from 47 classes and across 51 subrealms (Fig. S7; Data S1). The number of subrealms a species was found in was mostly 1 (64%) but ranged from 1 to 34 (Fig. S8). All urban affinity measures (i.e., urban affinity by subrealm measures) which we produced as part of our workflow are made available, as we hope to advance further testing of urban affinity among different taxonomic groups and regions, while highlighting that correct interpretation of these relative urban affinity values is essential before use.

Sampling biases are common in large biodiversity databases, including GBIF. For instance, urban areas are better sampled compared to remote regions, as contributors typically concentrate around areas with high human density. However, our approach mitigates this concern by calculating each species' urban affinity relative to the regional background of observations within the same subrealm. As a result, any broad-scale bias toward sampling in human-dominated landscapes affects all species within a region similarly, allowing meaningful comparisons among species rather than reliance on absolute estimates of urban occurrence. Importantly, our interpretation therefore focuses on relative differences among species within shared geographic contexts, rather than on absolute levels of urbanization. Previous work has found that this approach of assigning urban affinity is strongly correlated with occupancy-detection models where the target-background sampling is explicitly accounted for (see Figure S5 in [21]). As illustrative examples, these data can be used to better understand the differences in urban affinity among Hymenoptera in Northeast American Forests (Fig. S9), Lepidoptera in Southeast Asian Forests (Fig. S10), or Asterales in Scandinavia & West Boreal Forests (Fig. S11).

Species urbanness distributions

Our analysis of species urbanness distributions was descriptive in nature, relying on data visualization using ggplot2 to make histograms and density histograms of urban affinity values for each subrealm. In these analyses at the subrealm level, species are treated equally without any differentiation taxonomically, compared with the taxonomically-stratified analyses where species within each taxonomic rank are treated as similar (see below). To evaluate the consistency of SUD distributions across taxonomic levels and regions, we compared distributions among the most data-rich subrealms using violin plots for groups represented by ≥50 species (Supplementary Figures S2–S4).

Aggregating measures of body size

Our objective was to compile a dataset of species-specific measures of 'body size', or 'organism size' more broadly to integrate with our measures of species-specific urban affinity described above. We aimed to find measures for as many species as possible, maximizing our sample size for modeling. For plants, we used 'plant height' as a proxy for body size, and data were downloaded from the TRY database—a database compilation of plant traits from many different dataset[87]. For animals, body size can be measured in different ways, depending on the taxonomic group of interest (e.g., body length, wingspan, biomass, shell size, radius, forewing length, body mass, or biovolume). Therefore, our dataset was purposefully broad in its composition of body size estimates. Because 'body size' is the predominant form referred to in the literature, we use this throughout, but take it to broadly mean 'organism size' as discussed above.

To build the animal dataset, we first performed a semi-systematic broad literature search, using Web of Science, Google Scholar, Zenodo, Dryad, and Figshare with variations of the key words: “body size”, “organism size”, “body length”, “body mass” and “interspecific”, “global patterns”, “animals”, and higher-level groups such as classes (e.g., “Aves”, “Birds”, “Mammals”, “Mammalia”). We started by downloading known compilations for various taxa, for example mammals[88] or Odonata[89]. In these instances, we spent minimal further time searching for specific body size data for these larger taxonomic groups, assuming that these compilations had already aggregated the majority of data available. Following this, we conducted more detailed literature searches, predominantly using Google Scholar and Web of Science, which focused on our *a priori* list of species for which we had a measure of urban affinity (Data S1). These were conducted at class, order, or family taxonomic levels, but not at taxonomic levels below family. Multiple keywords were used for each group while searching when it was obvious to do so. For example, when searching for body size measures in Coccinellidae both “ladybirds”, “ladybugs”, and “Coccinellidae” were used in search strings, as well as “wing length”, “body length”, or “body size”. Search effort was qualitatively proportional to the number of species we had in each taxonomic level. For example, because we only had 43 species with urban scores from the class Diplopoda but 3,515 species from the order Lepidoptera, we spent proportionately more time and effort searching for body size data for Lepidoptera. Similarly, we spent more time on hard-to-find taxa, namely groups from Insecta. In our searches we generally ignored studies that were focused on intraspecific variation in body size for one or a few species, unless we found that the species was included in our urban affinity list. In addition to literature searches, we emailed networks of colleagues, looked at reference lists in papers that had data, and emailed corresponding authors of papers who had potentially relevant data but for which data were not accessible.

After this semi-systematic searching, we re-assessed the remaining species for which we had an urban affinity measure but not a measure of body size. We then performed a second-level targeted search (i.e., more systematic) for any family with at least 10 species remaining for which we had a measure of urban affinity. First, we searched Web of Science and Google Scholar one family at a time and looked at the first 100 hits, with the family name ‘and’ “body size” used as search terms. Second, we used Google search engine to search for these remaining species individually (N~3,100). We focused on including species for which Google immediately returned an estimate of body size (e.g., through Wikipedia, or an aggregating website), and did not go to original species descriptions. This detailed searching and the aggregation of body size measures concluded in June 2022.

Measurements of body size

In our searching for body size, we were agnostic to the type of body size measure, given that many different measures are used for quantifying body size, or proxies for body size. For each dataset we downloaded or processed, we kept track of the following key metadata properties: ‘type’, ‘units’, and ‘measurement detail’. Type refers to the different types of body size measurement, ranging from body length and body mass to Weber’s length in ants. Table S1 shows a list of the different body size types encompassed in our analysis (see statistical details below for how different body size types were accounted for in our analyses). For each dataset, we also kept track of the units (e.g., mm, g, mg cm^-2, or mm^3). And lastly, wherever possible, we noted the measurement detail of the body size measures, whether the mean, median, or maximum was used, or whether it was for males or females only. Many times, however, this information was not readily available, and thus this metadata field was not required in our dataset composition.

Taxonomic harmonization and dataset integration

Because body size data were aggregated across many potentially different datasets, we performed a taxonomic harmonization step to regain some species that did not match due to typos, spelling mistakes, or synonyms. For this, we treated Plantae and Animalia separately and used the taxize package[90] in R to search through the list of species and find any synonyms or fuzzy matches of other taxonomic entities, always matching back to the GBIF taxonomic backbone, given that our urban affinity measures follow this taxonomy (Data S1). With the possible synonyms and matches, we then integrated the urban affinity measures with the body size dataset using either direct matches or matches of synonyms. The taxonomic harmonization step regained a total of 831 species (see Fig. S12) that were integrated in the dataset for analysis. Data S3 provides details on the 223 different 'datasets' (i.e., downloaded data, or manually added data) that were processed as measures of body size. The most prevalent class in our final dataset (Fig. S13) was Insecta (N=7,526), followed by Magnoliopsida (N=4,872) and Aves (N=3,313).

Our final dataset for potential analysis and modeling (Data S2) included a total of 94,087 observations (i.e. unique combination of species urban affinity values, subrealm, and body size measure) for 20,957 species that had at least one measure of urban affinity and at least one measure of body size.

Quantifying the relationship between urban affinity and body size

Our objective here was to understand the relationship between urban affinity (the response variable) and body size (the predictor variable). Our dataset had potentially multiple measures of body size for an individual species, and differing levels of metadata. For example, some datasets may have specified whether the mean was used, or others might have specified for females only (see Table S1). Therefore, before modeling, our goal was to minimize the undue effect of having too many random effect levels. First, because an individual species could have multiple measures of body size, we selected the body size measure that was most common among the species in each family. For example, if a species had both a measure of body length and of body mass, we selected the measurement type that was most commonly available among the species in each family. Second, we further reduced the potential number of levels and variation in body size measurement by creating a synthetic "metadata" variable that was the combination of 'type', 'units', and 'measurement detail'. By doing this, we decreased the potential number of levels of a random effect from 223 (i.e., the number of data sources) to 71 (i.e., the combination of type, unit, and measurement detail). Third, several papers/data sources could have all reported the same metadata (e.g., maximum body length for females in mm), and instead of being treated as individual random effects because they were from different data sources, we assumed that these represented similar data and collapsed them into one random effect level (here, for maximum body length for females in mm). Importantly, this procedure did not result in the exclusion of species lacking a particular body size measurement type; rather, all species with at least one available body size estimate were retained, with measurement heterogeneity explicitly accounted for through hierarchical modeling.

Overall kingdom-level model construction

We used Bayesian hierarchical models to test for the effect of body size on urban affinity. In our models, urban affinity was the response variable and body size was the predictor variable of interest. To evaluate the overall relationship between body size and urban affinity, we fitted two comprehensive models that incorporated hierarchical taxonomic levels and the relationship with body size. The first model included fixed effects for kingdom and log-transformed body size due to its skewed distribution, along with their interaction, to investigate differences in the body size effect on urban affinity between plants and animals. The random effects accounted for hierarchical taxonomic levels, incorporating random intercepts and slopes for class, order, and family to capture variation at each level. Additional random effects for metadata and subrealm were included as random intercepts to control for study-specific differences in data and regional differences in urban affinity. The model formula was:

$$\text{urban affinity} \sim \text{body\_size\_scaled\_log10} * \text{kingdom} + (1 + \text{body\_size\_scaled\_log10} \mid$$

$$\text{class/order/family}) + (1 + \text{body\_size\_scaled\_log10} \mid \text{metadata}) + (1 \mid \text{subrealm}).$$

The second model built upon this structure but only included an interaction term between log-transformed body size and kingdom as well as kingdom as a fixed effect to determine if the effect of body size on urban affinity varied consistently across the plant and animal kingdom. It maintained the same hierarchical random effects structure as the first model, with class, order, and family nested to account for hierarchical variation, and metadata and subrealm included as additional grouping factors. The formula was:

$$\text{urban affinity} \sim \text{kingdom} + \text{body\_size\_scaled\_log10:kingdom} + (1 + \text{body\_size\_scaled\_log10} \mid \text{class/order/family}) + (1 + \text{body\_size\_scaled\_log10} \mid \text{metadata}) + (1 \mid \text{subrealm}).$$

Family-specific model construction

For our main analyses we chose to employ a ‘many models’ approach, where we fit individual models for each family that met a set of minimum criteria because many families do not have a known association or published information on the extent to which urban affinity associates with body size. A family was only included if there were at least 10 unique species with an urban affinity measure and body size measure, and a subrealm was only included if it had at least two species included to specify a random slope. For example, if there was only one species of a particular family included in our dataset, this family would not have received an independent model. We decided to focus our main analysis at the family level for three key reasons. First, for most of the taxonomic families included in our analyses there is little *a priori* expectation about the effect of body size on urban affinity (i.e., little to no literature on the subject; but see McClain and Boyer[39]), and therefore we wanted each model to represent an advance in knowledge of that relationship for that family. Second, there were large imbalances in the number of data points available for each taxonomic group, with some families having hundreds of species with available data and others with only a handful of species. Thus, we wanted to avoid shrinkage where the model results were primarily driven by the taxonomic groups with a larger number of data points represented. Third, we wanted to avoid an instance where a family (or other taxonomic grouping) could have little or no relationship between body size and urban affinity, but if included together in one model could result in a positive effect (see Fig. S14 for a simulated example). This was a smaller concern at the family level, which we present as the main analysis, because of the smaller imbalance in data availability across the taxa within each family.

When we fit the family-specific models, there were different requirements for the random effect structure depending on how many subrealms and metadata sources (i.e., types of body size measures) were available. In the simplest case, all species in a family were just from one subrealm and had just one data source for body size. But this was not always the case, and therefore we developed four different ‘types of models’ which varied in their treatment of random effect structure. Each ‘type’ of model, however, had the same overall objective—to quantify the relationship between body size and urban affinity. The four model types are as follows. Type 1: had at least two subrealms and at least two types of synthetic metadata (see above) sources included. Type 2: had data from only one subrealm and only one type of synthetic metadata source included (but could have data from more than one initial data source). Type 3: had at least two subrealms and only one type of synthetic metadata source included. Type 4: had data from only one subrealm and at least two types of synthetic metadata sources included. For all types of model fits, the response variable was the urban affinity measure, described above, and the fixed effect of interest was body size which was log10-transformed and scaled and centered by the synthetic metadata source. Type 1 had a random intercept and slope for subrealm, allowing the intercept and slope to vary across different levels of subrealm as well as a random intercept for the synthetic metadata source. Type 2 had no random effects. Type 3 had only a random intercept and slope for subrealm, allowing the intercept and slope to vary across different levels of subrealm. Type 4 had only a random intercept for the synthetic metadata source. Modeling was done using the ‘brm()’ function in R from the brms package[91,92,93]. For all model types we specified a standard normal prior, with a mean of 0 and a standard deviation of 1 applied to the fixed effects of the model. Models were fit with 1000 warmup iterations, 6000 iterations for the Markov Chain Monte Carlo sampling, 4 chains, and the adaptation target acceptance probability was set to 0.99.

For models of type 1 and type 4, where we combined metadata for body size measurements among different species, we also explored more complex model structures that included a random slope for body size by metadata source, in addition to subrealm. Such a model structure would allow the relationship between body size and urban affinity to vary across measurement types. However, these models often substantially reduced interpretability and inflated uncertainty around slope estimates, especially when metadata groups were sparsely represented, which was common. Additionally, many of the families only had 2 types of metadata, limiting our statistical power to fit random slopes. Comparative analyses showed that such models produced weaker or more uncertain estimates than our main model structure (i.e., random intercept for metadata of body size). We also note that to account for heterogeneity in body size measurement types, all body size values were log10-transformed, scaled, and centered by their metadata source prior to analysis, following standard practices in allometric studies. We use two illustrative examples (Figures S15 and S16) to illustrate the influence of including a random slope for metadata source.

Additional analyses beyond family level

Although our main analysis was focused on the family level, one potential drawback is that species could be excluded from any of the analyses for a family that has a small number of species. Plus, because some analyses have previously been conducted at higher taxonomic levels (e.g., Lepidoptera), we repeated the above procedure described for family at the order (see Supplementary Text) and kingdom level.

Supplementary Materials

Supplementary Text

In addition to family-level effect sizes, we performed the analysis at the order level, and found similar heterogeneous results. Among the 128 orders, a total of 45 had some evidence of an effect of body size on urban affinity (14 weak, 6 moderate, and 25 strong). Some of the orders with the strongest positive effect size included Sapindales (dicots, soapberry plants) and Columbiformes (birds, doves and pigeons), and orders with the strongest negative effect sizes included Coleoptera (insects, beetles) and Piciformes (birds, woodpeckers). Of note are the differential responses down the taxonomic guilds, where some families can show contrasting results, but there may be a strong effect when looking at the order level, or higher (e.g., Fig. S2).

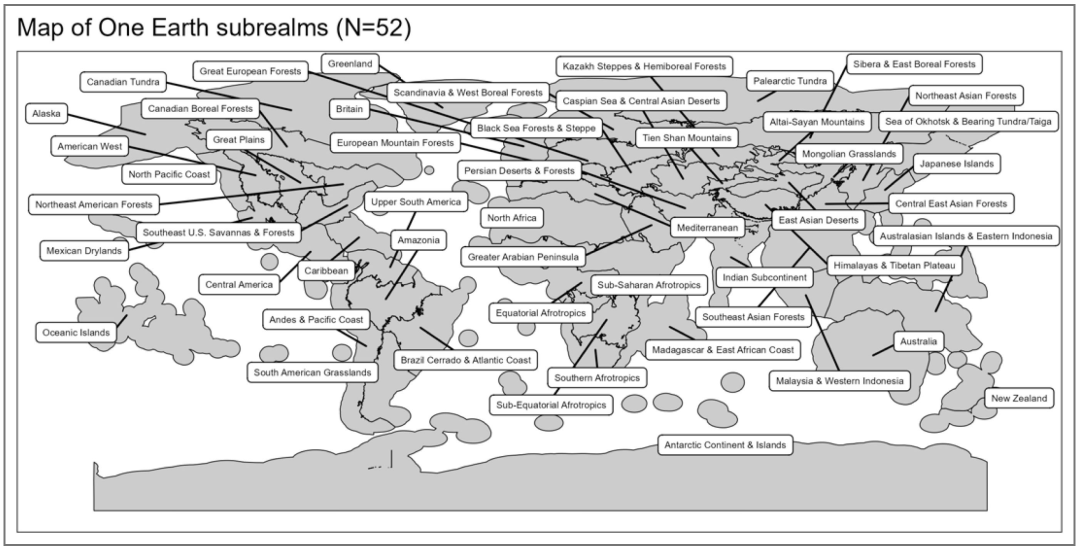

Fig. S1. **We used subrealms as our geographical aggregation.** Subrealms were quantified from aggregating bioregions as identified by One Earth (see more here: *https://www.oneearth.org/bioregions/*). The subrealms level was chosen after exploring the tradeoff between accounting for geographic differences in urban affinity and the number of species that could be included.

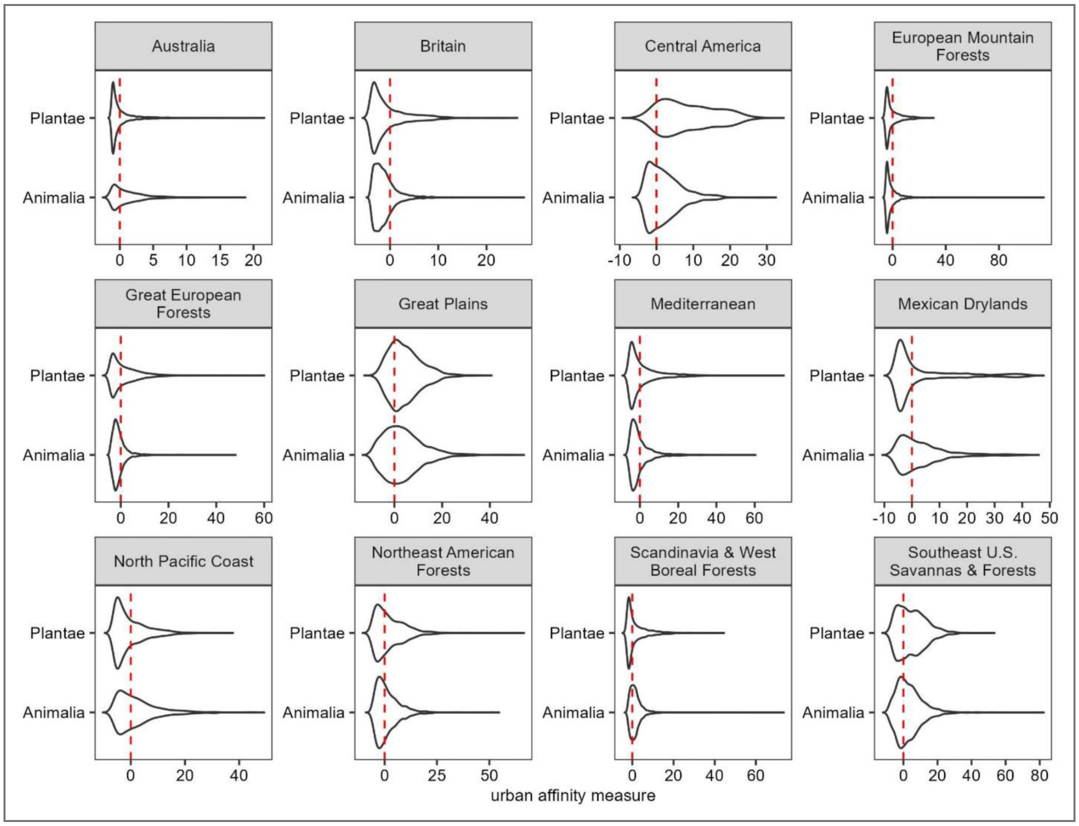

Fig. S2. **Violin plots showing the distribution of urban affinity values by kingdom across the 12 subrealms with the greatest sample sizes.**

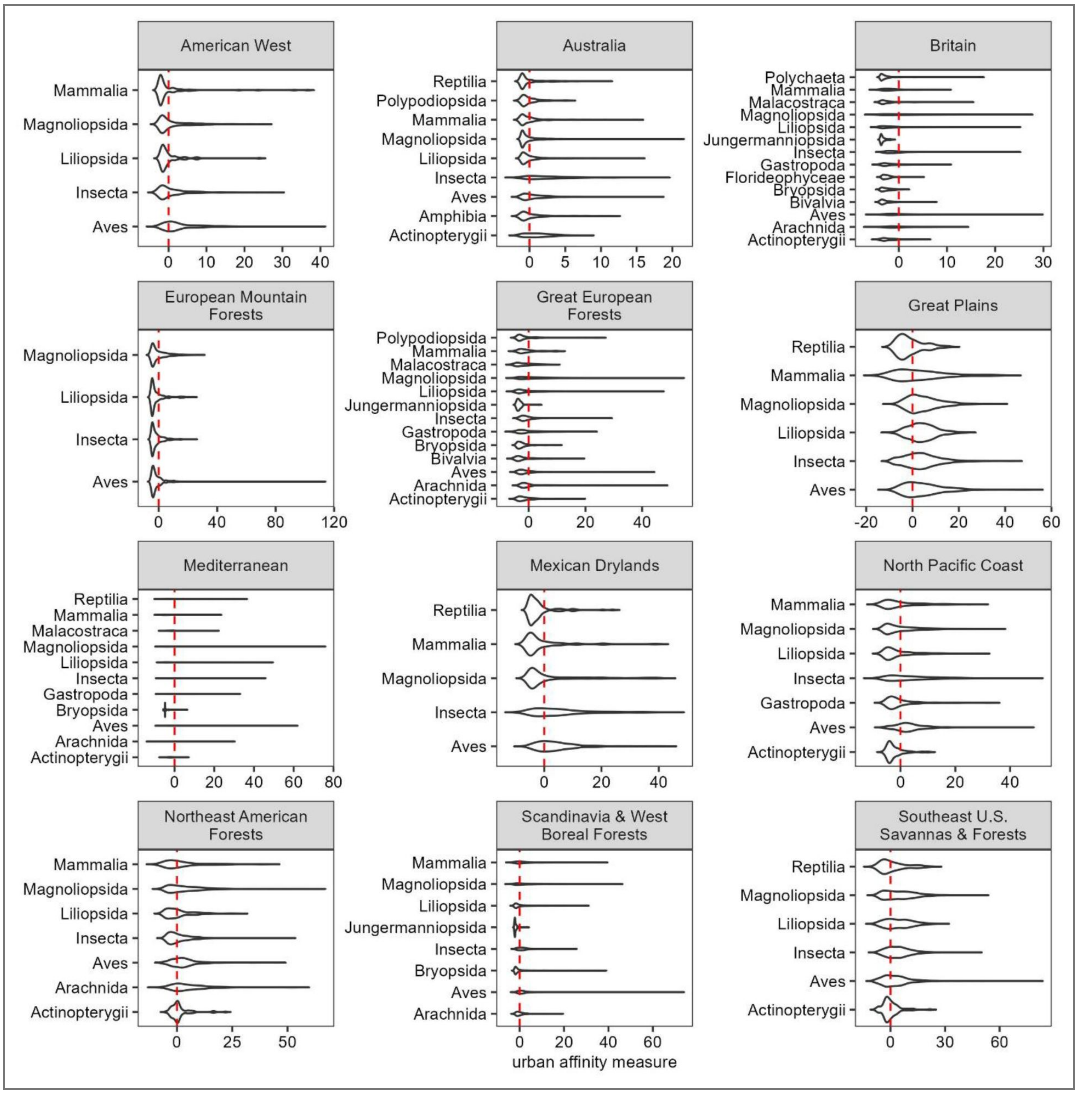

Fig. S3. **Violin plots showing the distribution of urban affinity values by class across the 12 subrealms with the greatest sample size.** Only classes represented by ≥ 50 species within a subrealm are included.

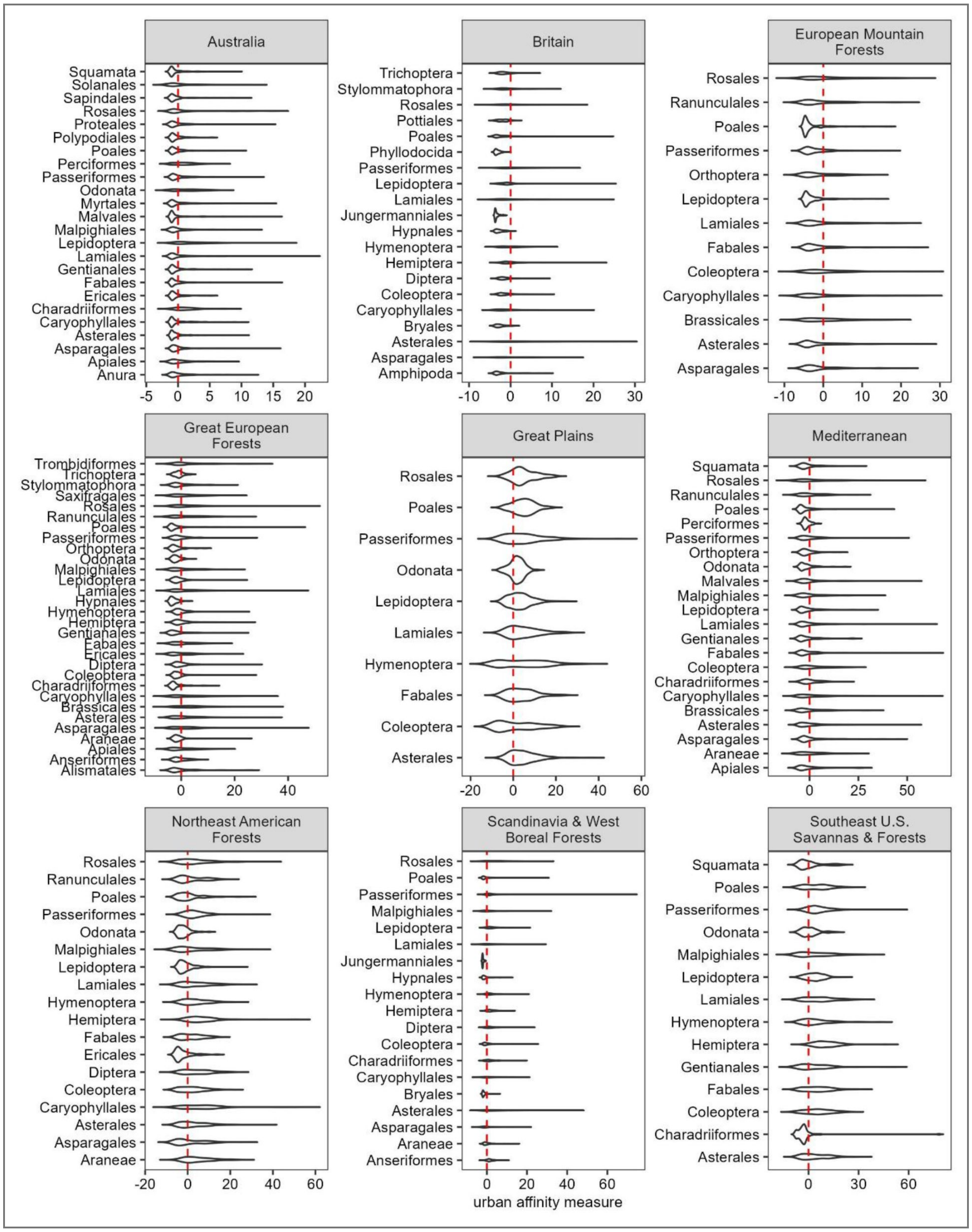

Fig. S4. Violin plots showing the distribution of urban affinity values by order across the 9 subrealms with the greatest sample size. Only orders represented by ≥ 50 species within a subrealm are included.

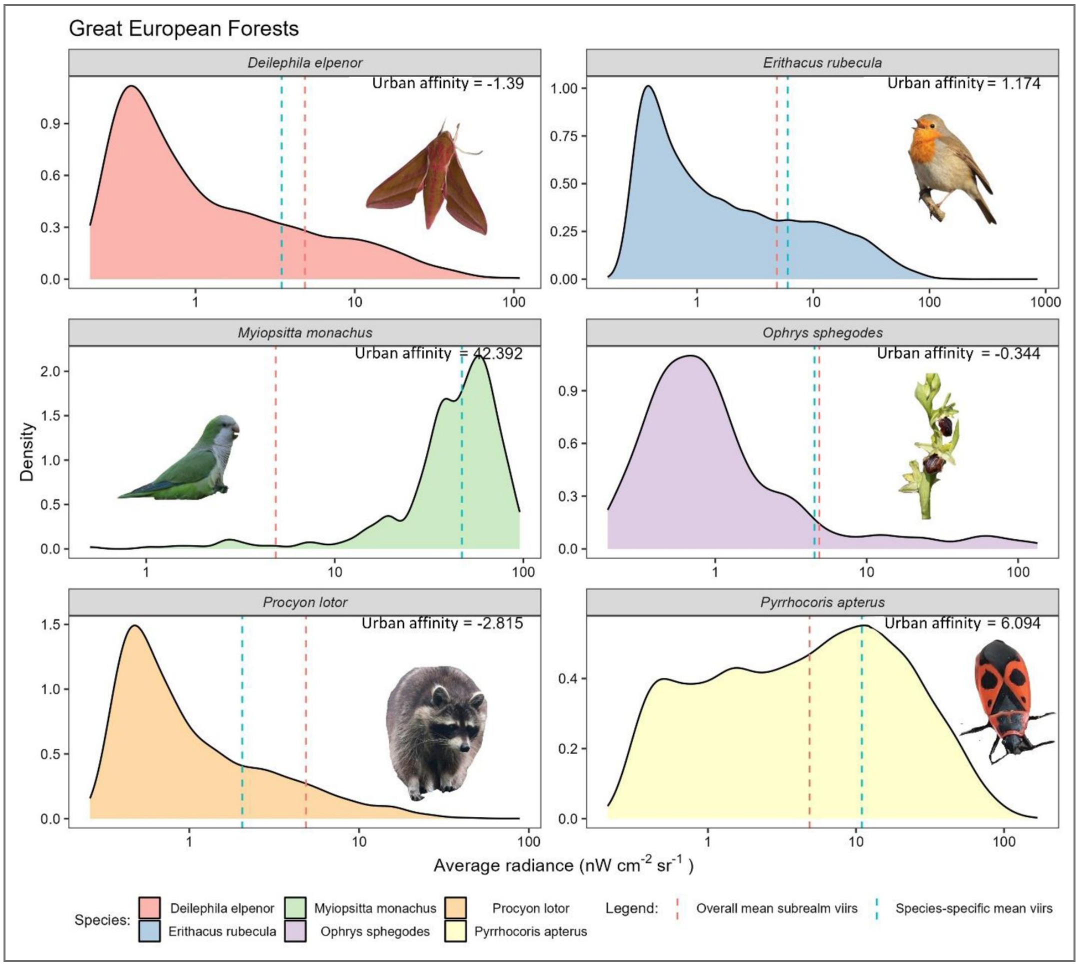

Fig. S5. **An illustration of the species-specific distribution of observations and the VIIRS values, in average radiance, of those observations for six different species within the Great European Forests subrealm.** Of note is that the urban affinity is not shown, as some are negative values, but these values are shown in the text.

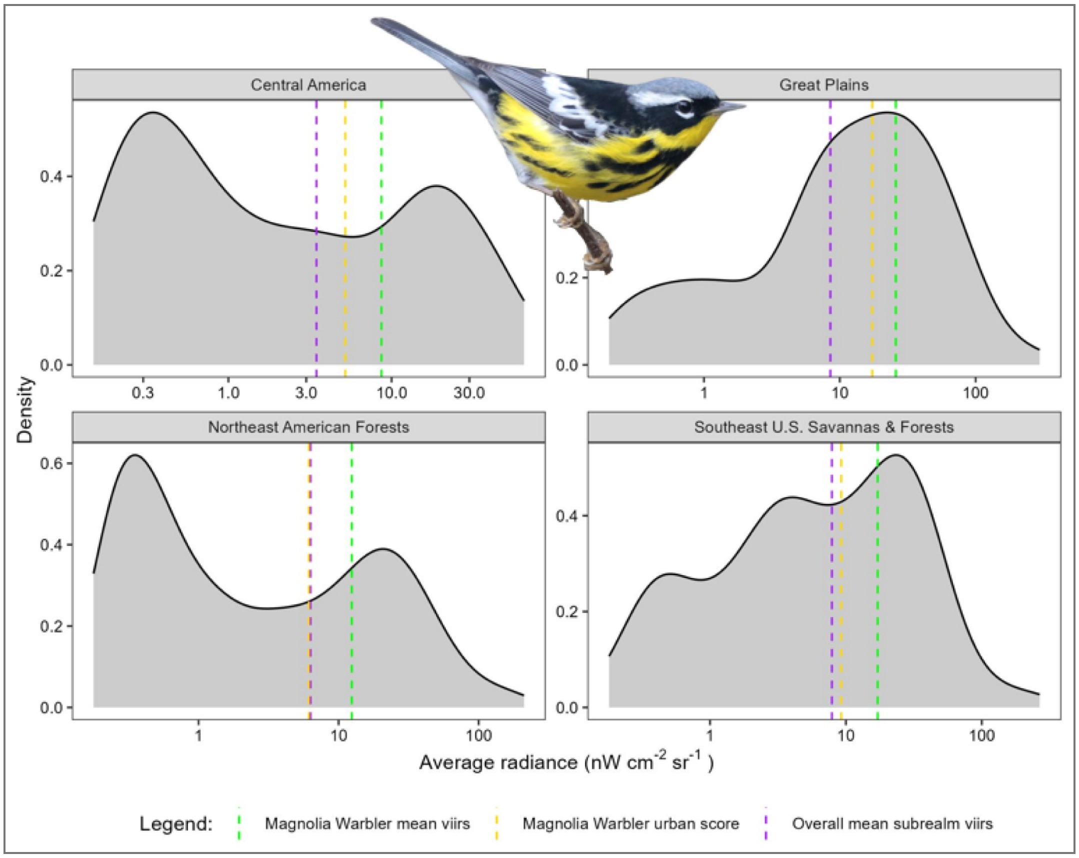

Fig. S6. **The distribution of Magnolia warbler *Setophaga magnolia* observations and the VIIRS values, in average radiance, of those observations in four different subrealms.** Shown using dashed lines are the species-specific mean (green), the subrealm-specific mean of VIIRS (violet), and the resulting urban affinity measure (yellow).

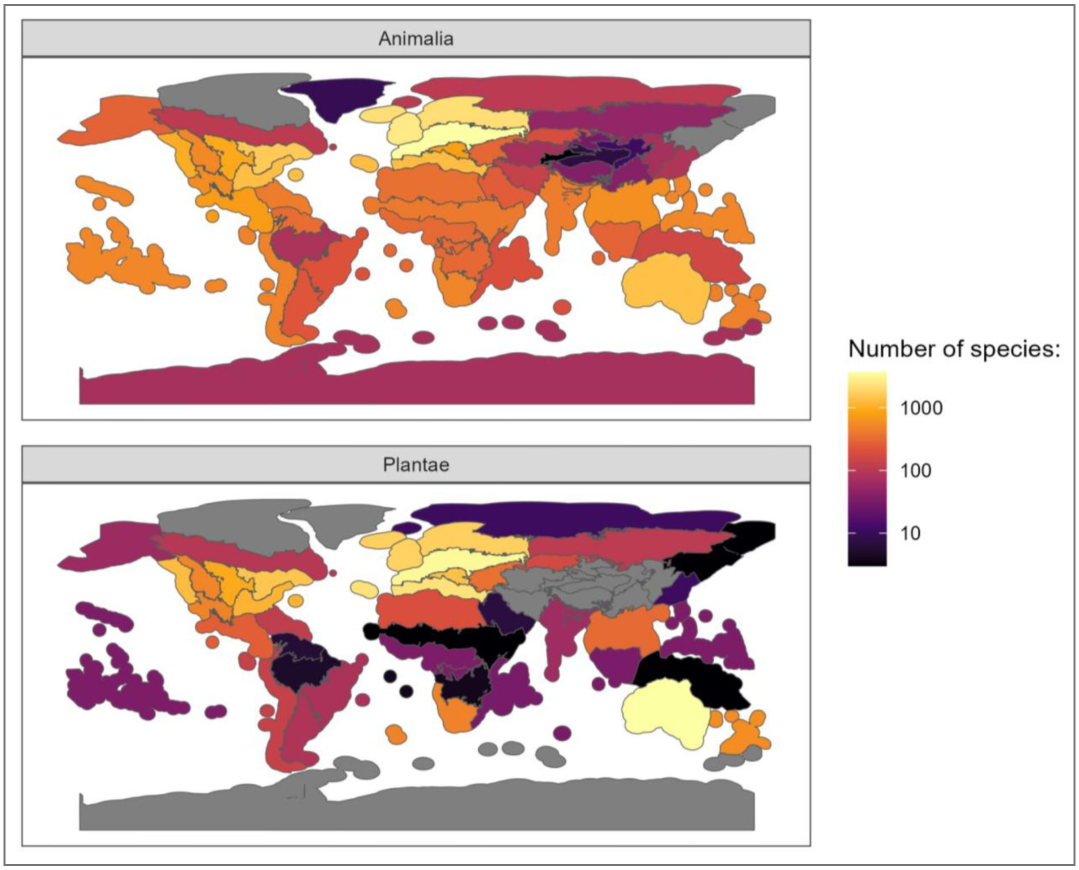

Fig. S7. The total number of species for which we calculated urban affinity scores, stratified by subrealm and shown separately for Animalia (top) and Plantae (bottom). The subrealms with their names are shown in Figure S1. The dataset of species' urban affinity scores is provided in Table S1.

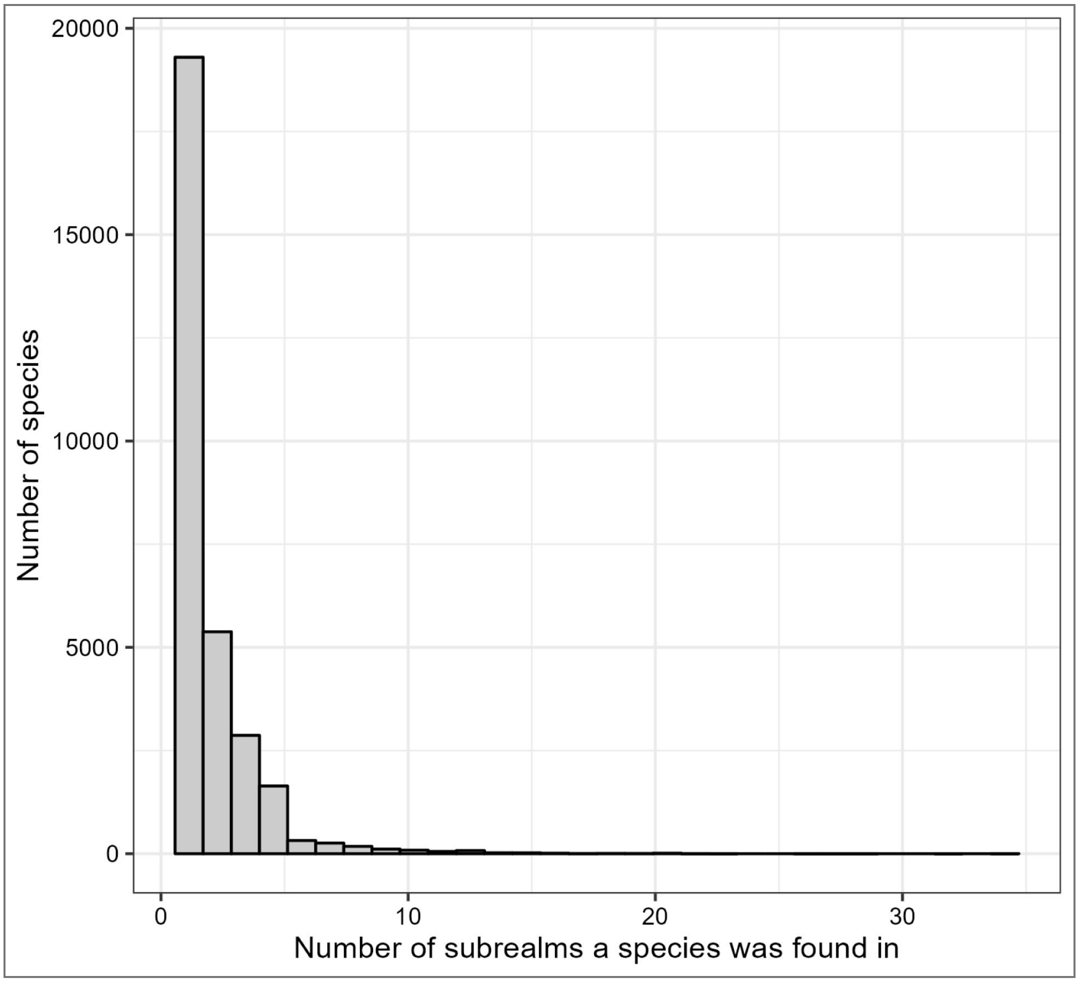

Fig. S8. **The total number of subrealms for which a species had an urban affinity score.** The majority of species (64%) only had an urban affinity score from one subrealm, but the range was from 1 to 34.

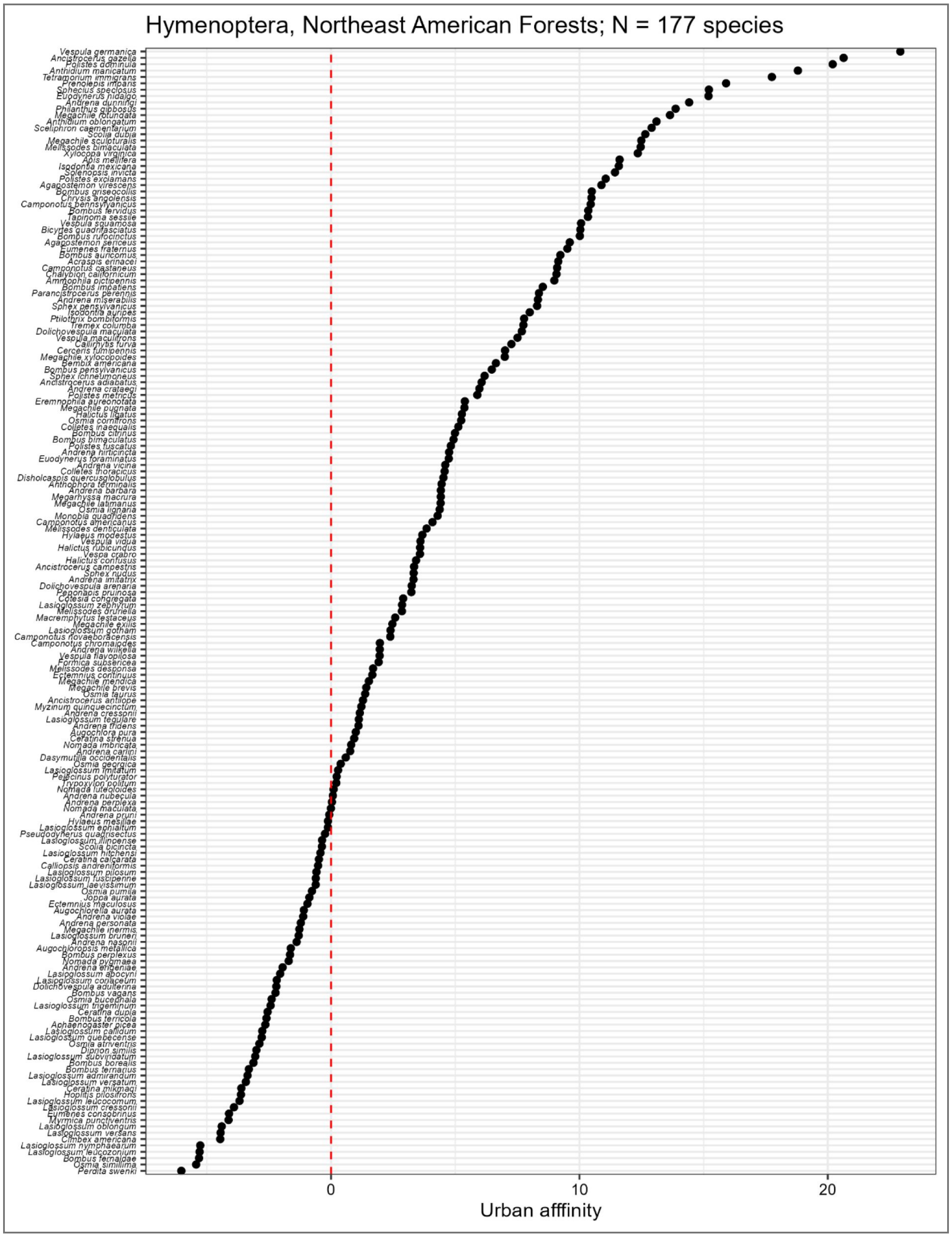

Fig. S9. **An illustrative example, showing the relative urban affinity scores for Hymenoptera in the Northeast American Forests subrealm.** The plot is for illustrative purposes and the values for each species can be found in Data S1.

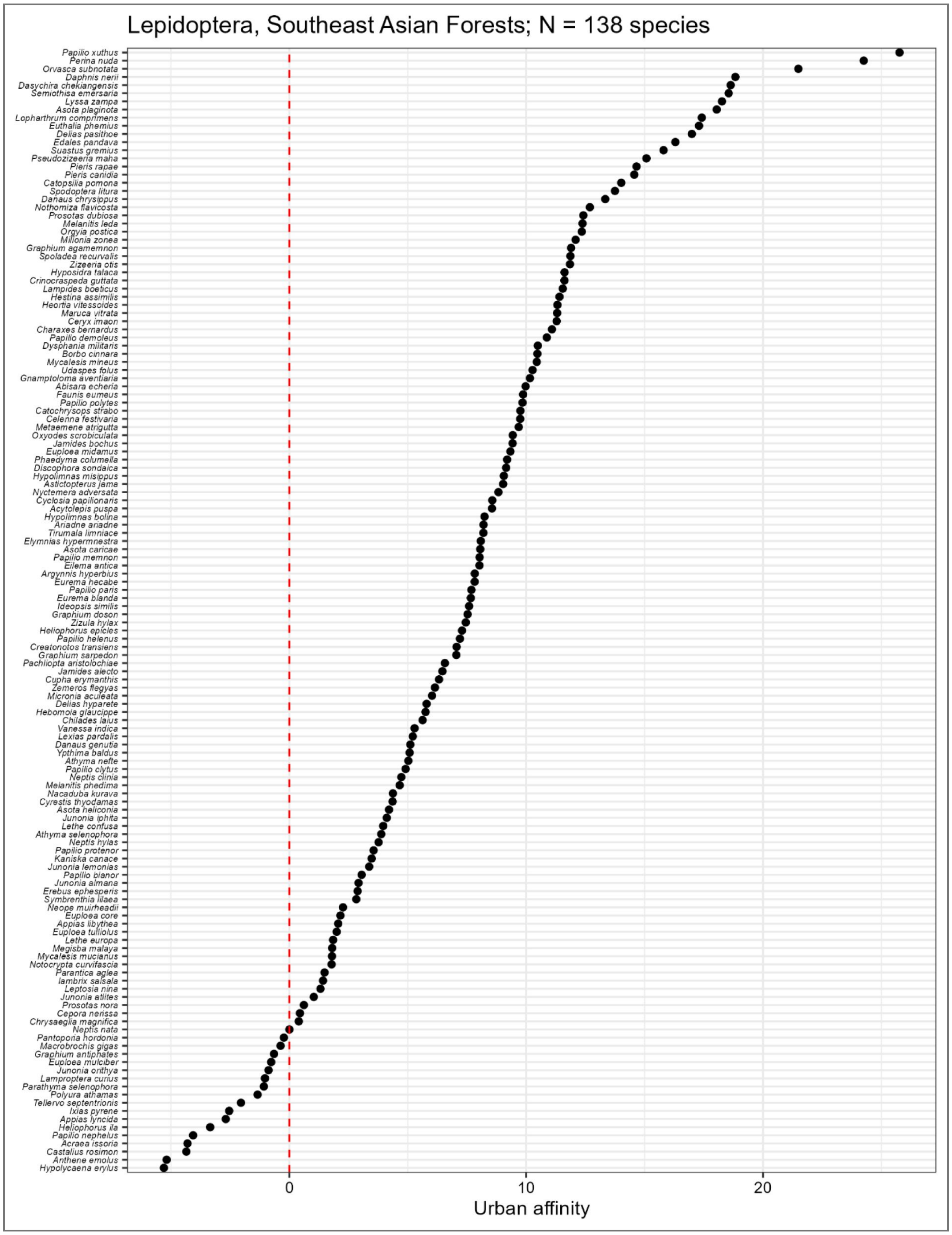

Fig. S10. **An illustrative example, showing the relative urban affinity scores for Lepidoptera in the Southeast Asian Forests subrealm.** The plot is for illustrative purposes and the values for each species can be found in Data S1.

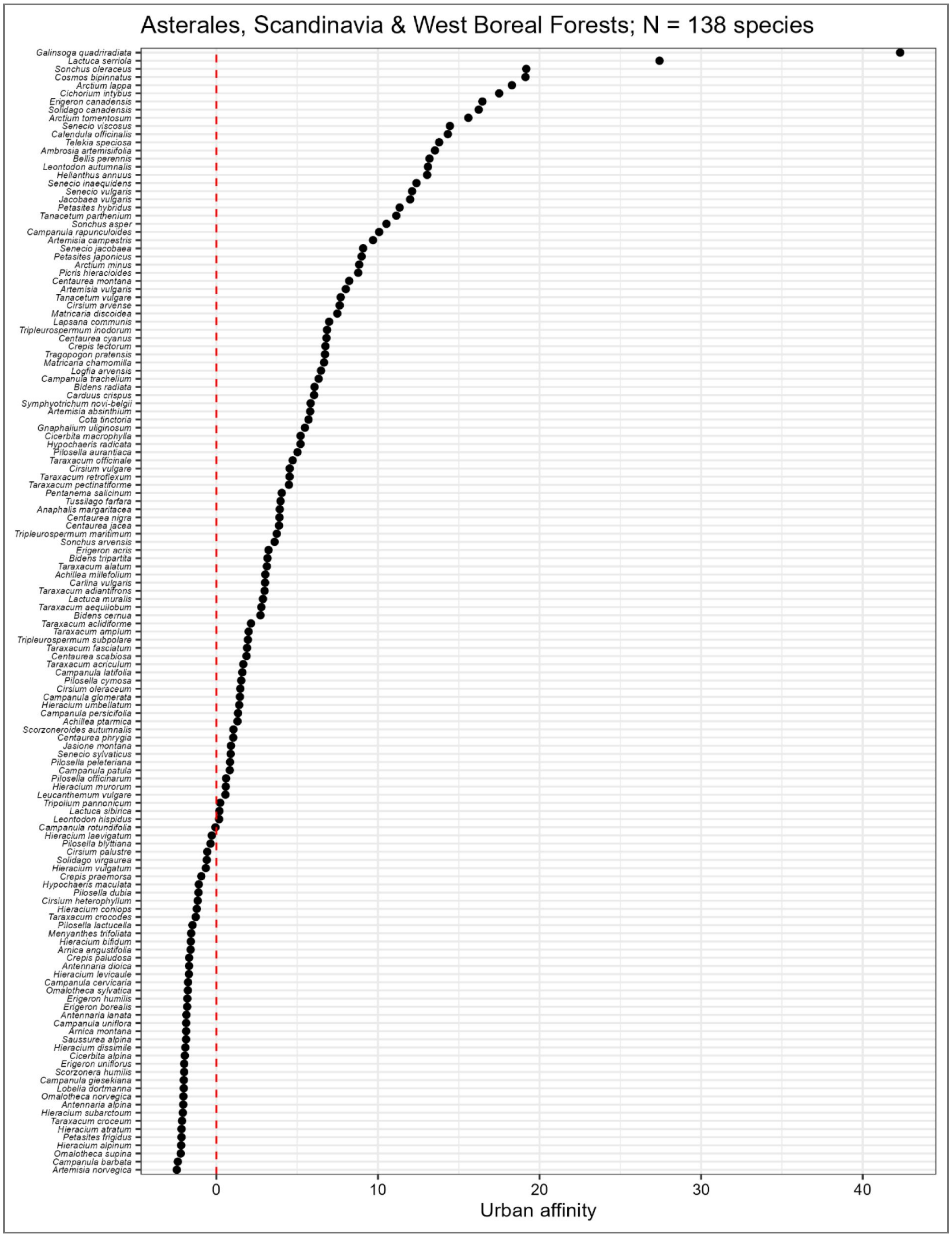

Fig. S11. **An illustrative example, showing the relative urban affinity scores for Asterales in the Scandinavia & West Boreal Forests subrealm.** The plot is for illustrative purposes and the values for each species can be found in Data S1.

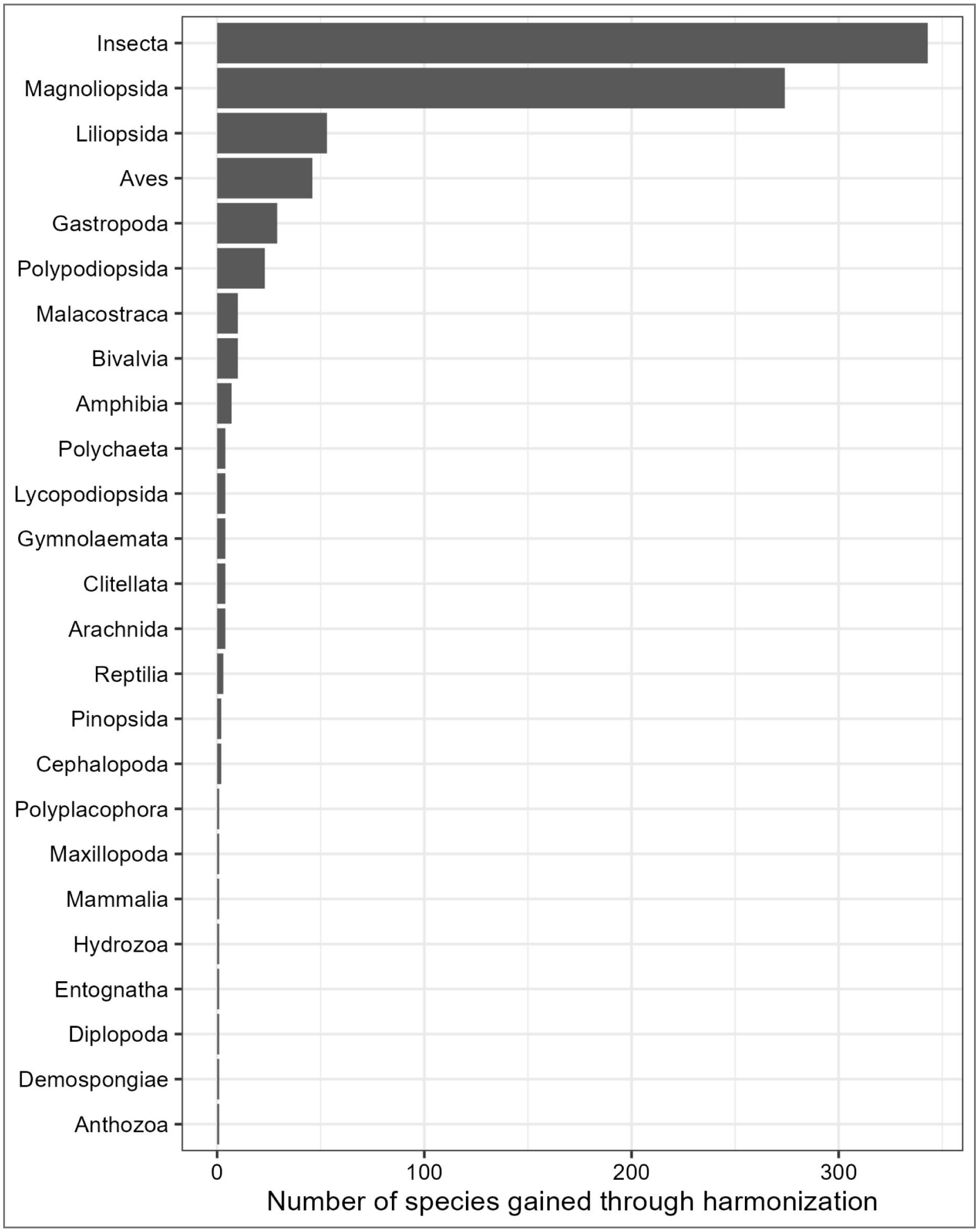

Fig. S12. **A summary of the number of species, shown per class, gained through taxonomic harmonization, and therefore included in the analysis dataset.**

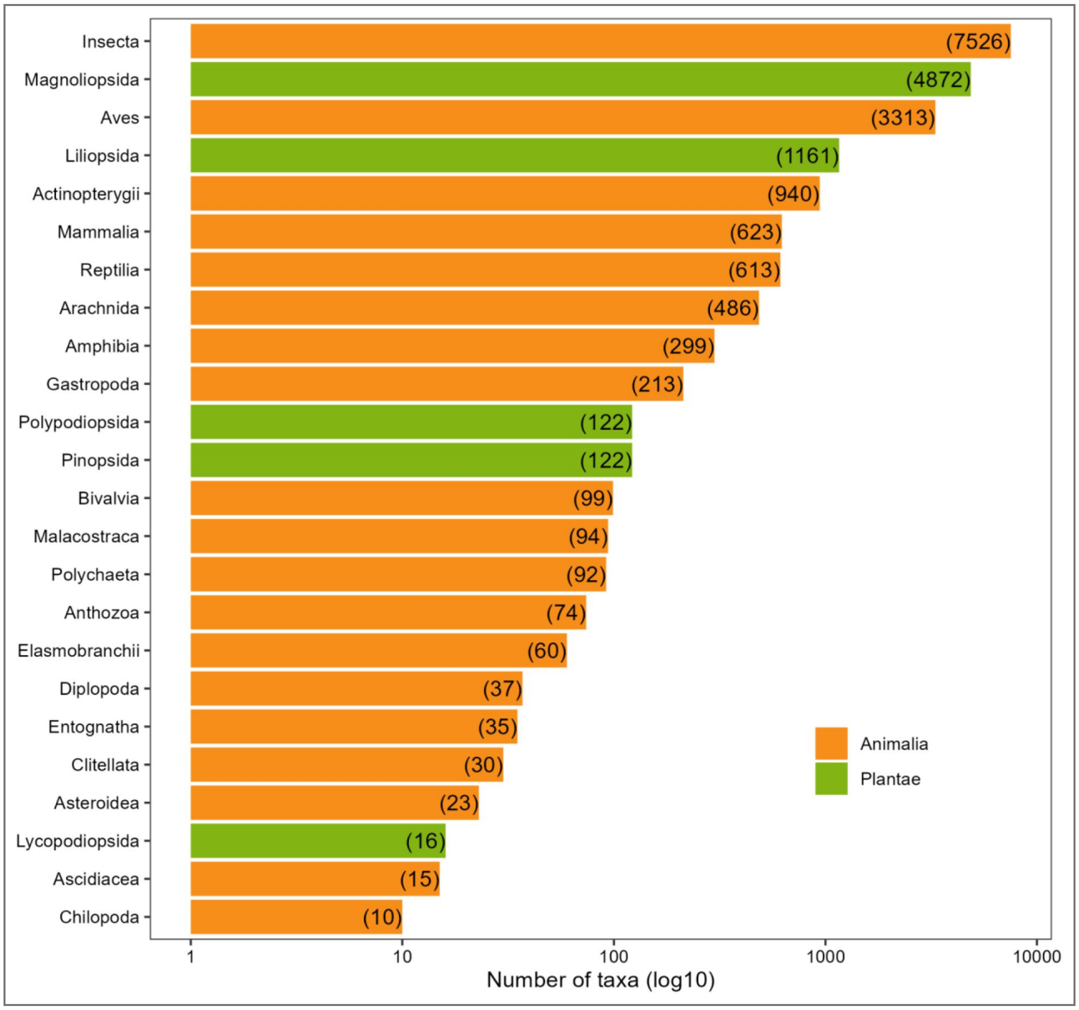

Fig. S13. The number of taxa, on a log10-transformed scale. These can be found in Table S3.

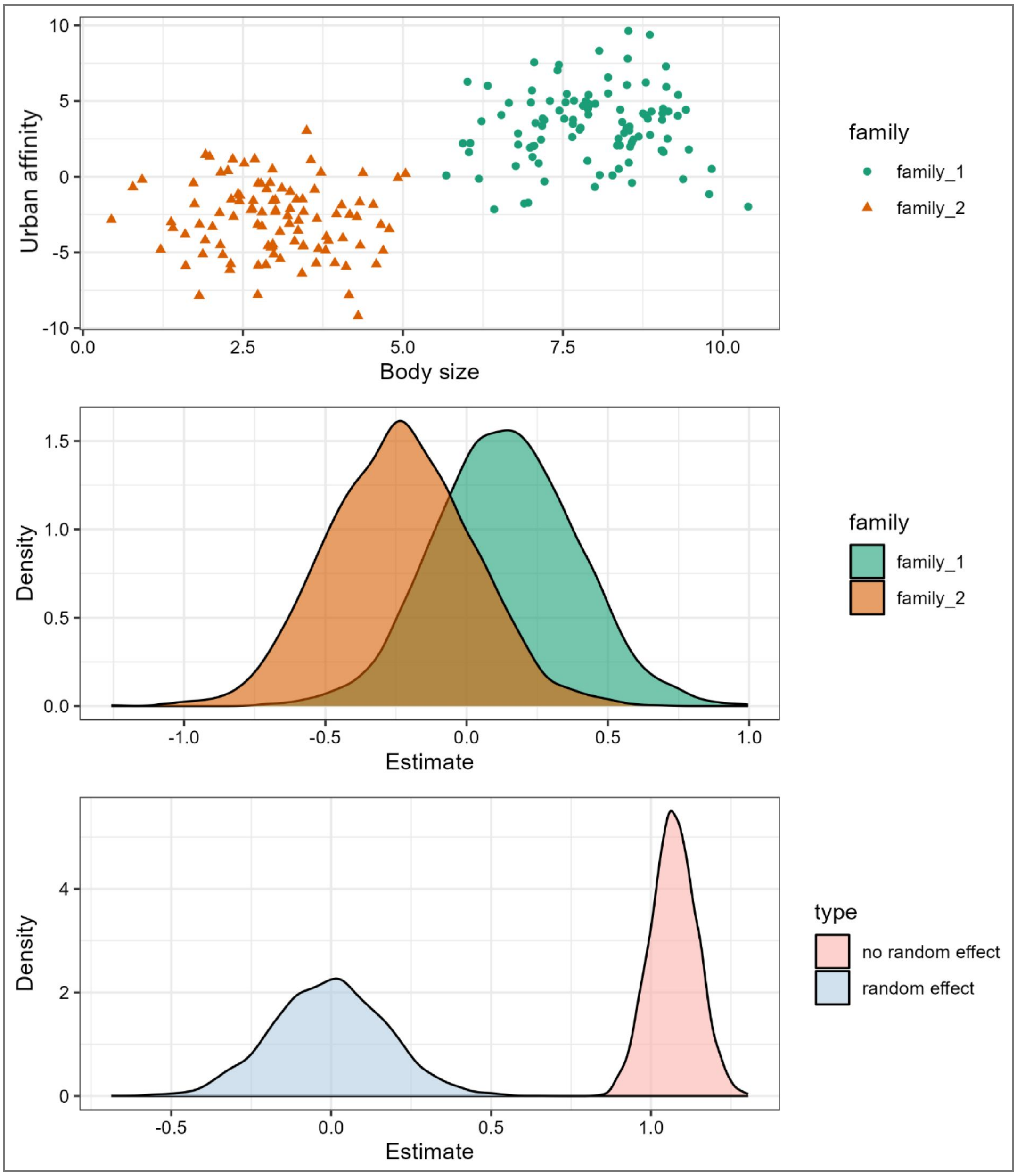

Fig. S14. **We chose to model each taxonomic group (i.e., family, order, class, phylum, and kingdom) independently of one another to avoid the influence of where individual families could have no effect but result in a positive effect if modeled jointly.** The top panel shows simulated raw data for two families; the middle panel shows the posterior distribution of a bayesian model fit for each of these families separately; the bottom panel shows the posterior distribution of a bayesian model fit for a model including family as a random effect and for a model not including family as a random effect.

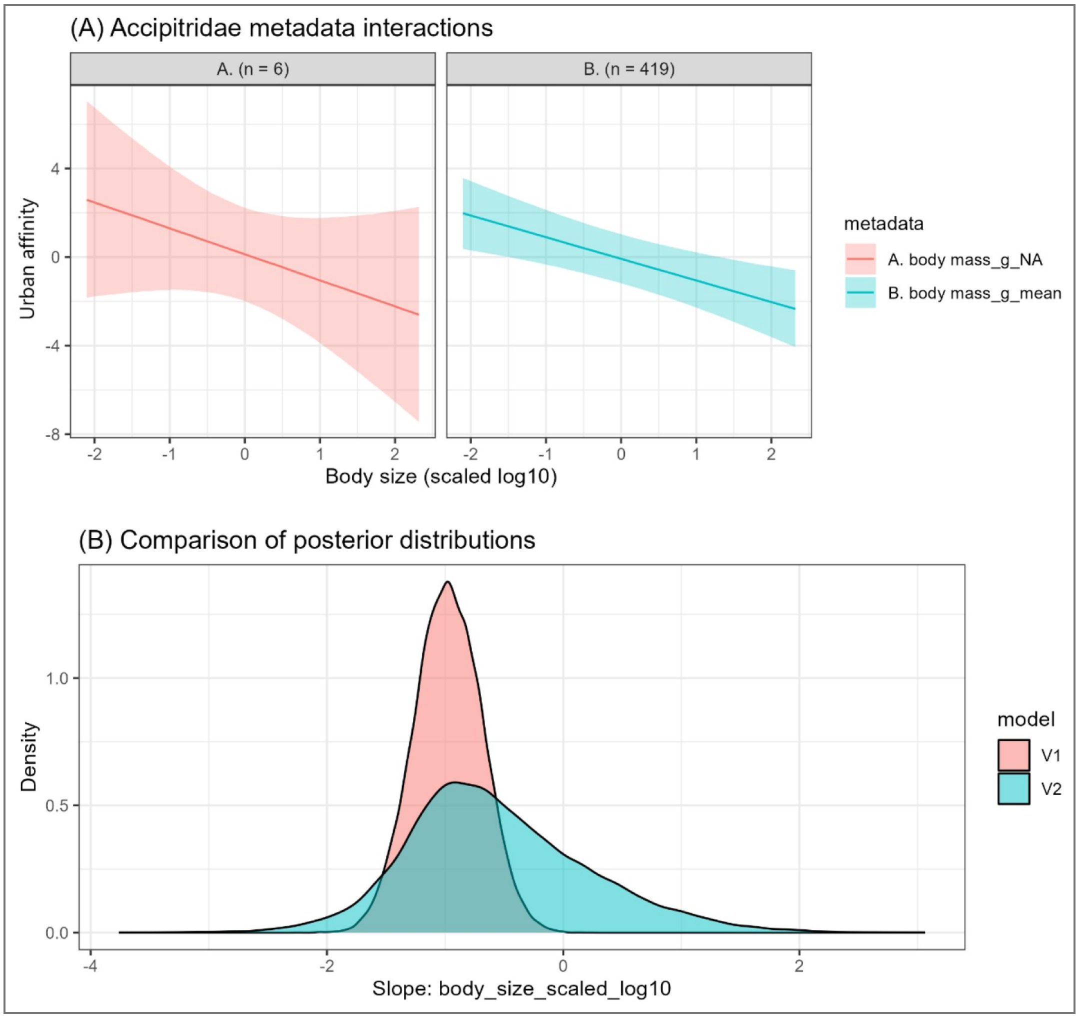

Fig. S15. An illustrative example showing the influence of using a random slope for body size, by showing the (A) Interaction between body size (scaled and log10 transformed) and body size measurement type (metadata; see Methods for details) for the family Accipitridae. Facets represent different types of body size metrics used in the dataset, labeled with a letter identifier and corresponding sample size (n). Lines represent predicted urban affinity based on body size, with 95% credible intervals shown as shaded ribbons. These are extracted from a model fit with an interaction between metadata and body size to purposefully investigate the influence of metadata and the relationship with body size. (B) Posterior distributions of the slope for body size (scaled and log10 transformed) under two model structures: V1 includes a random slope for body size by subrealm and a random intercept for metadata (as presented in main results), while V2 adds a random slope for body size by metadata. The inclusion of this additional random slope in V2 increases uncertainty and pulls slope estimates toward zero, particularly when data are sparse within body size measurement types as illustrated here. Also see Fig. S15.

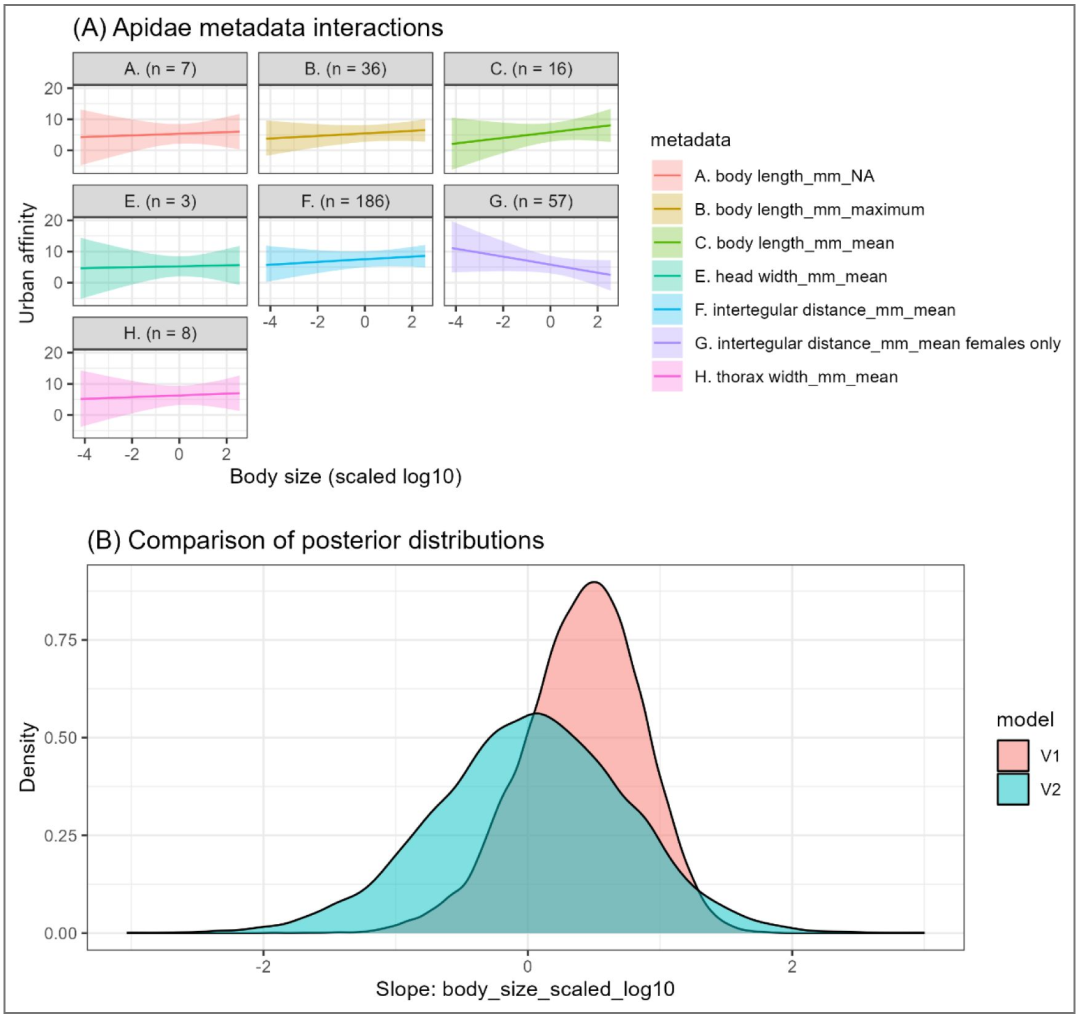

Fig. S16. **An illustrative example showing the influence of using a random slope for body size, by showing the (A) Interaction between body size (scaled and log10 transformed) and body size measurement type (metadata; see Methods for details) for the family Apidae.** Facets represent different types of body size metrics used in the dataset, labeled with a letter identifier and corresponding sample size (n). Lines represent predicted urban affinity based on body size, with 95% credible intervals shown as shaded ribbons. These are extracted from a model fit with an interaction between metadata and body size to purposefully investigate the influence of metadata and the relationship with body size. (B) Posterior distributions of the slope for body size (scaled and log10 transformed) under two model structures: V1 includes a random slope for body size by subrealm and a random intercept for metadata (as presented in main results), while V2 adds a random slope for body size by metadata. The inclusion of this additional random slope in V2 increases uncertainty and pulls slope estimates toward zero, particularly when data are sparse within body size measurement types as illustrated here. Also see Fig. S14.

Type of body size			
Weber's length	abdominal length	biovolume	body length
body mass	body mass female only	carapace width	cephalothorax width
colony height	column diameter	coral diameter	diameter
dorsal mantle length	dry mass	elytron length	femur length
forewing length	fork length	head height	head length
head width	height	hind tibia length	hindwing length
intertegular distance	longest length	plant height	pronotal width
radius	shell size	shell volume	snout vent length
standard length	thorax length	thorax width	total biomass
total length	wet mass	width	wing length
wingspan			

Table S1. A list of 41 potential 'types' of body size that were used for potential inclusion in our body size dataset. We aimed to incorporate as many types of body size measures as possible and were not restrictive in our searching for body size measures.

Data availability

All data analysis was conducted in R statistical software and relied heavily on tidyverse (Wickham et al. 2019). The DOI representing our download is: *https://doi.org/10.15468/dl.4dcbgt*. Our processing of the GBIF data to quantify urban scores is available here: *https://github.com/coreytcallaghan/body_size_vs_urban_tolerance*. Not all body size data can be openly shared due to copyright restrictions, however the freely available dataset, cleaned and processed for our analysis is available here: *https://github.com/coreytcallaghan/body_size_vs_urban_tolerance*. In this repository we did provide reproducible data and code, albeit not for the entire dataset of body sizes. We will archive a cleaned version of this repository in Zenodo upon acceptance of this manuscript.

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Additional information

Statement of authorship

CTC, DEB, TM conceptualized the project and developed project methodology. CTC, TM, VS, JHW, BMM conducted analyses. CTC conducted project administration and supervision. CTC, DEB, TM wrote the original draft, and CTC, DEB, VS, BMM, LA, IS, JHW, TM were involved in review and editing.

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Additional files

Data S1. The urban affinity values (N=56,181 total values (i.e., unique urban affinity score in a subrealm)) for potential inclusion in our analysis.

Data S2. A final dataset for potential analysis and modeling, including a total of 94,087 observations (unique combination of species urban affinity values, subrealm, and body size measure) of 20,957 species that had at least one measure of urban affinity and at least one measure of body size. Note, however, that not every body size measure is made available due to a lack of permissions to share some datasets.

Data S3. A list of the final potential 'datasets' that were used to aggregate measures of body size. Metadata refer to our naming scheme employed in our workflow; citation is a descriptor of either the paper citation or dataset citation or a descriptor of manual data aggregated by us; URL is the potential URL if applicable, and number of data points is the number of potential data points that could be used for the analysis.

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Peer reviews

Reviewer #2 (Public review):

I have completed a thorough review of this paper, which seeks to use the large datasets of species occurrences available through GBIF to estimate variation in how large numbers of plant and animal species are associated with urbanization throughout the world, describing what they call the "species urbanness distribution" or SUD. They explore how these SUDs differ between regions and different taxonomic levels. They then calculate a measure of urban tolerance and seek to explore whether organism size predicts variation in tolerance among species and across regions.

The study is impressive in many respects. Over the course of several papers, Callaghan and coauthors have been leaders in using "big [biodiversity] data" to create metrics of how species' occurrence data are associated with urban environments, and in describing variation in urban tolerance among taxa and regions. This work has been creative, novel, and it has pushed the boundaries of understanding how urbanization affects a wide diversity of taxa. The current paper takes this to a new level by performing analyses on over 94000 observations from >30,000 species of plants and animals, across more than 370 plant and animal taxonomic families. All of these analyses were focused on answering two main questions:

(1) What is the shape of species' urban tolerance distributions within regional communities?

(2) Does body size consistently correlate with species' urban tolerance across taxonomic groups and biogeographic contexts?

Overall, I think the questions are interesting and important, the size and scope of the data and analyses are impressive, and this paper has a potentially large contribution to make in pushing forward urban macroecology specifically and urban ecology and evolution more generally.

Despite my enthusiasm for this paper and its potential impact, there are aspects that could be improved, and I believe the paper requires major revision.

Some of these revisions ideally involve being clearer about the methodology or arguments being made. In other cases, I think their metrics of urban tolerance are flawed and need to be rethought and recalculated, and some of the conclusions are inaccurate. I hope the authors will address these comments carefully and thoroughly. I recognize that there is no obligation for authors to make revisions. However, revising the paper along the lines of the comments made below would increase the impact of the paper and its clarity to a broad readership.

Major Comments:

(1) Subrealms

Where does the concept of "subrealms" come from? No citation is given, and it could be said that this sounds like an idea straight out of Middle Earth. How do subrealms relate to known bioclimatic designations like Koppen Climate classifications, which would arguably be more appropriate? Or are subrealms more socio-ecologically oriented? From what I can tell, each subrealm lumps together climatically diverse areas. It might be better and more tractable to break things in terms of continents, as the rationale for subrealms is unclear, and it makes the analyses and results more confusing. The authors rationalized the use of subrealms to account for potential intraspecific differences in species' response to urbanization, but that is never a core part of the questions or interpretation in the paper, and averaging across subrealms also accounts for intraspecific variation. Another issue with using the subrealm approach is that the authors only included a species if it had 100 observations in a given subrealm, leading to a focus on only the most common species, which may be biased in their SUD distribution. How many more species would be included if they did their analysis at the continental or global scale, and would this change the shape of SUDs?

(2) Methods - urban score

The authors describe their "urban score" as being calculated as "the mean of the distribution of VIIRS values as a relative species-specific measure of a response to urban land cover."

I don't understand how this is a "relative species-specific measure". What is it relative to? Figures S4 and S5 show the mean distribution of VIIRS for various taxa, and this mean looks to be an absolute measure. Mean VIIRS for a given species would be fine and appropriate as an "urban score", but the authors then state in the next sentence: "this urban score represents the relative ranking of that species to other species in response to urban land cover".

That doesn't follow from the description of how this is calculated. Something is missing here. Please clarify and add an explicit equation for how the urban score is calculated because the text is unclear and confusing.

(3) Methods - urban tolerance

How the authors are defining and calculating tolerance is unclear, confusing, and flawed in my opinion.

Tolerance is a common concept in ecology, evolution, and physiology, typically defined as the ability for an organism to maintain some measure of performance (e.g., fitness, growth, physiological homeostasis) in the presence versus absence of some stressor. As one example, in the herbivory literature, tolerance is often measured as the absolute or relative difference in fitness of plants that are damaged versus undamaged (e.g., *https://academic.oup.com/evolut/article/62/9/2429/6853425?login=true*).

On line 309, after describing the calculation of urban scores across subrealms, they write: "Therefore, a species could be represented across multiple subrealms with differing measures of urban tolerance (Fig. S4). Importantly, this continuous metric of urban tolerance is a relative measure of a species' preference, or affinity, to urban areas: it should be interpreted only within each subrealm".

This is problematic on several fronts. First, the authors never define what they mean by the term "tolerance". Second, they refer to urban tolerance throughout the paper, but don't describe the calculation until lines 315-319, where they write (text in [ ] is from the reviewer):

"Within each subrealm, we further accounted for the potential of different levels of urbanization by scaling each species' urban score by subtracting the mean VIIRS of all observations in the subrealm (this value is hereafter referred to as urban tolerance). This 'urban tolerance' (Fig. S5) value can be negative - when species under-occupy urban areas [relative to the average across all species] suggesting they actively avoid them-or positive- when species over-occupy urban areas [relative to the average across all species] suggesting they prefer them (i.e., ranging from urban avoiders to urban exploiters, respectively).

They are taking a relativized urban score and then subtracting the mean VIIRS of all observations across species in a subrealm. How exactly one interprets the magnitude isn't clear and they admit this metric is "not interpretative across subrealms".

This is not a true measure of tolerance, at least not in the conventional sense of how tolerance is typically defined. The problem is that a species distribution isn't being compared to some metric of urbanness, but instead it is relative to other species' urban scores, where species may, on average, be highly urban or highly nonurban in their distribution, and this may vary from subrealm to subrealm. A measure of urban tolerance should be independent of how other species are responding, and should be interpretable across subrealms, continents, and the globe.

I propose the authors use one of two metrics of urban tolerance:

(i) Absolute Urban Tolerance = Mean VIIRS of species_i - Mean VIIRS of city centers

Here, the mean VIIRS of city centers could be taken from the center of multiple cities throughout a subrealm, across a continent, or across the world. Here, the units are in the original VIIRS units where 0 would correspond to species being centered on the most extreme urban habitats, and the most extreme negative values would correspond to species that occupy the most non-urban habitats (i.e., no artificial light at night). In essence, this measure of tolerance would quantify how far a species' distribution is shifted relative to the most highly urbanized habitat available.

(ii) % Urban Tolerance = (Mean VIIRS of species_i - Mean VIIRS of city centers)/MeanVIIRS of city centers * 100%

This metric provides a % change in species mean VIIRS distribution relative to the most urban habitats. This value could theoretically be negative or positive, but will typically be negative, with -100% being completely non-urban, and 0% being completely urban tolerant.

Both of these metrics can be compared across the world, as it would provide either absolute (equation 1) or relative (equation 2) metrics of urban tolerance that are comparable and easily interpretable in any region.

In summary, the definition of tolerance should be clear, the metric should be a true measure of tolerance that is comparable across regions, and an equation should be given.

(4) Figure 1: The figure does not stand alone. For example, what is the hypothesis for thermophily or the temperature-size rule? The authors should expand the legend slightly to make the hypotheses being illustrated clearer.

(5) SUDs: I don't agree with the conclusion given on line 83 ("pattern was consistent across subrealms and several taxonomic levels") or in the legend of Figure 2 ("there were consistent patterns for kingdoms, classes, and orders, as shown by generally similar density histograms shapes for each of these").

The shapes of the curves are quite different, especially for the two Kingdoms and the different classes. I agree they are relatively consistent for the different taxonomic Orders of insects.

Comments on revised version:

I believe their response is thorough and thoughtful. I still disagree with them on some fundamental points of their methodology. However, I would prefer to let my review and their response stand as is. This will allow engaged readers to see both sides of the arguments and judge for themselves whether they believe the revisions are sufficient and if my concerns are valid.

https://doi.org/10.7554/eLife.109047.2.sa1

Author response:

The following is the authors' response to the original reviews.

> ***eLife* Assessment**
>
> *This study provides an important assessment of how body size influences the occurrence of macro-organisms in urban areas across the globe. Size in most plants, but only some animal families, was positively associated with urban tolerance. The data set is impressive, but the evidence for broad-scale conclusions is incomplete due to methodological issues that need to be resolved.*

We have substantially revised the manuscript to resolve the methodological issues raised, including clarifying the definition, calculation, and interpretation of urban affinity (formerly named urban tolerance), and tightening the scope of our conclusions to align directly with the evidence presented.

> ***Public Reviews:***
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> ***Reviewer #1 (Public review):***
>
> *Summary:*
>
> *The authors integrate multiple large databases to test whether body sizes were positively associated with which species tolerate urban areas. In general, many plant families showed a positive association between body size and urban tolerance, whereas a smaller, though still non-trivial, percentage of animal families showed the same pattern. Notably, the authors are careful in the interpretation of their findings and provide helpful context for the ways that this analysis can be generative in shaping new hypotheses and theory around how urbanization influences biodiversity at large. They are careful to discuss how body size is an important trait, but the absence of a relationship between body size and urban tolerance in many families suggests a variety of other traits undergird urban success.*

We appreciate this thoughtful and balanced assessment of our work and fully agree with the reviewer's interpretation. In particular, we share the view that the heterogeneous and often weak association between body size and urban affinity across many families is an important result in its own right, underscoring that no single trait is likely to explain urban success across the tree of life. As the reviewer notes, our intention was not to present body size as a universal predictor, but rather as a widely available, integrative trait that can help reveal where general patterns do and do not emerge. We view the lack of a consistent relationship in many families as strong motivation for future work that explicitly integrates additional functional traits and ecological contexts, and we have clarified this perspective in the revised manuscript.

> *Strengths:*
>
> *The authors aggregated a large dataset, but they also applied robust filters to ensure they had an adequate and representative number of detections for a given species, family, geography, etc. The authors also applied their analysis at multiple taxonomic scales (family and order), which allowed for a better interpretation of the patterns in the data and at what taxonomic scale body size might be important.*

We thank the reviewer for highlighting these strengths of the study. Considerable effort went into assembling, harmonizing, and filtering these data across taxa, regions, and taxonomic resolutions, and we were deliberate in applying conservative thresholds to ensure that species-level urban affinity estimates were based on adequate and comparable sampling. We hope that, beyond the specific results presented here, the compiled dataset and analytical framework will serve as a valuable resource for future studies aiming to explore additional traits, taxa, or mechanisms underlying species' responses to urbanization.

> *Weaknesses:*
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> *My main concern is that it is not fully clear how the measure of body size might influence the result. The authors were unable to obtain consistent measures of body size (mean, median, maximum, or sex variation). This, of course, could be very consequential as means and medians can differ quite a bit, and they certainly will differ substantially from a maximum. And of course, sex differences can be marked in multiple directions or absent altogether. The authors do note that they selected the measure that was most common in a family, but it was not clear whether species in that family that did not have that measure were removed or not. This could potentially shape the variability in the dataset and obscure true patterns. This may require additional clarity from the authors and is also a real constraint in compiling large data from disparate sources.*

We appreciate this important point and agree that heterogeneity in how body size is measured (e.g., mean vs. maximum values, sex-specific measures) is a real but unavoidable challenge when compiling organismal trait data across such a broad taxonomic scope. We would like to clarify that our analytical approach was explicitly designed to minimize the influence of this heterogeneity rather than ignore it. Specifically, for each family we retained all species for which at least one body size estimate was available, rather than removing species that lacked a particular measurement type. When multiple body size measures existed for a species, we selected the measurement type that was most commonly available within that family in order to maximize comparability among species while retaining sample size. Importantly, differences among body size measurement types (including units, measurement detail, and whether values reflected means, maxima, or sex-specific estimates) were further accounted for by (i) log-transforming all body size values and (ii) centering and scaling body size values within each measurement type, which was included as a random effect in the hierarchical models. This approach reduces the influence of systematic differences among measurement types on estimated relationships with urban affinity. We have added a sentence to the methods clarifying that species with a single measurement type were not removed from analyses:

“Importantly, this procedure did not result in the exclusion of species lacking a particular body size measurement type; rather, all species with at least one available body size estimate were retained, with measurement heterogeneity explicitly accounted for through hierarchical modeling.”

We agree that variation in body size definitions may still contribute residual noise and potentially obscure weak relationships, and we now emphasize this more clearly as a limitation of large-scale trait syntheses. However, because our primary inference focuses on the presence, absence, and direction of size–urban affinity relationships across families, rather than precise effect sizes, we believe our approach provides a robust and conservative test of whether body size consistently predicts urban affinity across taxa. We highlight this point in the limitations section of our manuscript:

“One important limitation of our synthesis is the heterogeneity in how body size is measured across taxa, including differences among mean, maximum, and sex-specific estimates. While our analytical framework explicitly accounts for this variation through transformation, scaling, and hierarchical modeling with random intercepts (see Methods), residual measurement noise may still obscure weak size–urban affinity relationships. This challenge is inherent to large-scale trait syntheses that integrate data from disparate sources, and highlights the need for continued efforts to standardize trait databases and expand the availability of harmonized organismal trait data across the tree of life.”

> ***Reviewer #2 (Public review):***
>
> *I have completed a thorough review of this paper, which seeks to use the large datasets of species occurrences available through GBIF to estimate variation in how large numbers of plant and animal species are associated with urbanization throughout the world, describing what they call the "species urbanness distribution" or SUD. They explore how these SUDs differ between regions and different taxonomic levels. They then calculate a measure of urban tolerance and seek to explore whether organism size predicts variation in tolerance among species and across regions.*
>
> *The study is impressive in many respects. Over the course of several papers, Callaghan and coauthors have been leaders in using "big [biodiversity] data" to create metrics of how species' occurrence data are associated with urban environments, and in describing variation in urban tolerance among taxa and regions. This work has been creative, novel, and it has pushed the boundaries of understanding how urbanization affects a wide diversity of taxa. The current paper takes this to a new level by performing analyses on over 94000 observations from >30,000 species of plants and animals, across more than 370 plant and animal taxonomic families. All of these analyses were focused on answering two main questions:*
>
> *(1) What is the shape of species' urban tolerance distributions within regional communities?*
>
> *(2) Does body size consistently correlate with species' urban tolerance across taxonomic groups and biogeographic contexts?*

We thank the reviewer for their careful reading of the manuscript and for this generous and accurate summary of the study's aims, scope, and contributions. We appreciate the recognition of our group's broader body of work using large biodiversity databases to quantify species' associations with urban environments, and we are grateful for the reviewer's acknowledgement that this study extends those efforts to an unprecedented taxonomic and geographic scale. We agree with the reviewer's articulation of the two core questions motivating the paper, and we have revised the manuscript to ensure that these questions are stated clearly and addressed consistently throughout.

> *Overall, I think the questions are interesting and important, the size and scope of the data and analyses are impressive, and this paper has a potentially large contribution to make in pushing forward urban macroecology specifically and urban ecology and evolution more generally.*

Thanks! We see this work as an effort to move beyond species-by-species descriptions of urban responses toward a community- and distribution-level perspective, where the shape of species' urban associations themselves becomes an object of study. By framing species' distributions along an urbanization gradient as a collective property of regional species pools, our approach opens a complementary way of thinking about how urbanization filters biodiversity.

> *Despite my enthusiasm for this paper and its potential impact, there are aspects that could be improved, and I believe the paper requires major revision.*
>
> *Some of these revisions ideally involve being clearer about the methodology or arguments being made. In other cases, I think their metrics of urban tolerance are flawed and need to be rethought and recalculated, and some of the conclusions are inaccurate. I hope the authors will address these comments carefully and thoroughly. I recognize that there is no obligation for authors to make revisions. However, revising the*

> *paper along the lines of the comments made below would increase the impact of the paper and its clarity to a broad readership.*

We appreciate the detailed comments provided and have addressed each point in turn - see detailed responses below. We took these concerns seriously and undertook a substantial revision of the manuscript. In summary, we clarified the conceptual framing of “urban tolerance” (now referred to as “urban affinity”), explicitly defined the metric and its interpretation, added equations and a step-by-step methodological roadmap, and expanded justification for our regional stratification. Where appropriate, we refined language in the Results and Discussion to ensure conclusions are tightly aligned with what the metric can and cannot support. We agree that these revisions materially improve the clarity, rigor, and interpretability of the study, and we appreciate the reviewer’s perspective on how doing so strengthens the paper’s contribution and accessibility to a broad readership.

> *Major Comments:*
>
> *(1) Subrealms*
>
> *Where does the concept of "subrealms" come from? No citation is given, and it could be said that this sounds like an idea straight out of Middle Earth. How do subrealms relate to known bioclimatic designations like Koppen Climate classifications, which would arguably be more appropriate? Or are subrealms more socio-ecologically oriented? From what I can tell, each subrealm lumps together climatically diverse areas. It might be better and more tractable to break things in terms of continents, as the rationale for subrealms is unclear, and it makes the analyses and results more confusing. The authors rationalized the use of subrealms to account for potential intraspecific differences in species' response to urbanization, but that is never a core part of the questions or interpretation in the paper, and averaging across subrealms also accounts for intraspecific variation. Another issue with using the subrealm approach is that the authors only included a species if it had 100 observations in a given subrealm, leading to a focus on only the most common species, which may be biased in their SUD distribution. How many more species would be included if they did their analysis at the continental or global scale, and would this change the shape of SUDs?*

We thank the reviewer for raising this point and agree that the rationale for using subrealms required clearer explanation. Next to allowing potential intraspecific differences in urban affinity across regions, our subrealm-based approach also provides a practical way to partition global biodiversity into ecologically meaningful regional assemblages while maintaining sufficient sample sizes for analysis. Urban affinity is likely to vary geographically within species due to differences in climate, habitat availability, urban form, and evolutionary history. By calculating urban affinity within subrealms rather than globally, our approach allows species to exhibit region-specific urban affinities while ensuring that comparisons are made among species co-occurring within the same regional ecological context. We have substantially revised the Methods to explicitly define subrealms, cite their origin, and clarify why this spatial stratification is appropriate for our study:

“Accounting for geographic context through subrealm stratification

To account for geographic heterogeneity in both species’ distributions and the baseline levels of urbanization, we stratified our analyses by global biogeographic subrealms (N=52; Fig. S1). Subrealms represent an intermediate hierarchical level within the One Earth [82] (*https://www.oneearth.org/bioregions/*) bioregionalization framework, grouping the 185 terrestrial bioregions into broader units that reflect shared species pools and ecological contexts while maintaining meaningful regional structure. This scale represents a practical compromise between analyzing data at the finer bioregion level (which would result in many regions with insufficient observations for robust analysis) and broader classifications such as continents or the 14 biogeographic realms, which aggregate ecologically distinct regions and species pools. This regionalization has been widely used in macroecological and biogeographic research to contextualize species–environment relationships because subrealms capture meaningful gradients in biotic assemblages that are not accounted for by climatic classifications alone [83,84].

This stratification allows species' associations with urban environments to be interpreted relative to the environments available within the regions they occupy. This is important, as previous work has shown that species' responses to urbanization are constrained by biogeographic context, because regional species pools reflect shared evolutionary, ecological, and historical filters [23]. Previous work has also shown that urban associations among species are context-dependent, and interpreting species' responses without accounting for regional baselines conflates availability of urban environments with species' affinity to them. This distinction is critical because identical levels of urbanization (e.g., VIIRS radiance) can have different ecological meanings across regions with different species pools and land-use histories. It avoids conflating species' urban affinity with global differences in urban availability."

We chose subrealms rather than Köppen climate classifications or continental units because our objective was not to partition species by climatic similarity per se, but to evaluate species' associations with urban environments relative to the ecological and biogeographic contexts in which they occur. Climatic classifications such as Köppen are highly effective for addressing climate–species relationships, but they do not explicitly capture differences in species pools, evolutionary history, or land-use legacies that strongly shape how species interact with urbanization. Likewise, continents often aggregate ecologically disparate regions and species pools, potentially obscuring meaningful variation in baseline urbanization and species' realized distributions.

Importantly, urban affinity in our framework is a relative, context-dependent metric, explicitly interpreted within regions. Identical levels of urbanization (e.g., VIIRS radiance values) can have different ecological meanings across regions with distinct species pools, land-use histories, and settlement patterns. Stratifying analyses by subrealm therefore avoids conflating species' affinity to urban environments with global or continental differences in the availability and intensity of urban land cover. We have clarified this distinction and motivation in the revised Methods (see responses below).

Regarding the concern that requiring ≥100 observations per species per subrealm biases analyses toward common species: we agree that this threshold focuses the analysis on well-sampled species. This choice was intentional and follows previous work showing that such cutoffs are necessary to robustly characterize species' responses to urbanization using occurrence data. While a global or continental analysis would indeed include additional, rarer species, it would also substantially increase uncertainty and conflate species' responses across ecologically distinct contexts. Our study is therefore best interpreted as a macroecological synthesis of common species, which are also the taxa that disproportionately structure urban communities and drive the shape of Species Urbanness Distributions (SUDs). We now clarify this scope and limitation more explicitly in the introduction:

"Our aim is to identify broad, cross-taxonomic patterns in species' urban affinity at a global scale, rather than to resolve the specific causal mechanisms driving urban success or failure within individual taxa or cities.".

As well as in the discussion:

"Our synthesis complements taxon-specific, presence–absence trait studies by identifying broad, cross-taxonomic patterns that can motivate and contextualize more mechanistic analyses [17,23]."

Finally, while alternative spatial stratifications are possible, the central patterns we report particularly the skewed shape of SUDs—are robust to the use of regional context rather than absolute global metrics. Exploring how SUDs change under different spatial frameworks (e.g., continents, climate zones) is an interesting avenue for future work, but we feel is beyond the scope of the present study.

> *(2) Methods - urban score*
>
> *The authors describe their "urban score" as being calculated as "the mean of the distribution of VIIRS values as a relative species specific measure of a response to urban land cover."*
>
> *I don't understand how this is a "relative species-specific measure". What is it relative to? Figures S4 and S5 show the mean distribution of VIIRS for various taxa, and this mean looks to be an absolute measure. Mean VIIRS for a given species would be fine and appropriate as an "urban score", but the authors then state in the next sentence: "this urban score represents the relative ranking of that species to other species in response to urban land cover".*

We agree that the wording in the original manuscript was unclear and conflated two distinct steps in the workflow. We have now revised the Methods to clearly distinguish between (i) the urban score, which is an absolute, descriptive summary of the mean VIIRS radiance associated with a species' occurrence locations, and (ii) urban affinity, which is the relative, region-specific metric derived from the urban score. Specifically, we rewrote the methods to have distinct steps as subheadings, as follows: (1) urban score; (2) subrealms and why; (3) urban affinity. In the revised Methods, we explicitly define the urban score:

"an absolute descriptive summary of the urbanization levels associated with a species' occurrence locations within a given subrealm".

We no longer describe the urban score itself as "relative" or as a ranking among species. Relative comparisons among species arise only in the subsequent step, where species-specific urban scores are expressed relative to the regional background level of urbanization within each subrealm to derive urban affinity.

We refer the Reviewer to the revised version which we feel is much clearer (lines 428-479)!

> *That doesn't follow from the description of how this is calculated. Something is missing here. Please clarify and add an explicit equation for how the urban score is calculated because the text is unclear and confusing.*

The previous response, where we discuss the description, hopefully clarifies this. Further, we have revised the Methods to clearly define the urban score and to include an explicit equation. In the revised manuscript, the urban score for species s is calculated as the mean VIIRS radiance across all occurrence locations of that species:

$$U_{s,r} = \frac{1}{n_{s,r}} \sum_{i=1}^{n_{s,r}} L_i$$

where $n_s$is the number of GBIF occurrence records for species s, and L_i is the VIIRS nighttime lights radiance value extracted at the location of occurrence i. We also clarify in the Methods that this urban score is an absolute summary statistic of observed urbanization at species occurrence locations

> *(3) Methods - urban tolerance*
>
> *How the authors are defining and calculating tolerance is unclear, confusing, and flawed in my opinion.*

> *Tolerance is a common concept in ecology, evolution, and physiology, typically defined as the ability for an organism to maintain some measure of performance (e.g., fitness, growth, physiological homeostasis) in the presence versus absence of some stressor. As one example, in the herbivory literature, tolerance is often measured as the absolute or relative difference in fitness of plants that are damaged versus undamaged*
>
> *(e.g., https://academic.oup.com/evolut/article/62/9/2429/6853425?login=true).*
>
> *On line 309, after describing the calculation of urban scores across subrealms, they write: "Therefore, a species could be represented across multiple subrealms with differing measures of urban tolerance (Fig. S4). Importantly, this continuous metric of urban tolerance is a relative measure of a species' preference, or affinity, to urban areas: it should be interpreted only within each subrealm". This is problematic on several fronts. First, the authors never define what they mean by the term "tolerance". Second, they refer to urban tolerance throughout the paper, but don't describe the calculation until, where they write (text in [ ] is from the reviewer): "Within each subrealm, we further accounted for the potential of different levels of urbanization by scaling each species' urban score by subtracting the mean VIIRS of all observations in the subrealm (this value is hereafter referred to as urban tolerance). This 'urban tolerance' (Fig. S5) value can be negative - when species under-occupy urban areas [relative to the average across all species] suggesting they actively avoid them-or positive-when species over-occupy urban areas [relative to the average across all species] suggesting they prefer them (i.e., ranging from urban avoiders to urban exploiters, respectively). They are taking a relativized urban score and then subtracting the mean VIIRS of all observations across species in a subrealm. How exactly one interprets the magnitude isn't clear and they admit this metric is "not interpretative across subrealms".*
>
> *This is not a true measure of tolerance, at least not in the conventional sense of how tolerance is typically defined. The problem is that a species distribution isn't being compared to some metric of urbanness, but instead it is relative to other species' urban scores, where species may, on average, be highly urban or highly nonurban in their distribution, and this may vary from subrealm to subrealm. A measure of urban tolerance should be independent of how other species are responding, and should be interpretable across subrealms, continents, and the globe.*

We thank the reviewer for this careful and important critique. We agree that the term “tolerance” is commonly used to describe the ability of an organism to maintain performance (e.g., fitness, growth, physiological homeostasis) in the presence of a stressor, and that our metric does not measure tolerance in this mechanistic or fitness-based sense. To address this directly and unambiguously, we have revised the manuscript to explicitly define the term “urban affinity” as opposed to urban tolerance.

In the revised Methods, we also reorganized and clarified the calculation of urban affinity, introduced explicit notation, and provided a formal equation. Specifically, we now define urban affinity for species s in subrealm r as:

$$A_{s,r} = U_{s,r} - \bar{U}_r$$

where $U_{s,r}$is the mean VIIRS radiance across all occurrence locations of species s within subrealm r, and $\bar{U}_r$is the mean VIIRS radiance across all occurrence records of all species in that subrealm. This transformation centers species’ urban scores on the regional background level of urbanization, yielding a relative measure of spatial association with urban environments.

We agree with the reviewer that this metric is not interpretable as an absolute measure of affinity, and we now state this explicitly. Urban affinity values are, by construction, relative measures, interpretable only within subrealms, and they quantify whether a species tends to occur in more or less urbanized environments than is typical for that region. The magnitude of the metric therefore reflects deviation from the regional baseline, not a universal or global scale of urbanization, and is not intended to be compared directly across subrealms.

We respectfully disagree, however, that this makes the metric flawed. Rather, it reflects a deliberate analytical choice aligned with our research questions. Our goal was not to estimate absolute urban exposure or physiological performance, but to compare species' realized spatial associations with urban environments within shared biogeographic contexts. Because baseline urbanization levels, settlement history, and species pools vary strongly across regions, a globally absolute metric would conflate species' affinities with regional availability of urban environments. By contrast, a relative, region-centered metric allows meaningful comparisons among species that coexist within the same ecological and biogeographic setting. This approach follows a growing body of macroecological work that infers species' environmental affinities from spatial distributions rather than direct performance measures (e.g., Callaghan et al. 2020; 2021; 2023), and we now cite these studies explicitly.

> *I propose the authors use one of two metrics of urban tolerance:*
>
> *(i) Absolute Urban Tolerance = Mean VIIRS of species_i - Mean VIIRS of city centers Here, the mean VIIRS of city centers could be taken from the center of multiple cities throughout a subrealm, across a continent, or across the world. Here, the units are in the original VIIRS units where 0 would correspond to species being centered on the most extreme urban habitats, and the most extreme negative values would correspond to species that occupy the most non-urban habitats (i.e., no artificial light at night). In essence, this measure of tolerance would quantify how far a species' distribution is shifted relative to the most highly urbanized habitat available.*
>
> *(ii) % Urban Tolerance = (Mean VIIRS of species_i - Mean VIIRS of city centers)/MeanVIIRS of city centers * 100%*
>
> *This metric provides a % change in species mean VIIRS distribution relative to the most urban habitats. This value could theoretically be negative or positive, but will typically be negative, with -100% being completely non-urban, and 0% being completely urban tolerant.*
>
> *Both of these metrics can be compared across the world, as it would provide either absolute (equation 1) or relative (equation 2) metrics of urban tolerance that are comparable and easily interpretable in any region.*
>
> *In summary, the definition of tolerance should be clear, the metric should be a true measure of tolerance that is comparable across regions, and an equation should be given.*

We thank the reviewer for this thoughtful and constructive suggestion, which raises an important conceptual issue regarding how "urban tolerance" should be defined and quantified. We agree that any such metric must be clearly defined, interpretable, and accompanied by an explicit equation, and we have revised the manuscript accordingly to clarify both our definition and its intended interpretation.

The alternative metrics proposed by the reviewer anchoring species' distributions to city centers or to the most highly urbanized habitats represent a valid and intuitive absolute framing of urban tolerance. Indeed, a closely related approach was explored and evaluated in Callaghan et al. (2020; *https://doi.org/10.1016/j.ecolind.2020.106905*), where species' occurrence-based urbanness scores derived from VIIRS night-time lights were compared against abundance-based estimates of urban tolerance using explicit urban–non-urban contrasts. That study further demonstrated that urbanness scores depend on the choice of spatial baseline (e.g., regional buffers around cities versus continental extents), and showed that different baselines capture complementary, but not identical, aspects of species–urban associations.

In the present study, we deliberately adopt a relative, regionally contextualized metric (now referred to as urban affinity), expressing each species' mean VIIRS association relative to the background urbanization of the biogeographic subrealm in which it occurs. This choice reflects our goal of comparing species' relative affinities to urban environments within shared ecological and biogeographic contexts. Importantly, identical VIIRS values can correspond to very different ecological conditions across regions, and anchoring all species to city centers or global urban maxima risks conflating species' affinities with regional differences in urban availability and infrastructure.

We now make this distinction explicit throughout the manuscript, including by (i) defining urban affinity as a relative, occurrence-based measure of urban affinity (rather than physiological or fitness-based tolerance), (ii) providing an explicit equation for its calculation, and (iii) clarifying that these values are interpretable within, but not across, biogeographic subrealms. We view absolute, city-center–anchored metrics and relative, regionally normalized metrics as complementary approaches, each suited to different questions; the latter is most appropriate for the macroecological, comparative analyses pursued here.

> *(4) Figure 1: The figure does not stand alone. For example, what is the hypothesis for thermophily or the temperature-size rule? The authors should expand the legend slightly to make the hypotheses being illustrated clearer.*

We now expanded the legend so that the figure and hypotheses presented can be understood based on just the figure and its legend; we did so by explaining the illustrated hypotheses as requested by the Reviewer. The figure legend now reads as follows:

"Fig. 1: Conceptual framework illustrating hypothesized mechanisms linking urban affinity to interspecific body-size shifts. These include dispersal and mobility constraints under habitat fragmentation [44,45], thermophily and the temperature–size rule driven by the urban heat island effect [15,30], size-biased competition and survival [94,95], and size-biased human preferences [64]. Urban fragmentation of habitat resources can select for increased mobility (e.g., larger butterflies) or reduced mobility (e.g., larger seeds) depending on isolation severity. Elevated urban temperatures favor thermophily, which often negatively correlates with size as it affects the heat balance via thermal inertia. Similarly, these higher temperatures generally favor smaller-bodied adult ectotherms because they accelerate development and reduce time available for growth (i.e., temperature-size rule). In plants, the increased CO_2 and nutrient availability associated with anthropogenic environments due to heating- and traffic-related CO2 emissions and eutrophication provides a competitive advantage to larger plant species, and human preferences too may favor larger species (e.g., tree-lined streets), whereas smaller species may be advantaged in colonizing built infrastructure."

> *(5) SUDs: I don't agree with the conclusion given on line 83 ("pattern was consistent across subrealms and several taxonomic levels") or in the legend of Figure 2 ("there were consistent patterns for kingdoms, classes, and orders, as shown by generally similar density histograms shapes for each of these").*
>
> *The shapes of the curves are quite different, especially for the two Kingdoms and the different classes. I agree they are relatively consistent for the different taxonomic Orders of insects.*

We agree that our original wording overstated the similarity of distributions across taxa and regions. We have revised the text to clarify that the consistency we refer to pertains primarily to central tendencies rather than identical distributional shapes. To address this directly, we conducted additional analyses comparing urban affinity distributions across subrealms for taxonomic groups with the largest sample sizes. These results, now presented in new Supplementary Figures (Fig. S2-S4), show that while distributional shapes vary among higher taxonomic groups, median values and overall spread are broadly similar within comparable taxonomic levels. We have updated the Results text and the Figure 2 legend accordingly to reflect this more precise interpretation.

“These patterns in central tendency were broadly consistent across subrealms and taxonomic levels, although distributional shapes varied among higher taxonomic groups (Fig. 2).”

“To evaluate this more formally, we compared distributions across subrealms for groups with the largest sample sizes and found that while distributional shapes varied among higher taxa, median values and overall spread were broadly similar within comparable taxonomic levels (Fig. S2–S4).”

Figure 2 caption: “There were consistent patterns for kingdoms, classes, and orders (B) as shown by similar central tendencies despite variation in distributional shape.”

We refer the Reviewer to the revised manuscript and supplementary material, but show the kindom level in Fig S2.

More broadly, our goal in introducing Species Urbanness Distributions (SUDs) is not to argue that their exact shapes are invariant, but rather to provide a generalizable framework for describing how assemblages are structured along an urbanization gradient. In this respect, SUDs are conceptually analogous to Species Abundance Distributions (SADs), where the precise functional form has long been debated, yet the framework itself has proven extremely valuable for ecology. We therefore emphasize the utility of SUDs as a descriptive and comparative tool for quantifying community-level responses to urbanization, rather than as a claim about strict uniformity in distributional shape across taxa or regions.

> ***Reviewer #3 (Public review):***
>
> *Summary:*
>
> *This paper reports on an association between body size and the occurrence of species in cities, which is quantified using an 'urban score' that can be visualized as a 'Species Urbanness*
>
> *Distribution' for particular taxa. The authors use species records from the Global Biodiversity Information Facility (GBIF) and link the occurrence data to nighttime lighting quantified using satellite data (Visible Infrared Imaging Radiometer Suite-VIIRS). They link the urban score to body size data to find 'heterogeneous relationship between body size and urban tolerance across the tree'. The results are then discussed with reference to potential mechanisms that could possibly produce the observed effects (cf. Figure 1).*

We thank the reviewer for this clear and accurate summary of the study. We agree that the primary contribution of this work lies in the scale and taxonomic breadth of the analysis, and in introducing a framework (Species Urbanness Distributions) for quantifying species’ relative affinities to urban environments using globally available data. We have revised the manuscript to further clarify the scope of inference and the distinction between descriptive macroecological patterns and mechanistic explanations.

> *Strengths:*
>
> *The novelty of this study lies in the huge number of species analyzed and the comparison of results among animal taxa, rather than in a thorough analysis of what traits allow species to persist under urban conditions. Such analyses have been done using a much*

> *more thorough approach that employs presence-absence data as well as a suite of traits by other studies, for example, in (Hahs et al. 2023, Neate-Clegg et al. 2023). The dataset that the authors produced would also be very valuable if these raw data were published, both the cleaned species records as well as the body sizes. The paper could strongly add to our understanding of what species occur in cities when the open questions are addressed.*

We appreciate highlighting the novelty of the taxonomic breadth and scale of our analysis. We agree that our approach is complementary to more detailed, taxon-specific trait studies based on presence–absence data. In response, we have further emphasized this distinction in the Discussion:

“Our synthesis complements taxon-specific, presence–absence trait studies by identifying broad, cross-taxonomic patterns that can motivate and contextualize more mechanistic analyses17,23.”

We also agree that the cleaned occurrence data and body size information represent a valuable resource, and all data will be made available, with the exception of some body size datasets which we are not able to make available.

> *Weaknesses:*
>
> *I value the approach of the authors, but I think the paper needs to be revised.*
>
> *In my view, the authors could more carefully validate their approach. Currently, any weakness or biases in the approach are quickly explained away rather than carefully explored. This concerns particularly the use of presence-only data, but also the calculation of the urban score.*
>
> *The vast majority of data in GBIF is presence-only data. This produces a strong bias in the analysis presented in the paper. For some taxa, it is likely that occurrences within the city are overrepresented, and for other taxa, the opposite is true (cf. Sweet et al. 2022). I think the authors should try to address this problem.*

We thank the reviewer for raising this important point. We fully agree that GBIF occurrence data are subject to well-known sampling biases, including uneven geographic coverage, observer effort, and taxonomic focus. These limitations are now more explicitly acknowledged in the revised manuscript. At the same time, GBIF currently represents the only global biodiversity database that allows the scope of analysis undertaken here, spanning thousands of species across multiple taxonomic groups and regions. Systematic monitoring datasets that provide presence–absence data are typically restricted to particular taxa (often vertebrates or plants) and are geographically concentrated in the Global North, which would substantially limit the taxonomic and geographic breadth of our analysis.

Importantly, our objective was not to estimate absolute species-specific responses to urbanization, but rather to examine relative patterns of urban affinity across species and families within comparable regional contexts. To address this, we structured our analyses at the subrealm level, which aggregates observations across large spatial extents and reduces sensitivity to fine-scale sampling biases associated with individual cities or urban–rural gradients. In addition, we restricted analyses to species with ≥100 observations per subrealm to focus on well-sampled taxa and reduce the influence of extremely sparse occurrence records. While these steps cannot fully eliminate sampling biases inherent to occurrence data, they substantially mitigate their influence when examining broad comparative patterns.

Recent work has also evaluated the performance of GBIF data in urban biodiversity contexts. For example, Sweet et al. (2022) compared GBIF-derived species richness patterns with independent state-level biodiversity databases across cities and surrounding regions, finding that GBIF provided comparable or broader coverage across taxa and spatial extents. Their analysis showed that species richness was consistently higher in the surrounding region than in the city itself, suggesting that GBIF data capture broad urban–regional biodiversity gradients rather than systematically overrepresenting urban occurrences. Although our analysis differs in design, these results support the use of GBIF as a valuable resource for examining large-scale biodiversity patterns.

More broadly, occurrence databases such as GBIF have become widely used for analyzing species–environment relationships at macroecological scales. While they may be insufficient for estimating precise species-specific environmental tolerances, they are informative for identifying broad patterns across taxa and regions. Our goal here is therefore to identify large-scale comparative patterns in urban affinity and generate hypotheses about trait–urbanization relationships, which can subsequently be tested with more structured monitoring datasets where available.

Another important consideration is that our analyses focus on comparative differences among species within shared taxonomic and geographic contexts, rather than absolute estimates of urban affinity. Sampling biases in occurrence databases are often structured by observer behaviour (e.g., detectability, accessibility, or taxonomic interest), meaning that species recorded by similar observer communities are likely subject to similar sampling biases. Under these conditions, relative differences among species are expected to be preserved even when absolute occurrence frequencies are biased. This logic is consistent with the widely used target-group background approach in presence-only species distribution modelling, where species recorded by similar observer groups (often within the same taxonomic group) are used to control for shared sampling bias. Previous work by Callaghan et al. (2021; *https://doi.org/10.1111/gcb.15670*) performed additional validation analysis comparing our distribution-based urban affinity metric with estimates derived from occupancy modelling using well-sampled European butterflies (see Fig. S5 from the Callaghan et al. 2021 paper). The strong positive relationship between these approaches suggests that the broad patterns identified here are unlikely to arise solely from sampling artifacts.

Finally, in the revised manuscript we now include additional comparisons among well-sampled taxonomic groups (see responses to other comments throughout our response document for details), which show substantial variation in urban affinity even among taxa with extensive sampling. These results suggest that the patterns reported here are unlikely to arise solely from sampling artifacts, but instead reflect meaningful ecological variation in how species interact with urban environments.

> *The authors should compare their results to studies focusing on particular taxa where extensive trait-based analyses have already been performed, i.e., plants and birds. In fact, I strongly suggest that the authors should compare their results to previous studies on the relationship between traits, including body size and occurrences along a gradient of urbanisation, to draw conclusions about the validity of the approach used in the current study, which has a number of weaknesses.*

We agree that explicitly situating our findings within the existing trait-based urban ecology literature strengthens both interpretation and validation of our approach. We had already referenced several relevant studies (e.g., Hahs et al. 2023 and others) in the Introduction and Discussion, but we recognize that these comparisons were not sufficiently explicit. We have now added text to the Discussion directly comparing our results with previous trait-based studies across taxa:

“Our results are broadly consistent with prior taxon-specific trait-based studies (eg., Hahs et al.[17]), but also highlight that relationships between body size and urbanization vary across taxa and analytical frameworks. For example, global syntheses and regional studies have reported positive, negative, or null size–urbanization relationships depending on clade and spatial scale. A recent global analysis that compiled empirical occurrence data for multiple terrestrial faunal taxa across cities worldwide reported broadly similar body-size responses to urbanization [17]. For four of the five groups that overlap with our analysis—amphibians, bats, bees, and birds—the direction of the body-size relationship with urbanization was consistent between studies. The only exception was carabid beetles, which tended to be smaller-bodied in highly urbanized environments in that analysis, whereas we detected no significant size effect for this family. Studies on birds, for example, have found mixed results, including positive associations to urbanization in some regional assemblages [45], no global relationship in others [46] or an overall negative relationship globally [23], and negative relationships in particular clades such as raptors [40]. Such discrepancies likely arise because different studies quantify urbanization differently, focus on different spatial grains, or analyze different components of species responses (e.g., presence– absence, abundance, or occurrence distributions). Additionally, a study on multiple taxa including butterflies and moths found a positive relationship in butterfly and moth community-weighed mean body size with increases in urbanization level, similar to our findings [31]. Researchers have also found that smaller-bodied dung-associated beetles potentially benefit from urban environments, which is similar to the negative association we found between urbanization and body size in beetles [47]. Our approach complements these studies by estimating occurrence-based urban associations across thousands of taxa simultaneously, allowing comparison of how consistently body size predicts urban affinity across taxonomic groupings rather than within a single lineage. In this sense, variation among published results does not contradict our findings but instead reinforces the conclusion that body size is a context-dependent filter whose direction and strength depend on ecological setting, taxonomic scope, and the urbanization metric used.”

These additions highlight that published relationships between body size and urbanization vary widely across taxa, spatial scales, and analytical approaches. For example, prior studies have reported positive, negative, or null size–urbanization relationships depending on clade, geographic extent, and how urbanization or occurrence is quantified. Even within birds alone, the literature spans positive regional relationships, null global relationships, and negative relationships in particular clades such as raptors. We now explicitly discuss these contrasts and clarify that such discrepancies are expected because different studies measure different components of species’ responses (e.g., presence–absence vs. abundance vs. occurrence distributions), use different spatial grains, or focus on different taxonomic subsets.

We emphasize that our analysis is not intended to replace taxon-specific trait studies, but rather to complement them by providing a macroecological synthesis across thousands of species simultaneously. Importantly, the heterogeneity we observe among families is itself a key biological result, indicating that body size is not a universal predictor of urban affinity but instead a context-dependent filter whose direction and strength vary across ecological and phylogenetic settings. We now state this interpretation more clearly in the revised manuscript.

> *They should be be more careful in coming up with post-hoc explanations of why the pattern found in this study makes sense or suggests a particular mechanism. This reviewer considers that there is no way in which the current study can disentangle the different possible mechanisms without further analyses and data, so I would suggest pointing out carefully how the mechanisms could be studied.*

We agree that our study cannot disentangle the causal mechanisms underlying species’ responses to urbanization. Our intent in discussing potential mechanisms was not to claim definitive explanations, but rather to situate our findings within existing ecological theory and to highlight plausible, non-exclusive pathways that may generate the observed patterns.

To make this clearer, we have revised the Discussion to explicitly frame these interpretations as hypotheses rather than conclusions, and to emphasize that testing the underlying mechanisms will require additional data and approaches, such as targeted trait datasets, experimental manipulations, and longitudinal or within-city studies:

“Because our synthesis is correlative and macroecological in nature, the mechanisms discussed above are best viewed as hypotheses that can be evaluated through future work combining experimental, trait-based, and longitudinal data.”.

Additionally, we modified our overall goal to make it clear that this is not inherently a mechanistic study per se:

“Our aim is to identify broad, cross-taxonomic patterns in species’ urban affinity at a global scale, rather than to resolve the specific causal mechanisms driving urban success or failure within individual taxa or cities.”.

> *More details should be given about the methodology. The readers should be able to understand the methods without having to read a number of other papers.*

We have substantially revised and expanded the Methods section to ensure that all analytical steps can be understood directly from the manuscript without requiring consultation of prior publications. In particular, we now (i) provide a clear conceptual roadmap of the workflow at the start of the Methods, (ii) define all key metrics explicitly, including equations for both the urban score and urban affinity, and (iii) clarify the interpretation, assumptions, and limitations of each step. We also added text explaining the rationale for subrealm stratification and the intended interpretation of relative values. Together, these revisions make the methodological framework fully transparent and self-contained (see revised Methods and related responses above and below).

> *References:*
>
> *Hahs, A. K., B. Fournier, M. F. Aronson, C. H. Nilon, A. Herrera-Montes, A. B. Salisbury, C. G. Threlfall, C. C. Rega-Brodsky, C. A. Lepczyk, and F. A. La Sorte. 2023. Urbanisation generates multiple trait syndromes for terrestrial animal taxa worldwide. Nature Communications 14:4751.*
>
> *Neate-Clegg, M. H. C., B. A. Tonelli, C. Youngflesh, J. X. Wu, G. A. Montgomery, Ç. H. Şekercioğlu, and M. W. Tingley. 2023. Traits shaping urban tolerance in birds differ around the world. Current Biology 33:1677-1688.*
>
> *Sweet, F. S. T., B. Apfelbeck, M. Hanusch, C. Garland Monteagudo, and W. W. Weisser. 2022. Data from public and governmental databases show that a large proportion of the regional animal species pool occur in cities in Germany. Journal of Urban Ecology 8:juac002.*

We have incorporated these (and additional new references) into our revised manuscript.

> ***Recommendations for the authors:***
>
> ***Reviewing Editor Comments:***
>
> *As you see from the general comments above and the specific recommendations below, the reviewers are impressed by your comprehensive data set and the analytic approach. However, they ask you to clarify your measures of organism size, occurrence data (vs. presence/absence and corresponding sample-bias caveats), urbanness (lighting differences between cities and regions?), urban tolerance (measure should not be relative to other species and particular regions), and region ("subrealm" vs. more commonly used defintions of world regions such as continents). They also encourage you to*

> *compare your general results with more detailed local studies to better justify using size as the only, easily available trait.*

We thank the Editor for this clear synthesis of the key priorities for revision. We have carefully addressed each point and substantially revised the manuscript to improve clarity, methodological transparency, and interpretability. In particular:

We clarified how body size data were compiled, harmonized, and modeled, including explicit description of how different measurement types (mean, maximum, sex-specific) were retained and statistically accounted for through scaling and hierarchical modeling. We now state these procedures explicitly in the Methods.

We expanded the Methods and Discussion to clarify that our analyses rely on occurrence data rather than presence–absence or abundance data, and we now explicitly discuss the implications and limitations of presence-only datasets, including potential sampling biases and how these may influence inference.

We strengthened justification for using VIIRS night-time lights as a continuous proxy for urbanization, added supporting citations, and clarified that spatial heterogeneity in lighting primarily introduces additional variance rather than systematic bias. We also explicitly describe how urbanization values were calculated and interpreted.

We substantially revised the manuscript to clearly define urban affinity at the outset (including in the Abstract), distinguish it from physiological definitions of tolerance, and provide explicit equations and step-by-step descriptions of how both urban score and urban affinity are calculated and interpreted. We now emphasize that the metric is a relative, region-contextualized measure of occurrence-based urban affinity.

We added full justification, citations, and methodological explanation for the use of biogeographic subrealms, clarified how they differ from continents or climate zones, and explained why this stratification is appropriate for the ecological questions addressed. We also clarified the scope of inference and limitations of this approach.

We expanded the Discussion to explicitly compare our results with prior trait-based urban ecology studies across taxa (including birds and other groups), highlighting where results converge, diverge, and why such variation is expected across spatial scales, taxa, and analytical frameworks.

> ***Reviewer #1 (Recommendations for authors):***
>
> *(1) Abstract*
>
> *(a) Please define how tolerance is being used here*

We now use affinity throughout and it is defined in various places (see responses to other comments here).

> *(b) The abstract should clarify at what taxonomic scale body size is assessed. It is unclear in the abstract as to whether the reader expects intraspecific measures and interspecific, and at what resolution.*

We have revised the abstract by adding one sentence explicitly stating the scale body size was assessed:

“We then assessed whether body size, an integrative ecological trait fundamental to space use, mobility, metabolism, and environmental sensitivity, showed consistent associations with urban affinity among species and across 371 taxonomic families. Analyses were conducted at the interspecific level and focused primarily on variation among taxonomic families (provided with this paper is an accompanying application to view results).”

> *(2) Results/Discussion*
>
> *(a) The species urbanness distribution and comparison with the species abundance distribution is an interesting and conceptually useful contribution to urban ecology and underscores how urbanization functions on biodiversity at scale.*

We thank the reviewer for this positive assessment and are encouraged that they view the Species Urbanness Distribution (SUD) as a conceptually useful contribution to urban ecology. We see SUDs as a flexible framework that can be extended in several important directions, including comparisons across additional traits, cities of differing size and configuration, and temporal analyses that track how urbanness distributions shift with ongoing urban expansion or restoration. More broadly, we hope that SUDs can provide a framework to think about a macroecological understanding of how urbanization filters biodiversity.

> *(b) In our Lambert et al. (2023) study that you reference, we suggest that 'exaptation' may be valuable to explore in urban areas. Although body size wasn't the trait we were considering at that time, it may be worth putting your discussion around pre-adaptation in this context.*

We agree that exaptation provides a valuable conceptual lens for interpreting species’ responses to urban environments. We have revised the Discussion to explicitly frame species’ urban success in this context:

“Such traits “pre-adapted” to urban conditions allow for some species to not only persist but thrive in urban environments where most species cannot. Framing these patterns through the lens of exaptation may be particularly useful, as traits that evolved under non-urban selective pressures may incidentally confer advantages in urban environments without having arisen in response to urbanization per se (sensu Lambert et al.[4]). We therefore speculate that the skewed shape of SUDs may reflect the uneven distribution of exaptive traits across species pools, rather than widespread adaptive evolution to urban conditions.

Consistent with this interpretation, if exaptive traits that facilitate urban persistence are unevenly distributed across species pools, most species would be expected to exhibit avoidance rather than affinity of urban environments. Indeed, we found that the median urban affinity is most often below one, indicating widespread avoidance among species.”.

> *(c) Given the family-scale effect, it would be helpful to discuss how often species within a family co-occur in a given geographic region, how much other traits covary with size, etc. Do we have an a priori reason to expect family to be the taxonomic resolution at which body size seems to be most varied?*

Our exploratory and preliminary analyses revealed that variation in the body size– urban affinity relationship was strongest at the family level, which prompted us to focus our main analyses at this taxonomic resolution. (But we also present results on order as well). Families represent a biologically meaningful intermediate scale in taxonomy: species within families typically share broad morphological, ecological, and life-history characteristics, yet still exhibit substantial variation in body size and ecological strategies. Indeed, body size is well known to covary with multiple traits—including dispersal ability, metabolism, and space use —making it an integrative trait that captures several ecological dimensions simultaneously within and among families. These correlated traits likely contribute to the heterogeneous responses to urbanization observed among families.

Using the family level also provides a practical balance between biological relevance and statistical robustness. Many families contain sufficient numbers of species to allow independent model estimation while avoiding the strong data imbalance that would arise at higher taxonomic levels. In addition, family is a commonly used unit in macroecological trait analyses (e.g., Roy et al. 2009; Smith et al. 2004), and it often reflects major morphological and ecological similarities among species, as reflected in taxonomic identification frameworks.

Regarding co-occurrence, our analytical framework already accounts for geographic context by estimating urban affinity within subrealms. This ensures that species are compared within the same regional species pools and environmental contexts, rather than across globally disparate assemblages. Consequently, family-level effects emerge from comparisons among species that co-occur within shared biogeographic settings rather than from global taxonomic aggregation.

We have added a short clarification in the manuscript to emphasize that body size functions as an integrative trait that covaries with multiple ecological attributes, and that family-level analyses represent a balance between ecological interpretability and data availability:

“Because body size covaries with multiple ecological traits (e.g., dispersal ability and metabolic rate), we focused on family-level analyses to capture shared ecological strategies while still allowing sufficient variation among species to detect trait– environment relationships [39]”.

> *(d) The result that body size shows a stronger effect in plants perhaps could suggest that plant records in GBIF are more sensitive to potential collection bias, perhaps due to detectability differences or preferences for where botanists and citizen scientists collect plant data? You mention ornamental plants late, but it may be worth discussing this here, too.*

We agree that this is a possible mechanism, which likely conflates detectability and ecological signal. We have expanded this point in the discusssion to better address this:

“These human-driven preferences may also influence detectability and recording effort, as larger and more conspicuous plant species are more likely to be planted, maintained, and documented in urban environments, and thus be available in GBIF for our analyses. However, we suggest that this is not purely a sampling artifact, but such processes likely interact with ecological filtering to shape the realized size structure of urban plant communities.”.

> *(e) I appreciate the additional taxonomic layering to the discussion. Seeing patterns at the family and order levels is helpful for generating new theory and predictions about how urbanization structures biodiversity at different taxonomic scales.*

We agree that examining patterns across multiple taxonomic scales is particularly valuable for generating testable hypotheses about how urbanization structures biodiversity, as different mechanisms may emerge or break down depending on the resolution of analysis. We hope this multi-scale perspective helps stimulate new theory and predictions about the ecological processes shaping urban biodiversity across the tree of life.

> *(3) Methods*
>
> *(a) The methodology provides a scalable, consistent, and reasonable measure of both urbanness and species-level urban tolerance. The urban tolerance measure will, of course, not be useful for certain types of research (e.g., animal behavior), but it is appropriate for the resolution of this study.*

We agree that the urban affinity metric presented here is intended for broad-scale, comparative analyses and is not designed to capture fine-scale processes such as individual behavior or short-term demographic responses. Our goal was to develop a scalable and consistent measure that enables cross-taxon and cross-region comparisons at a global extent, which we believe is appropriate for addressing the questions posed in this study. We have sought to be explicit about this scope throughout the manuscript (e.g., to better alleviate Reviewer #1 concerns) and emphasize that the framework is complementary to, rather than a replacement for, more mechanistic or organism-focused approaches.

> *(b) I'm concerned that the authors were not able to constrain their dataset to mean, median, or maximum, not potentially sex variability in sizes. Later in the methods, the authors state that they selected the measure of size that was most common within a family. Does this mean that species within a given family that didn't have that measure of body size were removed from the analysis?*

We appreciate this important point and agree that heterogeneity in how body size is measured (e.g., mean, maximum, or sex-specific estimates) is a real and unavoidable challenge in large-scale trait syntheses. Our analytical approach was explicitly designed to minimize the influence of this heterogeneity while retaining as many species as possible, rather than excluding species based on inconsistent trait metadata.

Specifically, species within a family were not removed based on the availability of a particular body size definition. All species with at least one body size estimate were retained. When multiple measures existed for a species, we selected the measurement type that was most commonly available within each family to maximize comparability while preserving sample size. Remaining heterogeneity among measurement types (including units, measurement detail, and whether values reflected means, maxima, or sex-specific estimates) was explicitly accounted for through log-transformation and metadata-aware centering and scaling, with measurement metadata included as random intercepts in the hierarchical models. We have clarified this point in the Methods:

“Importantly, this procedure did not result in the exclusion of species lacking a particular body size definition; rather, all species with at least one available body size estimate were retained, with measurement heterogeneity explicitly accounted for through metadata-aware scaling and hierarchical modeling.”

In addition, our taxonomic modeling strategy was intentionally hierarchical. Species belonging to families that did not meet the minimum threshold for family-level modeling (≥10 species) were not discarded; rather, they were included in higher-level taxonomic analyses (e.g., order- or class-level models), ensuring that available information was retained wherever statistically appropriate. This approach reflects our broader goal of maximizing data inclusion while matching inference to the resolution supported by the data.

> ***Reviewer #2 (Recommendations for the authors):***
>
> *(1) Overlap between VIIRS and GBIF data: While it would have been nice for the GBIF records and VIIRS timescales to match, the degree of mismatch isn't overly large (2010-2021 vs 2015-2021), and any bias or inaccuracies should be minimal. I am mainly making this comment as a potential counterpoint to a possible criticism from other reviewers.*

We thank the reviewer for this helpful observation and agree with their assessment. While the temporal coverage of GBIF occurrence records (2010–2021) and VIIRS night-time lights data (2015–2021) does not perfectly overlap, the mismatch is relatively small and unlikely to introduce substantial bias, particularly given our focus on broad, global patterns of urban affinity rather than fine-scale temporal dynamics. We appreciate the reviewer highlighting this point as a potential counterargument to concerns about temporal alignment.

> *(2) Line 87: "only a select few species seem to possess traits that enable them to thrive in urban...".*

> *This seems like an odd statement, given how many of these species have positive urban tolerance measures.*

Agreed that this was oddly worded. We have revised for clarity, focusing on the magnitude of urban affinity:

“Similarly, much like the skewed distributions observed in SADs [24,26], the skewed shape of SUDs indicates that while many species exhibit some degree of urban affinity, a relatively small subset of species attain high levels of urban affinity and dominate urban environments.”

> *(3) Line 81: "skewed shape of SUDs suggests that traits enabling species to tolerate urban environments are both rare and specific".*

Again, based on the shape of some of these curves, I'm not convinced that it is rare, and there is nothing about these curves that suggests it is something "specific". Indeed, urban tolerance could be very multivariate, and the authors' own results suggest this is indeed the case.

We have revised the sentence to retain a focus on traits while avoiding overinterpretation of adaptation from the distributional patterns alone. The revised wording emphasizes the uneven expression of high urban affinity across species without implying rarity or trait specificity:

“The skewed shape of SUDs suggests that traits enabling species to tolerate urban environments are unevenly expressed, given that only a handful of species show extreme urban affinity values, but our results suggest this is geographically widespread across taxa.”.

We also agree with the likelihood that it is multivariate, and return to this in the conclusion in a stronger sense:

“Although body size emerged as a predictor of urban affinity, we found not only substantial heterogeneity across families and orders, but also that body size filtering alone is unlikely to explain the consistently skewed SUD shape. Taken together, these patterns suggest that urban affinity likely emerges from multiple trait combinations rather than a single, universally advantageous trait, and that strong affinity to urban environments is not uniformly expressed across taxa, despite occurring broadly across regions.”.

> *(4) Line 100: "UHI", avoid abbreviations unless absolutely necessary.*

We have removed this abbreviation throughout.

> *(5) Body size: focusing on one trait seems like a shot in the dark, and so it isn't too surprising that this didn't reveal a strong or consistent pattern. However, I also recognize that collecting consistent trait data across so many taxa is challenging, and size is a low-hanging fruit that correlates with multiple traits. Perhaps discuss more the range of traits you think are most likely to predict urban tolerance.*

Body size is indeed the ‘easiest’ to collect, but we acknowledge that there are other traits which could be important, and body size correlates with multiple traits. We revised our discussion to be more comprehensive to discuss some of the additional traits, and be explicit about the shortfalls of body size:

“Ultimately, the heterogeneous and sometimes weak relationships between body size and urban affinity suggests that body size alone cannot explain the emergence of extreme urban exploiters and the skewed shape of SUDs. Focusing on body size as a focal trait necessarily represents a simplification of the multidimensional processes underlying species’ responses to urbanization, driven in part by data availability when conducting a taxonomically-broad synthesis. Instead, urban affinity likely depends on multivariate trait combinations [17,58] that vary among taxa [59] and ecological contexts [60]. Traits that are likely to correlate with urban affinity include dispersal capacity, behavioral flexibility, diet breadth, reproductive strategy, thermoregulatory ability, and, in plants, life history traits such as growth form, clonality, phenology, and seed size. The diversity of trait pathways through which species may persist or thrive in urban environments is consistent with the pronounced taxonomic heterogeneity we observe and helps explain why body size alone does not yield a universal pattern."

> *(6) Figure S2: This figure and analysis appear to 'come out of nowhere'. I think this is distracting and tangential, and it should be removed. I have the same thoughts about Figure S3. While I do think a discussion of other traits to measure is well warranted and needed, the inclusion of "preliminary' results that aren't motivated by clear questions, appropriate context, and rigorous analysis should be discouraged.*

We have removed Figure S2 and Figure S3 in response to this comment.

> *I hope the authors find my constructive comments useful in their revision process.*

This was a very thorough and thoughtful review. We are greatly appreciative of the opportunity and guidance to improve our work!

> ***Reviewer #3 (Recommendations for the authors):***
>
> *Here is a list of a number of further points that the authors may want to address:*
>
> *(1) Figure 1 somehow misses the fact that humans simply do not want very large animals in the city. We kill large predators if they come too close to cities, and the same for large herbivores such as wild boar or deer.*

We agree that direct human persecution and management of large-bodied species can influence which species occur in urban environments, particularly for large predators and herbivores. Such processes represent important mechanisms shaping urban species assemblages and represent an entire field of socio-ecological dynamics. We have now clarified this point in the Discussion by noting that human–wildlife conflict, management, and persecution could contribute to observed size–urbanization relationships for some taxa, and that disentangling these mechanisms represents an important direction for future research. We added some text to highlight this point):

"Similarly, human–wildlife conflict and active management of large-bodied animals in cities may influence which species persist in urban environments, potentially constraining the upper end of the body size distribution. Taken together, these examples illustrate the importance of considering the socio-ecological context of urban species assemblages [65]".

> *(2) Line 270. So you removed all data from the grid-based survey?*

We did not remove all data originating from grid-based surveys or gridded products. Rather, we retained GBIF point-occurrence records and applied a standard spatial filtering step, removing only those individual observations with reported coordinate uncertainty greater than 1 km. This was done to ensure reliable alignment between species occurrence points and remotely sensed environmental layers. We have clarified this distinction in the Methods to avoid confusion:

"Due to uncertainty in matching observations with remotely-sensed products, any GBIF observation with a coordinate uncertainty > 1 km was removed. This filtering step removed individual observations with high spatial uncertainty, rather than excluding entire datasets or survey types.".

> *(3) Line 278. Human population density?*

Yes, we have added ‘human’ here (and elsewhere in this section) to make this clearer to the reader.

> *(4) Line 284. What is a pixel?*

We have modified the text to make this clearer:

“VIIRS Stray Light Corrected Nighttime Day/Night Band Composites product, representing monthly composites, (i.e., this dataset in Google Earth Engine: NOAA/VIIRS/DNB/MONTHLY_V1/VCMSLCFG) with a native resolution of ~500 m^2. We took the median of all monthly composites for each pixel (i.e., a single grid cell of the night-time lights raster representing a fixed ground area) to calculate a pixel-level urbanization value, measured in average radiance, and used imagery from January 2015 to January 2021 to calculate this median”.

> *(5) Line 292. It seems to me that lighting is different in different types of cities with the same level of impervious surface, depending on local customs of how many lights are installed, left switched on, etc. I guess that petrol stations and strongly lit industrial areas both produce high levels of light, while for the industrial areas, there could be lawn or other vegetation?*

We thank the reviewer for this thoughtful observation and agree that night-time lighting can vary across cities with similar levels of impervious surface due to differences in land use, infrastructure, and cultural lighting practices. We do not interpret VIIRS night-time lights as a direct measure of any single urban feature, but rather as a continuous, integrative proxy for urbanization that captures the combined footprint of human activity, infrastructure intensity, and energy use. VIIRS radiance has been repeatedly shown to correlate strongly with human population density, built infrastructure, and urban extent, while being negatively correlated with vegetation cover (e.g., EVI). It is repeatedly used in remote sensing and urban sustainability literature. This approach is widely supported in the literature, for example:

Panić et al. used night-time lights were to map spatial and temporal patterns of artificial lighting as a proxy for human population distribution and activity, distinguishing areas of urban and rural occupancy.

(*https://www.ceeol.com/search/article-detail?id=1035395*)

Zhou et al. used night-time light observations were to develop a globally consistent time series of annual urban extent, delineating urban clusters and quantifying global urban growth over decades. (*https://doi.org/10.1016/j.rse.2018.10.015*)

Chakraborty & Stokes used night-time light time series with machine learning to detect and quantify urban change processes—identifying deviations from expected radiance trends to monitor diverse urban transitions.

(*https://doi.org/10.1016/j.rse.2023.113818*)

Zhao et al. reviewed night-time light remote sensing was for its broad capacity to quantify human activities and socioeconomic dynamics—such as urbanization, economic change, and environmental impacts—across scales.

(*https://doi.org/10.3390/rs11171971*)

Zheng et al. used VIIRS nightime lights across 30 global megacities to produce a classification scheme to disentangle urban land changes into five categories, and assess global urbanization processes. (*https://doi.org/10.1016/j.isprsjprs.2021.01.002*)

Zhao et al. argue that nighttime lights provide a consistent dataset to model and interpret urbanization dynamics and use this to track urban dynamics in Southeast Asia. (*https://doi.org/10.1016/j.rse.2020.111980*)

While localized mismatches may occur (e.g., brightly lit industrial areas with surrounding vegetation), such heterogeneity is expected to introduce additional variance rather than systematic bias in the measure of urbanization, making our inference conservative. We have clarified this interpretation and added additional supporting references in the Methods:

"Previous work has shown that VIIRS night-time lights is negatively correlated with greenness measured through the Enhanced Vegetation Index (EVI) and positively correlated with human population density [69,71]. Although night-time light intensity can vary among cities with similar impervious surface due to differences in land use, infrastructure, and cultural lighting practices, at broad spatial scales it functions as an integrative proxy of urbanization [75,76,77,78,79,80], with localized heterogeneity contributing primarily to additional variance rather than systematic bias."

> *(6) Line 295. How did you reconcile the spatial uncertainty of >1km with an urbanization pixel of 150m2? For how many species did you have a higher uncertainty than pixel size? In my experience, your ca. 39m accuracy is a strong assumption for GBIF data.*

We would like to clarify that we do not assume species occurrence accuracy at the scale of the geohash blocks (i.e., tens of meters), and we do not interpret GBIF records as having ca. 39 m positional accuracy. The use of geohash7 (~150 m blocks) reflects a computational indexing choice, not an assumption about biological or observational precision. All GBIF observations with reported coordinate uncertainty greater than 1 km were removed prior to analysis, ensuring that retained occurrences were compatible with the effective spatial resolution of the remotely sensed urbanization data. Importantly, the effective spatial resolution of our urbanization metric remains that of the VIIRS night-time lights product (~500 m). Geohash encoding at a finer resolution was used solely to efficiently associate point occurrences with the appropriate VIIRS pixel while avoiding redundant extraction or averaging across adjacent pixels. This approach does not increase the effective spatial precision of the analysis, nor does it imply sub-pixel inference. We have clarified this in the Methods:

"The VIIRS night-time lights data, with a native resolution of ~500 m^2, was then matched to these blocks by assigning each geohash7 block the average VIIRS radiance value that intersects it. We do not assume positional accuracy at the scale of the geohash blocks, but geohash encoding was used solely for computational indexing, while the effective spatial resolution of the urbanization metric is that of the VIIRS data (~500 m). This approach allows us to avoid unnecessary redundancy in the data while maintaining the original VIIRS resolution".

> *(7) Line 296. Why this high resolution in the species data when your light data is 500m2?*

The apparent mismatch in resolution reflects a distinction between data handling resolution and analytical resolution. Species occurrence records were retained at their native point-level precision to avoid premature spatial aggregation and to ensure that each observation could be accurately matched to the appropriate VIIRS night-time lights pixel. The finer-resolution geohash encoding does not imply that species data were analyzed at that scale, nor does it increase the effective spatial resolution of the analysis. We note, however, that the reported spatial uncertainty of some GBIF records may approach or exceed the resolution of the VIIRS data. Retaining such records represents a deliberate trade-off between spatial precision and data coverage, and is necessary to maximize taxonomic and geographic representation in a global analysis of this scope. Importantly, any residual spatial uncertainty is expected to introduce additional noise rather than systematic bias, making our estimates of species–urban affinity relationships conservative.

> *(8) If you could show how your results match the results of Hahs et al and others with respect to occurrence and traits, this would strengthen your approach.*

We agree that explicitly comparing our findings with prior trait-based studies strengthens the interpretability of our approach. We have now added text to the Discussion that directly compares our results with published analyses, including Hahs et al. (2023) and other taxon-specific studies. In particular, we highlight where our occurrencebased estimates recover similar body size–urbanization relationships (four of five taxa in Hahs et al.) and where they differ (e.g., carabids), and we discuss how such differences likely arise from variation in spatial grain, response variables, and definitions of urbanization. These additions clarify how our framework aligns with, complements, and extends existing trait-based work rather than replacing it.

> *(9) I wonder whether you could run your analysis with simplified data. In the end, you do not talk much about how high the urban score is, so you may also aggregate values to "highly lighted", "lighted", "some light" and "dark" and re-do the analysis, after checking how these scores correlate with e.g. impervious surface in a slightly larger area than what you used (maybe 50x50m).*

Our analytical framework—and the concept of Species Urbanness Distributions (SUDs) in particular—relies on retaining the continuous nature of the underlying urbanization metric. Discretizing night-time light values would necessarily introduce arbitrary thresholds, reduce information content, and obscure subtle but ecologically meaningful variation in species' relative affinities to urban environments. Because we focus on relative affinity patterns rather than absolute urbanization classes, maintaining a continuous metric is central to both our methodological approach and conceptual contribution. That said, we agree that exploring how continuous urban affinity scores relate to categorical urban classes or alternative urbanization proxies (e.g., impervious surface at different spatial grains) represents a valuable direction for future work. Such analyses could be particularly informative for translating continuous affinity metrics into applied conservation or urban planning contexts.

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