

ARTICLE

Urban biotic homogenization: Approaches and knowledge gaps

Sophie Lokatis^{1,2,3}  | Jonathan M. Jeschke^{1,2,3} 

¹Institute of Biology, Freie Universität Berlin, Berlin, Germany

²Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

³Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

Correspondence

Sophie Lokatis

Email: sophie.lokatis@fu-berlin.de**Funding information**

Bundesministerium für Bildung und Forschung, Grant/Award Number: 01LC1501; Studienstiftung des deutschen Volkes

Handling Editor: Mary L. Cadenasso**Abstract**

Urbanization is restructuring ecosystems at an unprecedented pace, with complex and profound consequences for life on Earth. One of the hypothesized trajectories of urban ecosystems and species communities is biotic homogenization, possibly leading to very similar species assemblages in cities across the globe. Urbanization can, however, also have the opposite effect: biotic diversification, with cities, at least at the local scale, becoming biologically more diverse, mainly as a consequence of high species introduction rates and habitat diversification. Applying the hierarchy-of-hypotheses approach, we systematically map and structure the comprehensive body of literature on the urban biotic homogenization (UBH) hypothesis, comprising 225 individual studies (i.e., tests of the hypothesis) retrieved from 145 publications. The UBH hypothesis is studied at multiple levels with a multitude of approaches and underlying assumptions. We show that UBH is generally used with two very different connotations: about half of the studies investigated a potential increase in community similarity across cities, whereas the other half investigated biotic homogenization within cities, the latter being supported more frequently. We also found strong research biases: (1) a taxonomic bias towards birds and plants, (2) a bias towards small and medium distances (<5000 km) in comparisons across cities, (3) a dominance of studies substituting space for time versus true temporal studies, (4) a strong focus on terrestrial versus aquatic systems, (5) more extrarurban (including periurban) areas than natural or rural ecosystems for comparison to urban systems, (6) a bias towards taxonomic versus functional, phylogenetic, and temporal homogenization, and (7) more studies undertaken in Europe and North America than in other continents. The overall level of empirical support for the UBH hypothesis was mixed, with 55% of the studies reporting supporting evidence. Results significantly differed when a natural/nature reserve, an extrarurban, or rural/agricultural area served as reference to infer biotic homogenization, with homogenization being detected least frequently when urban systems were compared to agricultural, i.e., other anthropogenically influenced, study sites.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

We provide an evidence map and a bibliographic network and identify key references on UBH with the goal to enhance accessibility and orientation for future research on this topic.

KEYWORDS

bibliographic network, evidence map, hierarchy-of-hypotheses (HoH) approach, research biases, research synthesis, urban biotic homogenization (UBH)

INTRODUCTION

What we desire in evidence is not mere quantity, but diversity. Different kinds of test, under widely varying conditions, have a greater power to confirm than do repetitions of the same kind of test under the same conditions. More generally, variety in evidence makes for strength in confirmation.

Curd et al. (1998: 472) on Hempel's Diversity Principle of scientific reasoning.

Biotic homogenization is a globally studied phenomenon and a highly active research topic in urban ecology. The urban biotic homogenization (UBH) hypothesis posits an increase in the compositional similarity of urban biomes (Groffman et al., 2014; McKinney, 2002, 2006) and is thus a specific formulation of the more general biotic homogenization hypothesis, which is not limited to urban areas and well known to, for example, researchers working on biological invasions and conservation biology (Baiser et al., 2012; Olden, 2006). This more general hypothesis posits that massive interference with the original structure of ecosystems and the creation of global dispersal pathways leads to a restructuring of the natural ranges of organisms (Baiser et al., 2012; Olden, 2006; Smart et al., 2006). While some species benefit from anthropogenic impacts and expand globally, others have been decimated or disappeared (McKinney & Lockwood, 1999). As a result, the composition of biomes is becoming more similar worldwide, and may even eventually result in the dissolution of faunal barriers as predicted by Charles Elton (1958).

According to the UBH hypothesis, which is the focus of this study, homogenization of species communities is particularly pronounced in urban ecosystems: it could become more likely to find the same bird, tree, or lichen species in New York, Madrid, or Rome than in the original landscapes in which the cities were built. This figurative example represents the idea of homogenization across cities worldwide. It is this aspect of UBH that is highlighted in textbooks (e.g., Marzluff et al., 2008;

Seto et al., 2015; Ossola & Niemelä, 2018) and the focus of most early studies on UBH (Figure 1) as well as the most influential ones (Aronson et al., 2014; McKinney, 2006; Figure 5). The underlying causes are apparent: “Cities are habitats constructed almost exclusively to meet the relatively narrow demands of just one species, *Homo sapiens*. As a result, cities are physically very similar throughout the world: roads, skyscrapers, and residential housing in the suburbs are almost indistinguishable” (McKinney, 2006). This similarity of physical habitats in cities is a key reason for an increase in similarity of urban species communities postulated by the hypothesis, as similar habitats ask for similar species characteristics. In addition, urban areas provide dispersal pathways like trading of pets and ornamental plants, and a concentration of traffic and trade routes, which are of lesser importance in other areas, and many nonnative species are being introduced in this way to cities (Padayachee et al., 2017; Potgieter et al., 2022).

However, whether homogenization of biotic systems occurs depends on the proportion of immigration and extinction processes taking place. Depending on the magnitude and direction of these processes, they may also lead to more diverse species communities between urban areas (Olden & Poff, 2003), a process referred to as biotic differentiation. It is the opposite effect to biotic homogenization and has in an urban context been predominantly described in plants (e.g., Aronson et al., 2015; Brice et al., 2017; Ricotta et al., 2014). Changes in compositional similarity are usually measured as changes in beta diversity, which is the extent of change or dissimilarity between two or more communities. An increase in beta diversity leads to biotic differentiation, while a decrease leads to biotic homogenization.

Biotic homogenization is typically considered to occur at three different levels: phylogenetic, taxonomic, and functional (Olden & Rooney, 2006). A common approach to test UBH has been to use taxonomic diversity indices, but an increasing number of studies also examine functional (e.g., Devictor et al., 2007; Padullés Cubino et al., 2020; Sonnier et al., 2014) or phylogenetic diversity (Ceplova et al., 2015; Ibanez-Alamo et al., 2017; Padullés Cubino et al., 2020). Adding to the complexity of studies

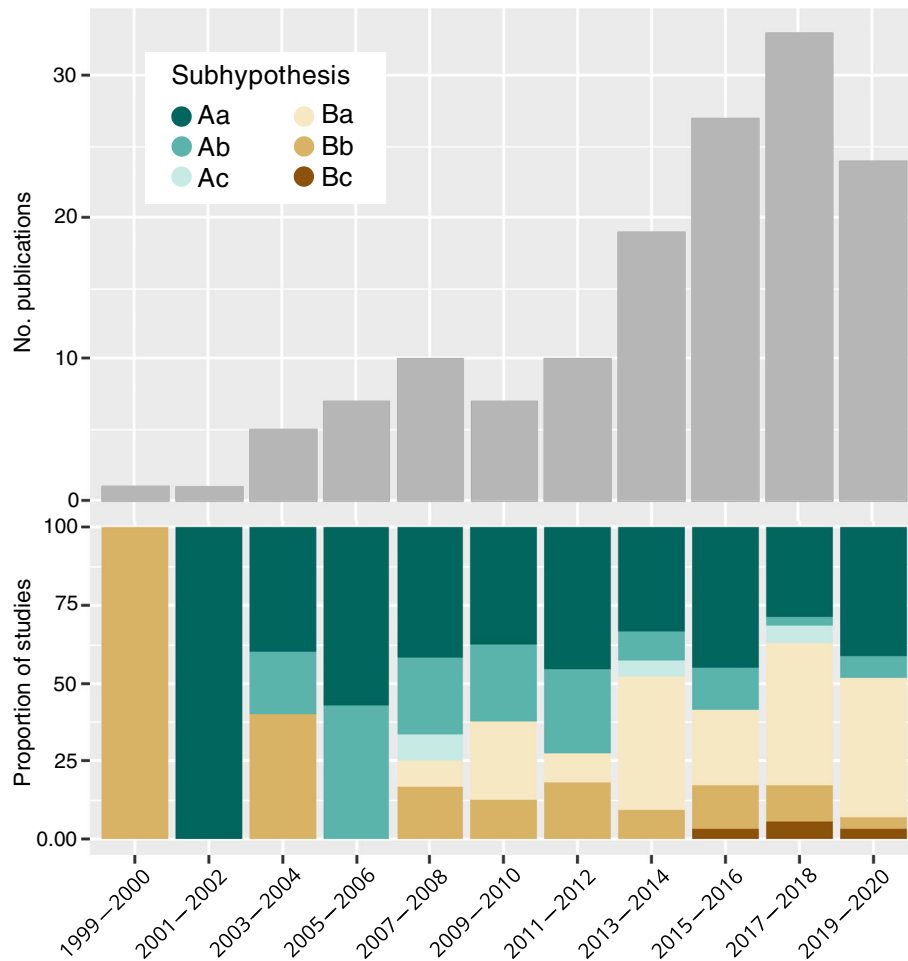


FIGURE 1 Number of publications on urban biotic homogenization over time (upper bars in gray). Bars below show the proportion of studies assessing six different types of sub-hypotheses: Aa, urbanization leads to an increase in community similarity across cities; Ab, urbanization leads to a decrease of specialist and endemic species and/or an increase in generalist, cosmopolitan, or urban tolerant species as an indication of biotic homogenization; Ac, other; Ba, urbanization leads to an increase in community similarity among communities within a city; Bb, urbanization leads to a decrease of specialist and endemic species and/or an increase in generalist, cosmopolitan, or urban tolerant species as an indication of biotic homogenization within a city, thus leading to biotic homogenization of more urban communities compared to less urban communities; Bc, other.

on UBH, patterns of beta diversity are highly scale-dependent, with different processes shaping those patterns, ranging from storms and fires at the local scale to plate tectonics at the global scale (Crawley & Harral, 2001; Willis & Whittaker, 2002). While beta diversity is generally increasing with geographic distance (Antão et al., 2019; Mac Nally et al., 2004), cities are highly novel and heterogeneous ecosystems that might stir up this perceived generality. Marina Alberti (2016) carved out the importance of scale in urban ecology: “At the scale of metres or smaller, urbanization might reduce the heterogeneity of land cover, but at patch level, [urbanization] might introduce highly heterogeneous [...] conditions [...]. As the scale increases, a further reduction in heterogeneity could occur, [...] so that habitats across

urban sites are more similar to one another than to their respective adjacent natural environment” (Alberti, 2016: 147).

To the UBH hypothesis thus applies what is also true for many other ecological hypotheses: it is so generally formulated that it cannot be empirically tested in its entire scope in a single study. Instead, it has been defined and tested in multiple ways (Olden et al., 2018). General hypotheses are typically (and often unconsciously) broken down into sub-hypotheses, which are tested in experiments or observational studies (Heger & Jeschke, 2018). Conclusions are then drawn about the general hypothesis based on the evidence for a narrower, or *operational* hypothesis (i.e., the specific hypothesis actually tested by an experimental or observational

study). The general hypothesis may be accepted as generally valid, whereas in reality it is only true under certain conditions and assumptions and might not even have been investigated in its full scope at all (Heger & Jeschke, 2018).

Philosophers of science have pointed out that studying a broad hypothesis with a diversity of approaches strengthens the scientific process (Curd et al., 1998). This advantage also comes with challenges, though, particularly that it is even hard for experts to keep an overview of the relevant studies. Focusing on UBH, we therefore aim to provide a systematic and structured overview of the comprehensive body of literature on this hypothesis. To do so, we implemented the method proposed by Nakagawa et al. (2019) to assess both evidence and influence (specifically systematic mapping and bibliometrics), an approach therein termed “research weaving.” To analyze the available evidence, we systematically reviewed the available studies on the UBH hypothesis and applied the hierarchy-of-hypotheses (HoH) approach to structure these studies according to the various sub-hypotheses of the broader concept that they address. These sub-hypotheses were thus not conceived a priori but were identified through the literature analysis. The HoH approach is a method to facilitate the synthesis of available studies for research questions, concepts and hypotheses that have been addressed in multiple ways by researchers (Heger et al., 2021; Heger & Jeschke, 2014, 2018; Jeschke et al., 2012). We combine this approach with evidence mapping and bibliometrics to offer an overview of evidence and influence, and thus a specific application of research weaving, focusing on a key hypothesis in urban ecology. Questions that we address are: Which approaches have been applied to study UBH, which systems and which taxonomic groups? Which elements, or sub-hypotheses, of the broad overall hypothesis are empirically supported, and which lack support? Does support for UBH depend on the methodology and type of sub-hypothesis assessed? Which are the most influential papers on UBH? Based on our findings we discuss critical biases and knowledge gaps in the investigation of UBH.

METHODS

Systematic literature search

We compiled a comprehensive collection of empirical studies addressing the urban biotic homogenization (UBH) hypothesis following the PRISMA protocol (Moher et al., 2009), see Appendix S1: Figure S3 for PRISMA flowchart. A search within the ISI Web of

Science was performed on 9 June 2020 using the following terms: “(urban* OR city OR cities) AND (biotic homogenization OR ((biodivers* OR taxonomic diversity OR functional diversity OR genetic diversity OR evolutionary diversity OR species diversity OR trait diversity OR species composition OR habitat diversity) AND homogenization)).”

This search yielded 560 hits, which were screened for relevance (abstract and title) and from these, 385 articles were assessed (full text) and included in our database if (1) the publication addressed the UBH hypothesis or biotic homogenization in cities or in response to urbanization and (2) biotic homogenization was studied empirically by either direct testing, or inferential reasoning from qualitative evidence. We thus included a wider range of publications than for a formal meta-analysis. We excluded publications if (1) neither quantitative nor qualitative evidence was provided on the UBH hypothesis or (2) two entries described the same study or presented the same analyses (e.g., doctoral dissertation and subsequent publication of results). For preprints and theses, we checked in Google Scholar and personal profiles of first authors, e.g., on ResearchGate, whether a more recent publication of the results in an English journal was available and included it instead if available. We also searched manually whether non-English and non-German publications that were retained after the first screening had since been published in English, or else excluded them from the analysis. A total of 145 articles fulfilled these criteria and were thus included in our data set.

Hierarchy of hypotheses

Following the hierarchy-of-hypotheses (HoH) approach (references cited above), we divided the UBH hypothesis into sub- and sub-sub-hypotheses following an iterative bottom-up process (cf. Heger et al., 2021): For each study, we identified how the authors assessed and/or described biotic homogenization in cities and formulated a hypothesis that described the assumptions of the study. For example, the actually tested (sub-)hypothesis of a given study could be “an increase in the percentage of built-up area leads to an increase in Jaccard similarity coefficient among 25 communities of woodland arthropods in a Mediterranean city.” We revised that to “urbanization leads to an increase in community similarity/decrease in beta diversity among communities.” The formulation of a hypothesis in the main text of a study did not necessarily match the actual (sub-)hypothesis that was tested based on the definition of the UBH and its sub-hypotheses applied here. Since it is important to be consistent across all studies, we

critically reflected for each study what aspect of UBH was assessed, and if the definition used by its authors was in congruence with other studies. If not, we adapted it, so that a consistent classification was achieved.

If a publication reported evidence for several (sub-) hypotheses or approaches (type of biotic homogenization, taxonomic focus, realm, temporal approach versus space-for-time substitution), we assessed each of these analyses separately: these are referred to as “studies,” as opposed to “publications,” which can thus contain several studies. For all studies, we gathered information on taxonomic focus; realm; scale; comparison to urban system; type of community data; and type of homogenization (see Lokatis & Jeschke, 2022).

The sub-hypotheses we identified with the described iterative bottom-up approach are the following:

A. *Urbanization leads to biotic homogenization across cities* (as opposed to patterns of homogenization within cities, see sub-hypothesis B below). Studies addressing this sub-hypothesis are based on comparisons across two or more cities, independent of distance: they include comparisons from a regional to global scale.

A.a. *Urbanization leads to an increase in community similarity across cities* ($n = 87$ studies from 63 publications). This sub-hypothesis can, for example, be assessed by calculating measurement pairs for beta diversity of different cities and their respective surrounding/natural areas in comparison with beta diversity between the studied cities, or by analyzing whether beta diversity between pairs of cities show no or less decrease in similarity with increasing distance between study sites, compared to beta diversity between pairs of non-urban sites.

A.b. *Urbanization leads to an increase in generalist, cosmopolitan, or nonnative species across cities, or to a decrease of rare, endemic, or specialist species* ($n = 25$ studies from 21 publications). This sub-hypothesis is, for example, addressed by studying a consistent increase in cosmopolitan species across multiple cities in comparison with pristine sites or historical baselines.

A.c. Other approaches across cities ($n = 5$ studies from four publications), comprising studies on functional or phylogenetic homogenization with alternative approaches to assess homogenization.

B. *Urbanization leads to biotic homogenization within cities.*

B.a. *Urbanization leads to an increase in community similarity among communities within cities* ($n = 83$ studies from 48 publications). Urbanization is, in this connotation of the UBH hypothesis, assumed to lead to biotic homogenization on the scale of cities, meaning that the highly urbanized parts of a city are more similar in their species composition than less urban areas in or around the same city.

B.b. *Urbanization leads to an increase in generalist, cosmopolitan or nonnative species within cities, or to a decrease of rare, endemic, or specialist species* ($n = 21$ studies from 19 publications). Can be assessed by studying species communities along an urbanization gradient within a city, for example by investigating the proportion of nonnative or endangered species.

B.c. Other approaches within cities ($n = 4$ studies from four publications), comprising alternative taxonomic and functional assessments, as well as one taxonomic study that used alpha diversity as indicator.

Scoring empirical evidence for urban biotic homogenization

The studies collected for our analysis are very heterogeneous in their approaches and the presented evidence for UBH. Depending on the sub-hypothesis that was addressed and the type of study system, this evidence was either provided by a (1) visual and/or (2) statistical analysis of several measures of beta diversity, (3) a numerical or (4) qualitative estimate of the proportion of nonnative/generalist/urban-tolerant and/or specialist/rare/endemic species. Each study or part of a study that provided such evidence for a sub-hypothesis was classified as either supporting (i.e., evidence is in line with the addressed hypothesis), mixed/undecided (i.e., provided inconclusive evidence or evidence both for and against the hypothesis) or questioning it (i.e., provided evidence opposing the hypothesis). In a few cases, we changed the authors' original interpretation of the results in order to be consistent in how each approach was used to infer support or refusal of a hypothesis.

This ordinal scoring approach follows earlier applications of the HoH approach. It needs to be distinguished from vote counting, which is simply based on the statistical significance of studies and can yield misleading results (Borenstein et al. 2009; Heger & Jeschke, 2018; Koricheva et al. 2013). The ordinal scoring approach applied here is certainly less powerful than a formal meta-analytic approach, which was, however, not feasible given the heterogeneous hypotheses and approaches used by the studies in our data set. Evidence mapping can also be used as a tool to identify subfields of a broader research field that are “ripe” for meta-analysis, and a formal meta-analysis can be applied for a subset of the data in the future.

Statistical analyses

All statistical tests were carried out in R version 4.0.3 (R Core Team, 2013). We calculated a multinomial

regression (R Package *nnet* version 7.3-15, Ripley et al., 2016) to test for whether the identified sub-hypotheses Aa–c and Ba–c are studied by different approaches/operational hypotheses. Specific attributes of the studies were grouped into tangible categories as follows: taxonomic focus (birds, plants, or else); type of study system (land, freshwater, marine); scale (local [within the same city or town], small [<500 km distance], medium [500–5000 km], large [>5000 km distance]); comparison to urban system (natural, agricultural/rural, urban, and extraurban [comprising all habitats that are neither (near-)natural nor urban, including, e.g., periurban areas, but excluding agricultural/rural areas]); type of community data (presence/absence based, abundance based); type of homogenization (taxonomic, functional, phylogenetic).

Studies in our data set alternately use attributes such as agricultural, extraurban, forest, high-vegetation cover, low urbanization, low disturbance, minimally disturbed, natural, natural greening, nature reserve, near-natural, non-urban, periurban, regional, rural, semi-natural, suburban, or wild to describe their non-urban baseline. To detect methodological choices that could influence the outcome of a study, we grouped these terms into natural, extraurban, rural, and urban (the latter for those studies that did not use a non-urban baseline).

We applied Mann-Whitney (Wilcoxon rank-sum test with unpaired data) and Kruskal-Wallis tests for calculating differences in support, based on the ordinal scores.

Bibliographic network

To further visualize the scientific field and identify influential publications on UBH, we constructed a bibliographic network based on bibliographic coupling of 143 out of the 145 articles identified in the systematic literature search. For the two remaining articles, no bibliometric meta-information was available. The network was compiled in VOSviewer (version 1.6.16) based on bibliographic data from the Web of Science, retrieved on 29 January 2021. Connectivity between publications was based on bibliographic coupling, i.e., two or more publications are linked together if they cite the same reference. While co-citation networks link publications when they have been cited in the same context and are a tool to reconstruct the history of a publication network, bibliographic coupling allows us to link publications that have not been cited and thus incorporates also recent and little-cited studies. Links to a publication were weighted based on fractional counting to account for the number of co-authors per publication.

RESULTS

With which approaches has urban biotic homogenization been studied?

From the 145 publications included in our data set, 225 studies of urban biotic homogenization (UBH) were identified. Research intensity on the UBH hypothesis has increased through time: early publications are from the turn of the millennium when only few articles appeared per year, whereas now about 20 new publications can be found in the literature each year (Figure 1). In total, studies assessing a change in similarity based on an estimate of beta diversity comprise the wide majority of our data set ($n = 170$ studies, 108 publications), compared to 46 studies that look at a decrease of specialist and endemic species and/or an increase in generalist, cosmopolitan or urban tolerant species as an indication of biotic homogenization (112 vs. 40 publications).

One of the most prominent differences in application of the UBH hypothesis is the interpretation of scope: Urban biotic homogenization is assumed to occur across different cities as a result of urbanization. About half of all studies in our data set (52%, 117 studies, 79 publications) assessed homogenization in this way, and thus compared different cities in their analyses. The other half (48%, 108 studies, 69 publications) assessed if urbanization (mostly along an urbanization gradient) leads to biotic homogenization within cities, thus comparing taxonomic composition and other units of biotic homogenization (e.g., phylogenetic or functional) of several sites within a city. This leads to two distinct UBH sub-hypotheses that form the first branch of a hierarchy of hypotheses (HoH): (A) urbanization leads to biotic homogenization across cities and (B) urbanization leads to biotic homogenization within cities.

In most cases, UBH studies across cities (sub-hypothesis A) have been performed at small (<500 km, 41 studies from 28 publications) or intermediate distances (500–5000 km, $n = 53$ studies from 37 publications). Only 21 studies (15 publications) included comparisons of urban areas with distances larger than 5000 km. As expected, biotic homogenization within cities (sub-hypothesis B) has been almost exclusively studied at local scales (i.e., city scale; 96 studies from 61 publications). However, few studies also looked at homogenization within several cities distributed at small and medium scales (11 studies from seven publications) by, e.g., pooling data from different urbanization level or habitat use, or for phylogenetic studies by comparing the evolutionary distinctiveness of these cities compared non-urban areas.

Each of these sub-hypotheses can be divided further into multiple branches. From the empirical data collected for this analysis, we identified two predominating approaches to study urban homogenization: (a) quantifying changes in beta diversity (170 studies from 108 publications in total, i.e., combining Aa and Ba) and (b) assessing the occurrence of species or traits that indicate or are associated with biotic homogenization (46 studies from 40 publications). The majority of articles quantified changes in beta diversity with indices based on presence–absence data ($n = 88$) like Jaccard (27 studies from 22 publications), Sørensen (24 studies from 20 publications), and Simpson, including β_{sim} ($1 - \text{Simpson}$) (21 studies from 12 publications). Abundance-based data (64 studies) was most often analyzed with the Bray-Curtis dissimilarity index (52 studies from 38 publications). Other approaches predominantly relate to (c) a decreased phylogenetic or functional diversity as measures for homogenization. These are not shown in our figures due to small sample size (nine studies from eight publications). We observed a temporal change in focus on these different sub-hypotheses of UBH, with studies addressing biotic homogenization by quantifying changes in beta diversity within and across cities dominating the research field since 2013 (Figure 1). Biotic homogenization has been commonly assessed at taxonomic (172 studies from 124 publications), functional (31 studies from 26 publications), and genetic or phylogenetic level (14 studies from 11 publications), with recent studies also addressing temporal homogenization, for both taxonomic and functional diversity (eight studies from six publications).

Instead of further dividing the HoH into operational hypotheses, we decided, due to the large number of combinations, to visualize the variety of methodological approaches for these sub-hypotheses (Figure 2). Studies looking at different sub-hypotheses significantly differ in scale (analysis of variance for multinomial regression model, $p < 0.001$), but not in other aspects like taxonomic focus (see Appendix S1: Table S1 for full results). Across all sub-hypotheses, birds and plants have been the predominantly studied taxonomic groups, with more than one-third (34%) of the publications in our data set focusing on plants and 29% on birds. Other taxonomic groups have only been studied sparsely (one to nine studies from one to five publications for each group): mollusks, annelids, reptiles and amphibians, fish, algae, lichens and fungi, and bacteria. Mammals only appeared in two studies as part of cross-taxonomic data sets. The majority of publications have assessed UBH at local scales (42%; mainly those addressing homogenization within cities), followed by assessments at medium (26%), small (21%), and large (11%) scales. Space-for-time substitution (scope = spatial) has been applied in the vast majority of publications (84%), with true temporal

assessments being more frequent in publications addressing homogenization within cities. Taxonomic diversity has been assessed in 74% of all publications, and terrestrial study sites dominate in all sub-hypotheses (86%). The type of comparison, i.e., whether homogenization was inferred by using extrarurban, natural, rural or other urban sites as reference, differed among sub-hypotheses, with extrarurban being most frequent (41%), and rural not being represented in sub-hypothesis Bb.

Does support for urban biotic homogenization depend on the applied approach?

Overall support for the UBH hypothesis was mixed, with 80 publications (55%) supporting, 33 publications (23%) questioning, and 32 publications (22%) providing mixed evidence (Figure 3). Support for biotic homogenization within cities (B) was higher than across cities (A), but this difference was not statistically significant (Mann-Whitney, $W = 2314$, $p = 0.06$). Further, publications using different measures of beta diversity (a) significantly less frequently supported UBH than studies assessing species or traits associated with UBH (b; Mann-Whitney, $W = 1592.5$, $p = 0.00721$). Publications using other approaches did not significantly differ from those based on either a or b.

We visualize the disparity in the distribution of studies assessing different sub-hypotheses with different methodological approaches in an evidence map (Figure 4; equivalent to splitting the studies at the level of operational hypotheses, compare Figure 2). There are a number of clear differences. For example, plants are the most frequently studied taxonomic group for sub-hypothesis Ba, whereas other groups are more frequently studied for sub-hypothesis Aa. Within each cell shown in Figure 4, we also compared the level of empirical support, with the caveat of low sample sizes for several cells. In this analysis, only two factors of methodological approach had a significant effect on how strong UBH was supported: type of biological diversity analyzed (i.e., taxonomic, functional, or phylogenetic and for each of these also seasonal [subsumed here into one category, due to small sample size]; analysis of variance for multinomial regression model, $p = 0.0334$), and “type of comparison”, i.e., whether a natural/nature reserve, an extrarurban area, a rural area or other urban habitats served as reference to infer biotic homogenization in the urban study system (analysis of variance for multinomial regression model, $p = 0.00815$, see Appendix S1: Table S2 for full results). Post hoc Wilcoxon tests yielded no significant differences between natural and extrarurban ($W = 2242$, $p = 0.0885$), but significant differences between

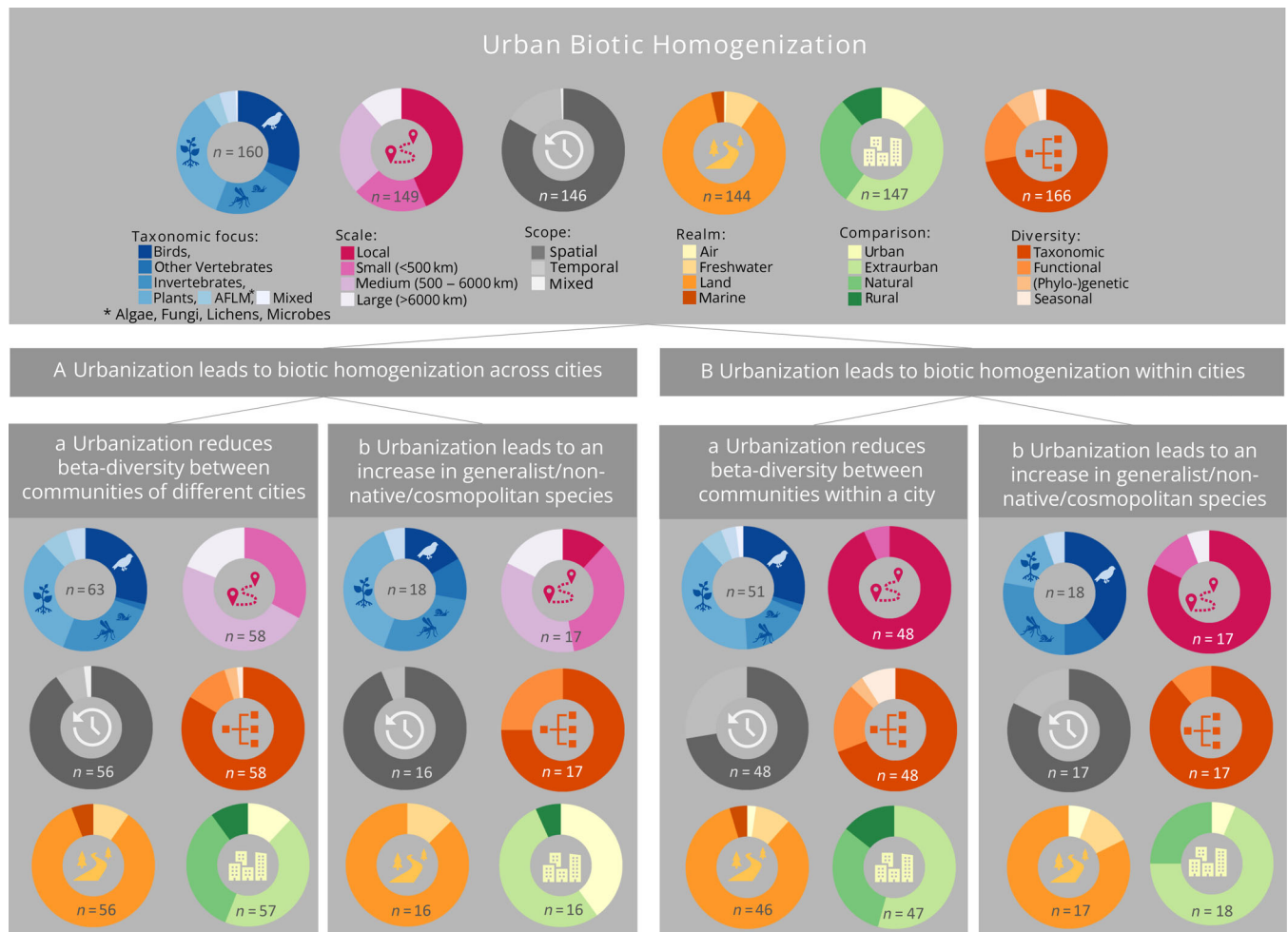


FIGURE 2 Variation in methodological approaches used in four of the six urban biotic homogenization (UBH) sub-hypotheses. Here, n is the number of times an approach was applied across all publications, meaning that, for example, a publication assessing birds and plants in a terrestrial system will appear twice in the plot depicting taxonomic focus (birds and plants), but only once in the plot depicting realm (terrestrial); this leads to diverging sample sizes. Sub-hypotheses Ac and Bc are not included here because of low sample sizes for these two sub-hypotheses.

urban and extraurban areas ($W = 1478$, $p = 0.0458$), and between rural and natural areas ($W = 898.5$, $p = 0.00966$).

Are publications on urban biotic homogenization geographically biased?

We found a strong geographic bias in publications on the UBH hypothesis, with the vast majority of studies coming from Europe and North America, compared to only few in Africa, Central Asia, the Middle East and island states in the western Pacific (see Appendix S1: Figure S1). More specifically, 41% of the publications are from Europe (60 publications and 98 studies), 40% from North America (59 publications and 84 studies), with a third coming from the United States (47 publications, 73 studies), the country with by far the highest

number of studies. The following continents were South America (29 publications, 41 studies), Asia (16 publications, 31 studies), Australia/Oceania (12 publications, 21 studies), and Africa (12 publications, 20 studies).

Bibliometric analysis: Mapping research on urban biotic homogenization

The network based on bibliographic coupling of the scientific literature highlights the two most influential research articles on UBH (Figure 5): McKinney (2006, 1611 citations until 29 January 2021 in the Web of Science) and Aronson et al. (2014, 494 citations); for the 25 most cited articles, see Appendix S1: Table S3. We provide three visualizations of the network, one showing the year of publication for each article and thus

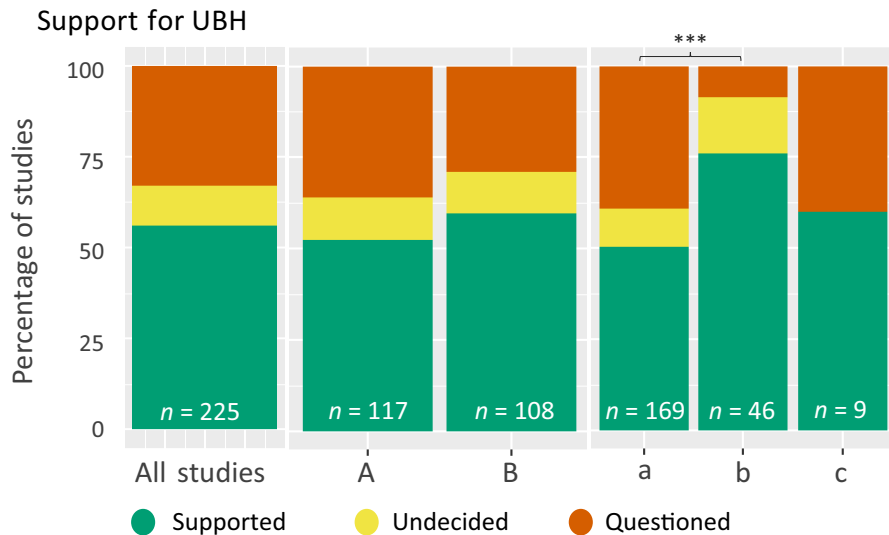


FIGURE 3 Support for urban biotic homogenization for all publications (left bar), and publications using different connotations of the main hypothesis A across versus B within cities (center bars), and different homogenization/diversity measures, based on (a) beta diversity, (b) certain species (e.g., generalist, nonnative, cosmopolitan species) and (c) other approaches. ****p* < 0.01, Mann-Whitney test.

a rough temporal development from the top to the bottom of the network; the second one illustrating the distribution of the two main sub-hypotheses A (*urbanization leads to biotic homogenization across cities*) and B (*urbanization leads to biotic homogenization within cities*); and the third one showing the focal study taxon of each publication. This latter network illustrates that articles segregate according to taxonomic group and roughly match the innate clustering calculated by VosViewer based on connectivity of the publications, not attributes of studies (see Appendix S1: Figure S2). The two most influential studies, McKinney (2006) and Aronson et al. (2014), assessed both birds and plants as taxonomic groups (i.e., they were cross-taxonomic), whereas most other studies focused on a single taxonomic group. The two influential studies also focused on sub-hypothesis A, similarly to most other early publications on UBH (cf. Figure 1).

DISCUSSION

Different connotations and sub-hypotheses of urban biotic homogenization

We showed that two very different connotations of UBH are frequently used by urban ecologists: an increase in biotic homogenization across cities, including an increased likelihood of meeting the same species in cities worldwide, and an increase in biotic homogenization within a particular city. Looking more closely at studies on UBH, this is not the only aspect in which they differ: similar to other major ecological hypotheses, existing

studies addressing UBH do in fact address different variants, i.e., sub-hypotheses, of the overarching hypothesis (cf. Heger & Jeschke, 2014 for the enemy release hypothesis, a major hypothesis about biological invasions). Accordingly, the hierarchy-of-hypotheses (HoH) approach (Heger et al., 2021 and further references cited above) has proven useful for structuring and assessing publications on UBH.

A key aspect we aimed to capture in our HoH is scale, hence we discriminated sub-hypothesis A (*urbanization leads to biotic homogenization across cities*) from sub-hypothesis B (*urbanization leads to biotic homogenization within cities*). Overall, sub-hypothesis B received more empirical support than sub-hypothesis A, although this difference was only marginally significant. Interestingly, sub-hypothesis B opposes the idea that urbanization leads to heterogeneous habitats, and that this heterogeneity leads to an increase in beta diversity within a city, thus benefiting a city’s total biodiversity (e.g., Pyšek, 1989, Sattler et al., 2010). Note that, even if sub-hypothesis B relates to comparisons within cities, their results may also be relevant for larger scales. This is especially true for studies looking at the distribution of widespread indicator species (i.e., generalist, cosmopolitan species); if such species are particularly abundant in urbanized areas within cities, that also leads to UBH across cities.

Olden and Rooney (2006) presented two notable definitions of biotic homogenization, one focusing on the process of nonnative species replacing resident species (based on McKinney & Lockwood, 1999), the other one focusing on the pattern of “increased similarity of biotas over time” (quoted from Rahel 2002). We paraphrased

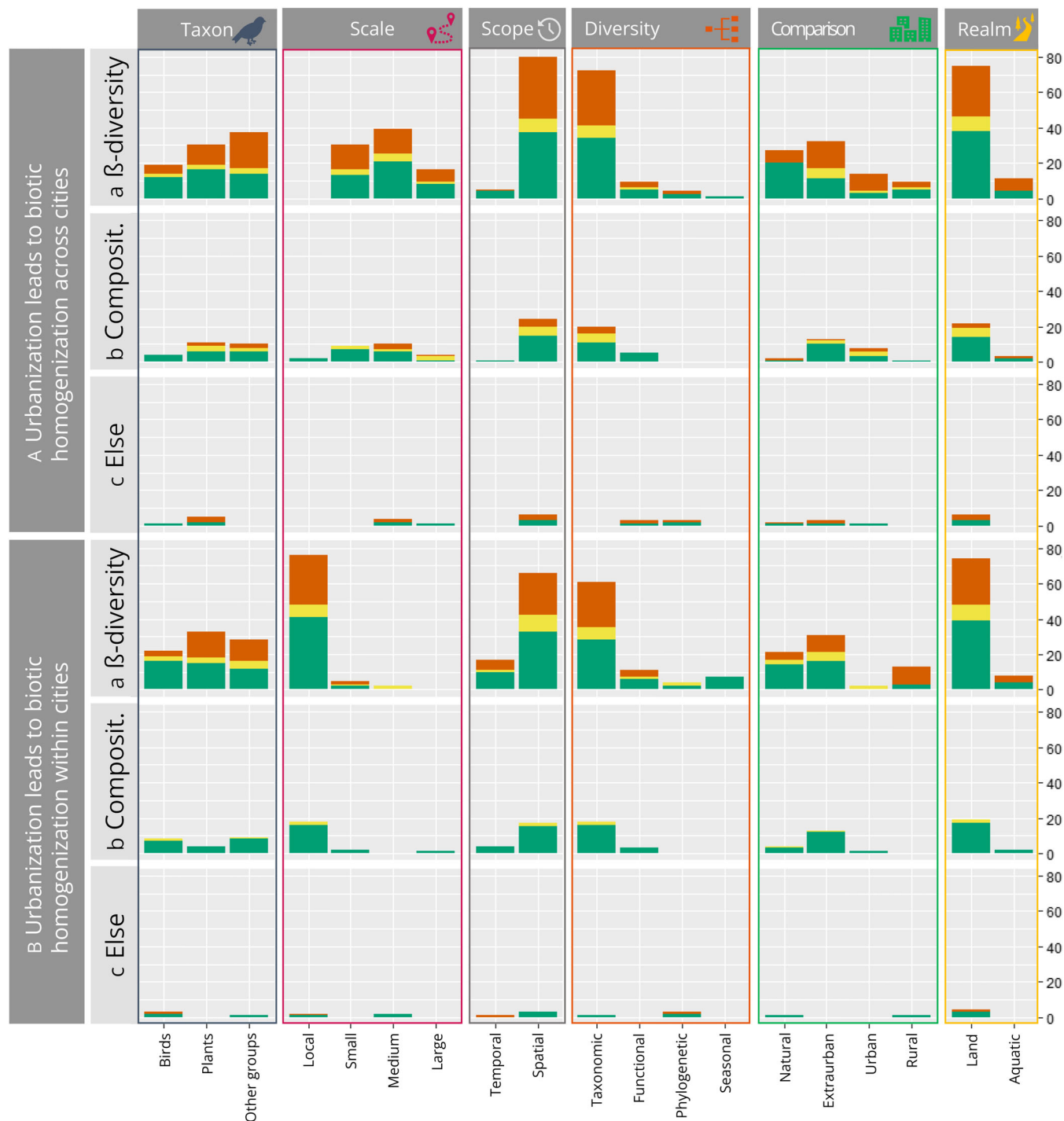


FIGURE 4 Evidence map for the different UBH sub-hypotheses Aa–Bc showing the distribution of available evidence for different approaches. Symbols and colors in the top row indicating different approaches match those in Figure 2.

these definitions and incorporated them as lower-level sub-hypotheses in our hierarchy of hypotheses, the latter as *urbanization leads to an increase in community similarity* (sub-hypothesis a), and the former as *urbanization leads to an increase in generalist, cosmopolitan, or nonnative species in cities, or to a decrease of rare, endemic, or specialist species* (sub-hypothesis b). Remaining studies that did not fit into either a or b were grouped into c (other

approaches). We found that publications addressing sub-hypothesis b reported supporting evidence for UBH significantly more frequently than studies addressing sub-hypothesis a. It is possible that this approach is more susceptible to certain biases (discussed in the next section, *What has been studied and how?*) and thus overestimates total biotic homogenization. On the other hand, it might be more sensitive to processes of ongoing homogenization,

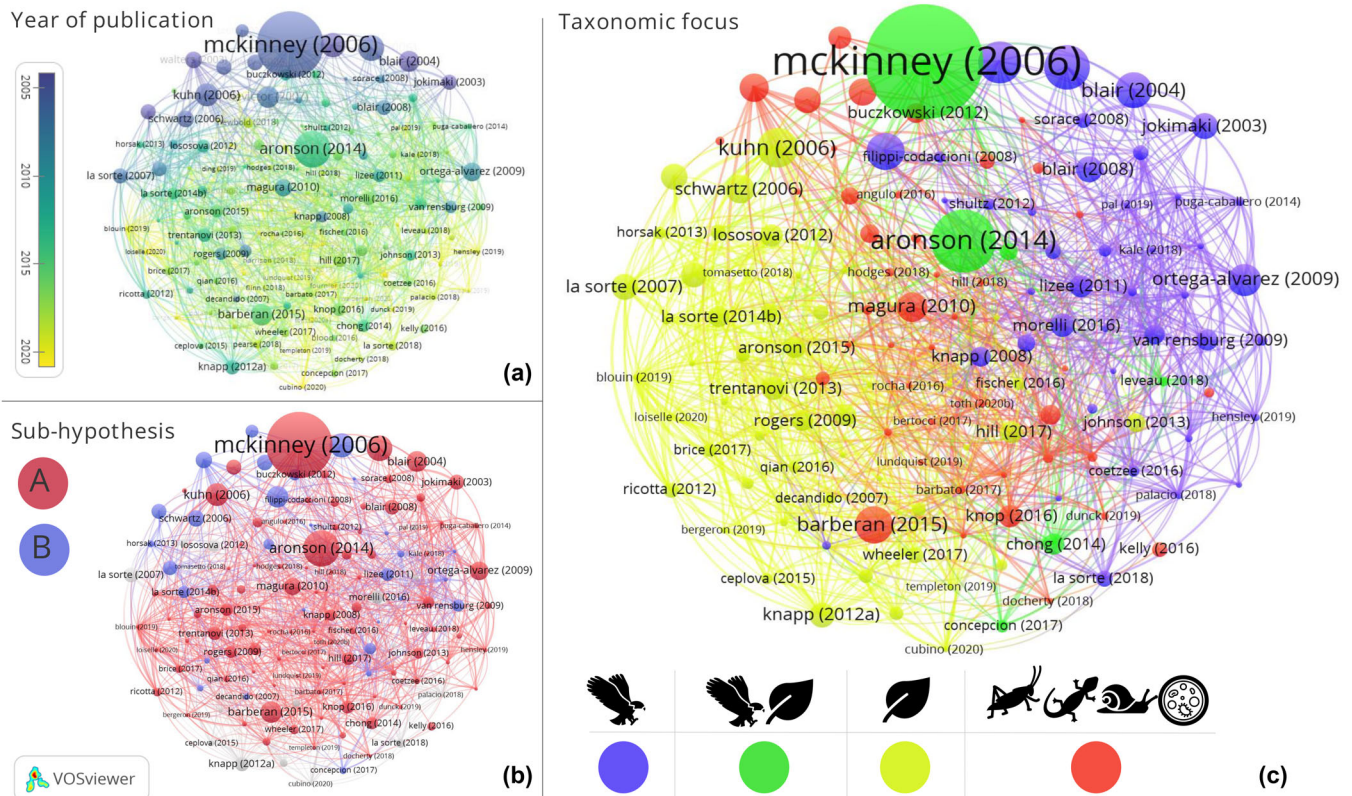


FIGURE 5 A map of publications on urban biotic homogenization, based on bibliographic coupling. (a) A gradient from blue to yellow indicates the time of publication from 2006 to 2020; (b) the two main hypotheses highlighted in red and blue; (c) the taxonomic focus of a study is highlighted in yellow (plants), blue (birds), green (plants and birds), or red (all other groups, e.g., insects, reptiles, and microbes). References attributed to the nodes are available in Appendix S1.

e.g., identifying the presence of known indicator taxa, that are not (yet) apparent in comparative analyses of beta diversity and can only be detected with a delay. The difference we observed in empirical support between sub-hypotheses a and b might thus reflect real differences.

Studies that quantify UBH using estimates for changes in beta diversity (sub-hypothesis a) make up more than two-thirds of all studies. Anderson et al. (2011) identified a series of “mission statements” that studies assessing beta diversity adhere to and that would constitute excellent sub-hypotheses if one wants to extend our HoH further. These mission statements cluster into two groups: variation and turnover, i.e., non-directional and directional differentiation, with variation being the exception in our data set (represented by Piano et al., 2020; Uchida et al., 2018). The wide majority of publications applied common measures of directional beta diversity, like Bray-Curtis dissimilarity index, Jaccard similarity index, Sørensen-Dice coefficient, or Simpson dissimilarity index.

There is an ongoing debate around the concept of beta diversity and its application. The choice of (dis)similarity metrics and “mission statement” (using the term from Anderson et al., 2011) has been shown

to influence the results when quantifying changes in dissimilarity and are thus highly relevant to the study of biotic homogenization: compositional turnover versus variation, calculating average pairwise dissimilarities versus multiple site dissimilarity (see, e.g., Baselga, 2013 or La Sorte et al., 2014), using presence/absence versus abundance based indices (see, e.g., McKinney & Lockwood, 2005), differentiating between turnover and nestedness components of beta diversity (Baselga, 2010) or even reflecting on the question whether what is measured is in fact true beta diversity (Tuomisto, 2010). These questions go beyond the scope of this literature assessment and we highly recommend the respective literature.

Sub-hypothesis b focuses on the presence/absence, proportion or abundance of “indicator species” for UBH. Methods and reasoning of studies belonging to this group are diverse. One approach is to use (dis)similarity indices to quantify patterns of homogenization as described above, but instead of measuring total community (dis)similarity, the focus here is on the change in indicator species, e.g., rare species (Schwartz et al., 2006), urban exploiters (Starry et al., 2018), nonnative species (Horsak et al., 2013; Lososova et al., 2012; Padullés

Cubino et al., 2019) or a combination of these (e.g., Paz Silva et al., 2016). The advantage of this selective assessment might be that it is more sensitive to detect processes of biotic homogenization that can be covered by parallel processes of community change and that it allows us to identify underlying causes of UBH, particularly when used in combination with overall quantification of homogenization, as in Lososova et al. (2012). Other approaches use, for example, the proportional change or relative abundance of these indicator species (Abilhoa & Amorin, 2017; Bigirimana et al., 2011).

Biotic homogenization can be associated with a decrease in species richness, but not inferred from it, and Olden and Poff (2003) argue that treating homogenization “erroneously as a synonym for species diversity loss” may be a major problem in studies on biotic homogenization. We rarely found this type of reasoning, however, and grouped them into sub-hypothesis c, together with publications on phylogenetic and functional homogenization that assess functional diversity loss or loss in phylogenetic or functional distinctiveness as indicators for homogenization.

What has been studied and how?

General ecological hypotheses are empirically tested at the level of operational hypotheses, which differ in study design and research approach. Studies on UBH differ in the type of biotic homogenization assessed (taxonomic, phylogenetic, functional), taxonomic focus (here mostly simplified to birds, plants, and other groups, but see Figure 2 and the openly provided data set for a more detailed distinction), geographic location, realm (land, freshwater, marine), scale (local, small, medium, and large), baseline comparison (urban, extraurban, rural, and natural), whether they are performed as field studies or analyses of data compilations, size of the data set, and (statistical or inferential) method.

Of particular interest, and potentially problematic, is the quantification of temporal change. Olden and Rooney (2006) emphasized that, following McKinney and Lockwood (1999), biotic homogenization has been seen as “the process by which species similarity across space increases over time due to species invasions and extinctions, as opposed to the pattern resulting from this process.” Yet, <15% of all publications include true temporal data in their analysis, most of them covering time periods of up to 30 years. Only a handful of studies used longer-term data, particularly Knapp et al. (2017), DeCandido et al. (2007), and Dolan et al. (2017): they all compared recent data on plant communities with historical inventories. Studies that simultaneously study

temporal homogenization at multiple sites and spanning various degrees of urbanization, an approach highly recommended by Olden and Rooney (2006), are particularly rare (Rogers et al., 2009). The most common way to quantify the intrinsically temporal process of UBH is space-for-time substitution, which “infer[s] a temporal trend from a study of different aged sites” (Pickett, 1989), with the modification that the degree of urbanization, or urban areas when compared to non-urban sites, is assumed to allow inferring an underlying process to the observed pattern. Space-for-time substitution has been criticized to have less explanatory power than true temporal studies (Damgaard, 2019), and Olden and Rooney (2006) urged researchers to include the temporal dimension in their analyses of biotic homogenization, or else risk losing explanatory power. Studies on UBH that use space-for-time substitution need to be aware of confounding factors, especially in a world where almost every type of ecosystem is anthropogenically affected: pristine natural areas that could serve as comparative baseline for changes in urban systems are rare and they are especially hard to find in regions where cities are located because these are by definition densely populated by humans (Riggio et al., 2020).

Space-for-time substitution: What is the non-urban baseline?

Studies that analyze biotic homogenization usually need a non-urban baseline to infer patterns of homogenization in urban areas. Exceptions are temporal studies of urban focal areas, assessing the presence of “indicator species” for homogenization or the quantification of distance decay, e.g., comparing the similarity of communities within one city to communities in remote cities.

Using (near-) natural reference sites as non-urban baseline leads to a significant increase in the probability to detect UBH, while rural sites decrease this probability. Agricultural sites in particular might lead to a possible underestimation or even covering of UBH when used as non-urban baseline, probably because of similar processes of homogenization in this habitat: agricultural areas are far from being natural, and patterns of biotic homogenization have been reported there repeatedly (Ekroos et al., 2010; Karp et al., 2012; Solar et al., 2015).

The very heterogeneous use of non-urban baseline is partly founded in regional characteristics of study sites (the non-urban surrounding is highly heterogeneous and truly natural sites are hardly found anymore), but also linked to the question of how to quantify and define urbanization (and non-urbanization, conversely), an aspect that we cannot expand on in this article, but see the openly provided data set for an attempt to list

definitions and approaches on this; see, e.g., Alberti et al. (2001) and Schwarz (2010) for further discussion on this topic.

Where are biases and knowledge gaps?

We found a strong geographic bias in the investigation of UBH, with Europe and North America comprising more than two-thirds of all publications, and a few other “hot spots” of urban biodiversity research, e.g., China, Australia, and parts of South America, whereas other regions remain highly understudied. There is also the matter of climate regions that is highly relevant for studies on biotic homogenization, with a strong bias towards northern temperate climate, and few studies crossing climatic regions. Geographic biases have been reported in biodiversity research in general (e.g., Martin et al., 2012; Tydecks et al., 2018) and urban ecology in particular (e.g., Magle et al., 2012; Shwartz et al., 2014). They are a major concern in this field, as urbanization pressure is often high in regions that are poorly monitored for changes in biodiversity (Elmqvist et al., 2013); and contextual differences of cities in the Global South cannot be accounted for due to insufficient data (Shackleton et al., 2021).

Our data set also shows a strong bias towards terrestrial versus aquatic habitats, the latter comprising both marine and freshwater habitats: only about every 10th publication focused on aquatic systems. This bias is even more pronounced than the 20% aquatic studies reported in a recent comprehensive literature review on the impact of urbanization on biodiversity (McDonald et al., 2020).

Similarly, plants and birds have been studied much more frequently than other taxonomic groups. Mammals were highly underrepresented in our assessment, which is surprising, as Magle et al. (2012) report them to be in second place, after birds, in a cross-taxonomic review on urban wildlife research. However, while many studies focusing on mammals in cities focus on wildlife management and animal behavior, studies on UBH are currently rare. Our analysis also points to a serious knowledge gap about some species-rich taxonomic groups, such as insects, fungi, and bacteria (Hochkirch et al., 2021).

The largest fraction of UBH publications looks at taxonomic diversity, only comparatively few on functional, or phylogenetic and evolutionary homogenization, which have thus remained largely unexplored. An extension is the study of seasonal homogenization, for both taxonomic (La Sorte et al., 2014) and functional diversity (Leveau et al., 2018).

Not all studies explicitly stated a hypothesis in the way we defined it here. We included such studies if we found

them with our literature search, but we expect that there are a number of further studies reporting and analyzing suitable data sets that we did not find because they did not refer to biotic homogenization or a related keyword included in our query. The danger here is a reporting bias for the UBH hypothesis that emerges when the connection to UBH was only made when it was observed, a phenomenon called HARKing (Hypothesizing After the Results are Known, see, e.g., Lokatis & Jeschke, 2018). This phenomenon leads to a higher empirical support as reported in the literature (of studies being explicit about testing a hypothesis) compared to the actual support of all relevant studies (including those that do not explicitly refer to the hypothesis and those that never got published, see also Neuroskeptical, 2012).

CONCLUSIONS

By providing an overview of the conceptual structure of research on urban biotic homogenization, we highlight and aim to raise awareness of the fact that the concept is being used to describe patterns and processes from different perspectives, not only on the matter of comparing diversity within and across cities, but also due to different approaches and study systems. Inferring from any study that one will encounter the same birds or trees in cities around the world and that this is an ongoing process following urbanization will be difficult—unless that study actually compared the temporal development of species communities in multiple cities across the globe. The reality is that long-term studies as well as comparable research sites across the globe, especially in the southern hemisphere, are rare (Fidino & Magle, 2017; Wohner et al., 2021). While researchers draw on diverse approaches to partly overcome practical limitations (e.g., applying space-for-time substitution), and global research collaborations in urban ecology have been built in the past years (e.g., Magle et al., 2019; Pouyat et al., 2017), a strong need for more evenly distributed, long-term urban research sites remains.

ACKNOWLEDGMENTS

We appreciate helpful input from Maud Bernard-Verdier, Tina Heger, Chunlong Liu, Flavio Morelli, Tanja Straka, and three anonymous reviewers. Financial support has been provided by the Studienstiftung des deutschen Volkes to S. Lokatis and by the German Federal Ministry of Education and Research (BMBF) within the Collaborative Project “Bridging in Biodiversity Science (BIBS)” (funding number 01LC1501) to J. M. Jeschke. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Lokatis & Jeschke, 2022) are available in Dryad at <https://doi.org/10.5061/dryad.7sqv9s4v5>.

ORCID

Sophie Lokatis  <https://orcid.org/0000-0003-2178-3924>

Jonathan M. Jeschke  <https://orcid.org/0000-0003-3328-4217>

REFERENCES

- Abilhoa, V., and R. Amorin. 2017. "Effects of Urbanization on the Avian Community in a Southern Brazilian City." *Revista Brasileira De Ornitologia* 25(1): 31–9.
- Alberti, M. 2016. *Cities that Think like Planets: Complexity, Resilience, and Innovation in Hybrid Ecosystems*. Seattle, WA: University of Washington Press.
- Alberti, M., E. Botsford, and A. Cohen. 2001. "Quantifying the Urban Gradient: Linking Urban Planning and Ecology." In *Avian Ecology and Conservation in an Urbanizing World*, edited by J. M. Marzluff, R. Bowman, and R. Donnelly, 89–115. New York: Springer.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, et al. 2011. "Navigating the Multiple Meanings of β Diversity: A Roadmap for the Practicing Ecologist." *Ecology Letters* 14(1): 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>.
- Antão, L. H., B. McGill, A. E. Magurran, A. M. V. M. Soares, and M. Dornelas. 2019. " β -Diversity Scaling Patterns Are Consistent across Metrics and Taxa." *Ecography* 42(5): 1012–23. <https://doi.org/10.1111/ecog.04117>.
- Aronson, M. F. J., S. N. Handel, I. P. La Puma, and S. E. Clemants. 2015. "Urbanization Promotes Non-native Woody Species and Diverse Plant Assemblages in the New York Metropolitan Region." *Urban Ecosystem* 18(1): 31–45. <https://doi.org/10.1007/s11252-014-0382-z>.
- Aronson, M. F. J., F. A. La Sorte, C. H. Nilon, M. Katti, M. A. Goddard, C. A. Lepczyk, P. S. Warren, et al. 2014. "A Global Analysis of the Impacts of Urbanization on Bird and Plant Diversity Reveals Key Anthropogenic Drivers". *Proceedings of the Royal Society B: Biological Sciences* 281(1780): 20133330. <https://doi.org/10.1098/rspb.2013.3330>.
- Baiser, B., J. D. Olden, S. Record, J. L. Lockwood, and M. L. McKinney. 2012. "Pattern and Process of Biotic Homogenization in the New Pangaea." *Proceedings of the Royal Society B: Biological Sciences* 279(1748): 4772–7.
- Baselga, A. 2010. "Partitioning the Turnover and Nestedness Components of Beta Diversity." *Global Ecology and Biogeography* 19(1): 134–43.
- Baselga, A. 2013. "Multiple Site Dissimilarity Quantifies Compositional Heterogeneity among Several Sites, while Average Pairwise Dissimilarity May Be Misleading." *Ecography* 36(2): 124–8.
- Bigirimana, J., J. Bogaert, C. Canniere, J. Lejoly, and I. Parmentier. 2011. "Alien Plant Species Dominate the Vegetation in a City of Sub-Saharan Africa." *Landscape and Urban Planning* 100(3): 251–67. <https://doi.org/10.1016/j.landurbplan.2010.12.012>.
- Borenstein, M., H. Cooper, L. Hedges, and J. Valentine. 2009. "Effect Sizes for Continuous Data." In *The Handbook of Research Synthesis and Meta-Analysis*, edited by H. Cooper, L. V. Hedges, and J. C. Valentine, 2nd edn, 221–35. New York: Russell Sage Foundation.
- Brice, M.-H., S. Pellerin, and M. Poulin. 2017. "Does Urbanization Lead to Taxonomic and Functional Homogenization in Riparian Forests?" *Diversity and Distributions* 23(7): 828–40. <https://doi.org/10.1111/ddi.12565>.
- Ceplova, N., Z. Lososova, D. Zeleny, M. Chytry, J. Danihelka, K. Fajmon, D. Lanikova, Z. Preislerova, V. Rehorek, and L. Tichy. 2015. "Phylogenetic Diversity of Central-European Urban Plant Communities: Effects of Alien Species and Habitat Types." *Preslia* 87(1): 1–16.
- Crawley, M. J., and J. Harral. 2001. "Scale Dependence in Plant Biodiversity." *Science* 291(5505): 864–8.
- Curd, M., J. A. Cover, and C. Pincock. 1998. *Philosophy of Science: The Central Issues*. New York, NY: Norton & Company.
- Damgaard, C. 2019. "A Critique of the Space-for-Time Substitution Practice in Community Ecology." *Trends in Ecology & Evolution* 34(5): 416–21. <https://doi.org/10.1016/j.tree.2019.01.013>.
- DeCandido, R., N. Calvanese, R. V. Alvarez, M. I. Brown, and T. M. Nelson. 2007. "The Naturally Occurring Historical and Extant Flora of Central Park, New York City, New York 1857–2007." *Journal of the Torrey Botanical Society* 134(4): 552–69. <https://doi.org/10.3159/07-RA-002.1>.
- Devictor, V., R. Julliard, D. Couvet, A. Lee, and F. Jiguet. 2007. "Functional Homogenization Effect of Urbanization on Bird Communities." *Conservation Biology* 21(3): 741–51. <https://doi.org/10.1111/j.1523-1739.2007.00671.x>.
- Dolan, R. W., M. F. J. Aronson, and A. L. Hipp. 2017. "Floristic Response to Urbanization: Filtering of the Bioregional Flora in Indianapolis, Indiana, USA." *American Journal of Botany* 104(8): 1179–87. <https://doi.org/10.3732/ajb.1700136>.
- Ekroos, J., J. Heliölä, and M. Kuussaari. 2010. "Homogenization of Lepidopteran Communities in Intensively Cultivated Agricultural Landscapes." *Journal of Applied Ecology* 47(2): 459–67.
- Elmqvist, T., M. Fragkias, J. Goodness, B. Güneralp, P. J. Marcotullio, R. I. McDonald, S. Parnell, M. Schewenius, M. Sendstad, and K. C. Seto. 2013. *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment*. Urbanization, Biodiversity and Ecosystem Services: Springer.
- Elton, C. S. 1958. "Wallace's Realms: The Archipelago of Continents." In *The Ecology of Invasions by Animals and Plants*, 33–49. Boston: Springer.
- Fidino, M., and S. B. Magle. 2017. "Trends in Long-Term Urban Bird Research." In *Ecology and Conservation of Birds in Urban Environments*, edited by E. Murgui and M. Hedblom, 161–84. Cham: Springer.
- Groffman, P. M., J. Cavender-Bares, N. D. Bettez, J. M. Grove, S. J. Hall, J. B. Heffernan, S. E. Hobbie, K. L. Larson, J. L. Morse, and C. Neill. 2014. "Ecological Homogenization of Urban USA." *Frontiers in Ecology and the Environment* 12(1): 74–81.
- Heger, T., C. A. Aguilar-Trigueros, I. Bartram, R. R. Braga, G. P. Dietl, M. Enders, D. J. Gibson, L. Gómez-Aparicio, P. Gras, and K. Jax. 2021. "The Hierarchy-of-Hypotheses Approach: A Synthesis Method for Enhancing Theory

- Development in Ecology and Evolution.” *Bioscience* 71(4): 337–49.
- Heger, T., and J. M. Jeschke. 2014. “The Enemy Release Hypothesis as a Hierarchy of Hypotheses.” *Oikos* 123(6): 741–50.
- Heger, T., and J. M. Jeschke. 2018. “The Hierarchy-of-Hypotheses Approach.” In *Invasion Biology. Hypotheses and Evidence*, edited by J. M. Jeschke and T. Heger, 14–8. Wallingford: CABI.
- Hochkirch, A., M. J. Samways, J. Gerlach, M. Böhm, P. Williams, P. Cardoso, N. Cumberlidge, et al. 2021. “A Strategy for the Next Decade to Address Data Deficiency in Neglected Biodiversity.” *Conservation Biology* 35(2): 502–9. <https://doi.org/10.1111/cobi.13589>.
- Horsak, M., Z. Lososova, T. Cejka, L. Jurickova, and M. Chytry. 2013. “Diversity and Biotic Homogenization of Urban Land-Snail Faunas in Relation to Habitat Types and Macroclimate in 32 Central European Cities.” *PLoS One* 8(8): e71783. <https://doi.org/10.1371/journal.pone.0071783>.
- Ibanez-Alamo, J. D., E. Rubio, Y. Benedetti, and F. Morelli. 2017. “Global Loss of Avian Evolutionary Uniqueness in Urban Areas.” *Global Change Biology* 23(8): 2990–8. <https://doi.org/10.1111/gcb.13567>.
- Jeschke, J. M., L. Gómez Aparicio, S. Haider, T. Heger, C. J. Lortie, P. Pyšek, and D. L. Strayer. 2012. “Support for Major Hypotheses in Invasion Biology Is Uneven and Declining.” *NeoBiota* 14: 1–20.
- Karp, D. S., A. J. Rominger, J. Zook, J. Ranganathan, P. R. Ehrlich, and G. C. Daily. 2012. “Intensive Agriculture Erodes β -Diversity at Large Scales.” *Ecology Letters* 15(9): 963–70.
- Knapp, S., M. Winter, and S. Klotz. 2017. “Increasing Species Richness but Decreasing Phylogenetic Richness and Divergence over a 320-Year Period of Urbanization.” *Journal of Applied Ecology* 54(4): 1152–60. <https://doi.org/10.1111/1365-2664.12826>.
- Koricheva, J., J. Gurevitch, and K. Mengersen, eds. 2013. *Handbook of Meta-Analysis in Ecology and Evolution*. Princeton, NJ: Princeton University Press.
- La Sorte, F. A., M. W. Tingley, and A. H. Hurlbert. 2014. “The Role of Urban and Agricultural Areas during Avian Migration: An Assessment of Within-Year Temporal Turnover.” *Global Ecology and Biogeography* 23(11): 1225–34. <https://doi.org/10.1111/geb.12199>.
- Leveau, L. M., F. I. Isla, and M. I. Bellocq. 2018. “Predicting the Seasonal Dynamics of Bird Communities along an Urban–Rural Gradient Using NDVI.” *Landscape and Urban Planning* 177: 103–13. <https://doi.org/10.1016/j.landurbplan.2018.04.007>.
- Lokatis, S., and J. M. Jeschke. 2018. “The Island Rule: An Assessment of Biases and Research Trends.” *Journal of Biogeography* 45(2): 289–303. <https://doi.org/10.1111/jbi.13160>.
- Lokatis, S., & Jeschke, J. M. (2022), “Urban Biotic Homogenization: Approaches and Knowledge Gaps.” Dryad, Dataset. <https://doi.org/10.5061/dryad.7sqv9s4v5>.
- Lososova, Z., M. Chytry, L. Tichy, J. Danihelka, K. Fajmon, O. Hajek, K. Kintrova, D. Lanikova, Z. Otypkova, and V. Rehorek. 2012. “Biotic Homogenization of Central European Urban Floras Depends on Residence Time of Alien Species and Habitat Types.” *Biological Conservation* 145(1): 179–84. <https://doi.org/10.1016/j.biocon.2011.11.003>.
- Mac Nally, R., E. Fleishman, L. P. Bulluck, and C. J. Betrus. 2004. “Comparative Influence of Spatial Scale on Beta Diversity within Regional Assemblages of Birds and Butterflies.” *Journal of Biogeography* 31(6): 917–29. <https://doi.org/10.1111/j.1365-2699.2004.01089.x>.
- Magle, S. B., M. Fidino, E. W. Lehrer, T. Gallo, M. P. Mulligan, M. J. Ríos, A. A. Ahlers, J. Angstmann, A. Belaire, and B. Dugelby. 2019. “Advancing Urban Wildlife Research through a Multi-City Collaboration.” *Frontiers in Ecology and the Environment* 17(4): 232–9.
- Magle, S. B., V. M. Hunt, M. Vernon, and K. R. Crooks. 2012. “Urban Wildlife Research: Past, Present, and Future.” *Biological Conservation* 155: 23–32.
- Martin, L. J., B. Blossey, and E. Ellis. 2012. “Mapping where Ecologists Work: Biases in the Global Distribution of Terrestrial Ecological Observations.” *Frontiers in Ecology and the Environment* 10(4): 195–201.
- Marzluff, J. M. S., E. Shulenberger, W. Endlicher, M. Alberti, G. Bradley, C. Ryan, U. Simon, and C. ZumBrunnen, eds. 2008. *Urban Ecology*. New York, NY: Springer. <https://doi.org/10.1007/978-0-387-73412-5>.
- McDonald, R. I., A. V. Mansur, F. Ascensão, M. L. Colbert, K. Crossman, T. Elmquist, A. Gonzalez, et al. 2020. “Research Gaps in Knowledge of the Impact of Urban Growth on Biodiversity.” *Nature Sustainability* 3(1): 16–24. <https://doi.org/10.1038/019-0436-6>.
- McKinney, M. L. 2002. “Urbanization, Biodiversity, and Conservation: The Impacts of Urbanization on Native Species Are Poorly Studied, but Educating a Highly Urbanized Human Population about these Impacts Can Greatly Improve Species Conservation in all Ecosystems.” *Bioscience* 52(10): 883–90.
- McKinney, M. L. 2006. “Urbanization as a Major Cause of Biotic Homogenization.” *Biological Conservation* 127(3): 247–60. <https://doi.org/10.1016/j.biocon.2005.09.005Y3-02.01.2021S1-14>.
- McKinney, M. L., and J. L. Lockwood. 1999. “Biotic Homogenization: A Few Winners Replacing Many Losers in the Next Mass Extinction.” *Trends in Ecology & Evolution* 14(11): 450–3.
- McKinney, M. L., and J. L. Lockwood. 2005. “Community Composition and Homogenization: Evenness and Abundance of Native and Exotic Plant Species.” In *Species Invasions—Insight into Ecology, Evolution and Biogeography*, edited by J. J. Stachowicz and D. Tilman, 365–80. Sunderland, MA: Sinauer Associates, Inc. Publishers.
- Moher, D., A. Liberati, J. Tetzlaff, D. G. Altman, and Group, P. 2009. “Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement.” *PLoS Medicine* 6(7): e1000097.
- Nakagawa, S., G. Samarasinghe, N. R. Haddaway, M. J. Westgate, R. E. O’Dea, D. W. Noble, and M. Lagisz. 2019. “Research Weaving: Visualizing the Future of Research Synthesis.” *Trends in Ecology & Evolution* 34(3): 224–38.
- Neuroskeptic. 2012. “The Nine Circles of Scientific Hell.” *Perspectives on Psychological Science* 7(6): 643–4. <https://doi.org/10.1177/1745691612459519>.
- Olden, J. D., L. Comte, and X. Giam. 2018. “The Homogocene: A Research Prospectus for the Study of Biotic Homogenisation.” *NeoBiota* 37: 23–36.

- Olden, J. D., and N. L. Poff. 2003. "Toward a Mechanistic Understanding and Prediction of Biotic Homogenization." *The American Naturalist* 162(4): 442–60. <https://doi.org/10.1086/378212>.
- Olden, J. D. 2006. "Biotic Homogenization: A New Research Agenda for Conservation Biogeography." *Journal of Biogeography* 33(12): 2027–39.
- Olden, J. D., and T. P. Rooney. 2006. "On Defining and Quantifying Biotic Homogenization." *Global Ecology and Biogeography* 15(2): 113–20. <https://doi.org/10.1111/j.1466-822X.2006.00214.x>.
- Ossola, A., and J. Niemelä. 2018. *Urban Biodiversity: From Research to Practice*. New York, NY: Routledge.
- Padayachee, A. L., U. M. Irlich, K. T. Faulkner, M. Gaertner, Ş. Procheş, J. R. Wilson, and M. Rouget. 2017. "How Do Invasive Species Travel to and through Urban Environments?" *Biological Invasions* 19(12): 3557–70.
- Padullés Cubino, J., J. Cavender-Bares, P. M. Groffman, M. L. Avolio, A. R. Bratt, S. J. Hall, K. L. Larson, et al. 2020. "Taxonomic, Phylogenetic, and Functional Composition and Homogenization of Residential Yard Vegetation with Contrasting Management." *Landscape & Urban Planning* 202: 103877.
- Padullés Cubino, J., J. Cavender-Bares, S. E. Hobbie, S. J. Hall, T. L. E. Trammell, C. Neill, M. L. Avolio, L. E. Darling, and P. M. Groffman. 2019. "Contribution of Non-native Plants to the Phylogenetic Homogenization of US Yard Floras." *Ecosphere* 10: e02638.
- Paz Silva, C., R. D. Sepulveda, and O. Barbosa. 2016. "Nonrandom Filtering Effect on Birds: Species and Guilds Response to Urbanization." *Ecology and Evolution* 6(11): 3711–20. <https://doi.org/10.1002/ece3.2144>.
- Piano, E., C. Souffreau, T. Merckx, L. F. Baardsen, T. Backeljau, D. Bonte, K. I. Brans, et al. 2020. "Urbanization Drives Cross-Taxon Declines in Abundance and Diversity at Multiple Spatial Scales." *Global Change Biology* 26(3): 1196–211. <https://doi.org/10.1111/gcb.14934>.
- Pickett, S. T. A. 1989. "Space-for-Time Substitution as an Alternative to Long-Term Studies." In *Long-Term Studies in Ecology*, edited by G. E. Likens, 110–35. New York, NY: Springer. https://doi.org/10.1007/978-1-4615-7358-6_5.
- Pouyat, R. V., H. Setälä, K. Szlavecz, I. D. Yesilonis, S. Cilliers, E. Hornung, S. Yarwood, D. J. Kotze, M. Dombos, and M. P. McGuire. 2017. "Introducing GLUSEEN: A New Open Access and Experimental Network in Urban Soil Ecology." *Journal of Urban Ecology* 3(1): jux002.
- Potgieter, L. J., M. F. J. Aronson, A. J. Brandt, C. N. Cook, M. Gaertner, N. E. Mandrak, and M. W. Cadotte. 2022. "Prioritization and Thresholds for Managing Biological Invasions in Urban Ecosystems." *Urban Ecosystem* 25(1): 253–71.
- Pyšek, P. 1989. "On the Richness of Central European Urban Flora." *Preslia* 61(4): 329.
- R Core Team. 2013. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rahel, F. J. 2002. "Homogenization of Freshwater Faunas." *Annual Review of Ecology and Systematics* 33(1): 291–315.
- Ricotta, C., L. Celesti-Grapow, I. Kühn, G. Rapson, P. Pyšek, F. A. La Sorte, and K. Thompson. 2014. "Geographical Constraints Are Stronger than Invasion Patterns for European Urban Floras." *PLoS One* 9(1): e85661.
- Riggio, J., J. E. M. Baillie, S. Brumby, E. Ellis, C. M. Kennedy, J. R. Oakleaf, A. Tait, et al. 2020. "Global Human Influence Maps Reveal Clear Opportunities in Conserving Earth's Remaining Intact Terrestrial Ecosystems." *Global Change Biology* 26(8): 4344–56. <https://doi.org/10.1111/gcb.15109>.
- Ripley, B., W. Venables, and M. B. Ripley. 2016. *Package 'nnet'*. R package version 7, 700. <https://cran.microsoft.com/web/packages/nnet/nnet.pdf>.
- Rogers, D. A., T. P. Rooney, T. J. Hawbaker, V. C. Radeloff, and D. M. Waller. 2009. "Paying the Extinction Debt in Southern Wisconsin Forest Understories." *Conservation Biology* 23(6): 1497–506. <https://doi.org/10.1111/j.1523-1739.2009.01256.x>.
- Sattler, T., P. Duelli, M. Obrist, R. Arlettaz, and M. Moretti. 2010. "Response of Arthropod Species Richness and Functional Groups to Urban Habitat Structure and Management." *Landscape Ecology* 25(6): 941–54.
- Schwartz, M. W., J. H. Thorne, and J. H. Viers. 2006. "Biotic Homogenization of the California Flora in Urban and Urbanizing Regions." *Biological Conservation* 127(3): 282–91. <https://doi.org/10.1016/j.biocon.2005.05.017>.
- Schwarz, N. 2010. "Urban Form Revisited—Selecting Indicators for Characterising European Cities." *Landscape and Urban Planning* 96(1): 29–47. <https://doi.org/10.1016/j.landurbplan.2010.01.007>.
- Seto, K. C., W. D. Solecki, and C. A. Griffith. 2015. *The Routledge Handbook of Urbanization and Global Environmental Change*. Milton Park: Routledge.
- Shackleton, C. M., S. S. Cilliers, M. J. du Toit, and E. Davoren. 2021. "The Need for an Urban Ecology of the Global South." In *Urban Ecology in the Global South*, edited by C. M. Shackleton, S. S. Cilliers, E. Davoren, and M. J. du Toit, 1–26. Cham: Springer.
- Shwartz, A., A. Turbé, R. Julliard, L. Simon, and A.-C. Prévot. 2014. "Outstanding Challenges for Urban Conservation Research and Action." *Global Environmental Change* 28: 39–49. <https://doi.org/10.1016/j.gloenvcha.2014.06.002>.
- Smart, S. M., K. Thompson, R. H. Marrs, M. G. Le Duc, L. C. Maskell, and L. G. Firbank. 2006. "Biotic Homogenization and Changes in Species Diversity across Human-Modified Ecosystems." *Proceedings of the Royal Society B: Biological Sciences* 273(1601): 2659–65.
- Solar, R. R. D. C., J. Barlow, J. Ferreira, E. Berenguer, A. C. Lees, J. R. Thomson, J. Louzada, M. Maués, N. G. Moura, and V. H. Oliveira. 2015. "How Pervasive Is Biotic Homogenization in Human-Modified Tropical Forest Landscapes?" *Ecology Letters* 18(10): 1108–18.
- Sonnier, G., S. E. Johnson, K. L. Amatangelo, D. A. Rogers, and D. M. Waller. 2014. "Is Taxonomic Homogenization Linked to Functional Homogenization in Temperate Forests?" *Global Ecology and Biogeography* 23(8): 894–902.
- Starry, O., S. Gonsalves, K. Ksiazek-Mikenas, J. S. MacIvor, M. Gardner, A. Szallies, and S. Brenneisen. 2018. "A Global Comparison of Beetle Community Composition on Green Roofs and the Potential for Homogenization." *Urban Naturalist, Special Issue No. 1*: 1–15.
- Tuomisto, H. 2010. "A Diversity of Beta Diversities: Straightening up a Concept Gone Awry. Part 1. Defining Beta Diversity as a Function of Alpha and Gamma Diversity." *Ecography* 33(1): 2–22.

- Tydecks, L., J. M. Jeschke, M. Wolf, G. Singer, and K. Tockner. 2018. "Spatial and Topical Imbalances in Biodiversity Research." *PLoS One* 13(7): e0199327.
- Uchida, K., H. Fujimoto, and A. Ushimaru. 2018. "Urbanization Promotes the Loss of Seasonal Dynamics in the Semi-Natural Grasslands of an East Asian Megacity." *Basic and Applied Ecology* 29: 1–11. <https://doi.org/10.1016/j.baae.2018.03.009>.
- Willis, K. J., and R. J. Whittaker. 2002. "Species Diversity—Scale Matters." *Science* 295(5558): 1245–8. <https://doi.org/10.1126/science.1067335>.
- Wohner, C., T. Ohnemus, S. Zacharias, H. Mollenhauer, E. C. Ellis, H. Klug, H. Shibata, and M. Mirtl. 2021. "Assessing the Biogeographical and Socio-Ecological Representativeness of the ILTER Site Network." *Ecological Indicators* 127: 107785.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lokatis, Sophie, and Jonathan M. Jeschke. 2022. "Urban Biotic Homogenization: Approaches and Knowledge Gaps." *Ecological Applications* 32(8): e2703. <https://doi.org/10.1002/eap.2703>