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Urban affinity and its associated traits: A global analysis of bats

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Abstract

Urbanization is a major contributor to the loss of biodiversity. Its rapid progress is mostly at the expense of natural ecosystems and the species inhabiting them. While some species can adjust quickly and thrive in cities, many others cannot. To support biodiversity conservation and guide management decisions in urban areas, it is important to find robust methods to estimate the urban affinity of species (i.e. their tendency to live in urban areas) and understand how it is associated with their traits. Since previous studies mainly relied on discrete classifications of species' urban affinity, often involving inconsistent assessments or variable parameters, their results were difficult to compare. To address this issue, we developed and evaluated a set of continuous indices that quantify species' urban affinity based on publicly available occurrence data. We investigated the extent to which a species' position along the urban affinity gradient depends on the chosen index and how this choice affects inferences about the relationship between urban affinity and a set of morphological, sensory and functional traits. While these indices are applicable to a wide range of taxonomic groups, we examined their performance using a global set of 356 bat species. As bats vary in sensitivity to anthropogenic disturbances, they provide an interesting case study. We found that different types of indices resulted in different rankings of species on the urban affinity spectrum, but this had little effect on the association of traits with urban affinity. Our results suggest that bat species predisposed to urban life are characterized by low echolocation call frequencies, relatively long call durations, small body size and flexibility in the selection of the roost type. We conclude that simple indices are appropriate and practical, and propose to apply them to more taxa to improve our understanding of how urbanization favours or filters species with particular traits.

KEYWORDS
biogeography, Chiroptera, GBIF, macroecology, species traits, urban avoiders, urban dwellers, urbanization, urbanity indices, urban–rural gradient

1 | INTRODUCTION

Human-induced land-use change is regarded as the primary threat to biodiversity (Newbold et al., 2015), and urbanization is one of the main and most rapidly growing land-use change processes. Urban expansion comes mostly at the expense of natural ecosystems (Seto et al., 2011; Vitousek et al., 1997) and is often associated with the destruction, fragmentation or isolation of natural or near-natural habitats (Liu et al., 2016). The conditions that characterize urban areas are thought to drive changes of species richness (Aronson et al., 2014; Kühn et al., 2004; McKinney, 2002, 2008) and the homogenization of biotic assemblages (Lockwood et al., 2000; McKinney, 2006; but Kühn & Klotz, 2006). Apparently, some species struggle with urban conditions and consequently are repressed from urban areas, while others quickly adjust, benefit from and thrive in these novel environments (Aronson et al., 2014; McKinney, 2002).

There have been many approaches to assess the urban affinity of species (i.e. their tendency to live in urban areas), especially in botany. While the term 'plantea urbanae' was already used two centuries ago to describe the urban association of certain plant species (Schouw, 1823), early 20th-century studies initially focused on the impact of humans on landscapes and ecosystems. The term 'hemeroby' was introduced to describe the degree of anthropogenic impact based on the disturbance of soil (Jalas, 1955). Later, this system was refined by classifying vegetation types and habitats on a scale from ahemerobic (natural) to polyhemerobic (unnatural; Sukopp, 1972) and a scale based on the absence or presence of a species in cities was introduced to describe its behaviour towards human settlements (Wittig et al., 1985). Similarly, a five-level scale to determine the urbanity of plants by comparing urban floras to the surrounding rural floras was created by Klotz et al. (2002). While all these approaches are classification systems, one study attempted to introduce two continuous measures for urbanity to plant ecology in Britain (Hill et al., 2002). The first one was based on the proportion of urban land cover in the vicinity of sample squares and the second one on the frequency of occurrences in highly urbanized grid squares. In a different approach, the occurrence probability of plant species in grid cells was modelled and correlated with the proportion of urban land use in the same grid cells (Knapp et al., 2009). The correlation coefficient then indicated how the probability of occurrence changed with increasing urban proportion.

Although botanical studies appear to have pioneered such quantification attempts, the number of studies focusing on other taxa has recently increased, especially in birds. Some of the used urban indices use occurrence frequency or abundance in cities compared to their surrounding more rural areas (Ferenc et al., 2018; Sayol et al., 2020; Sol et al., 2014), others are based on remote sensing measurements of artificial light at night (Callaghan et al., 2019). In a recent study on mammals, species were categorized into 'urban dwellers', 'urban visitors' or 'urban avoiders' according to the extent to which they breed and forage in urban areas (Santini et al., 2019). Such discrete classification methods were predominant in previous studies (Kark et al., 2007; McDonnell & Hahs, 2015; McKinney, 2002; Møller, 2009), and most studies focused on plants (Hill et al., 2002; Knapp et al., 2009; Thompson & McCarthy, 2008) and birds (Callaghan, Benedetti, et al., 2020; Ferenc et al., 2018; Sayol et al., 2020; Sol et al., 2014). The application of novel methods also enables investigations on previously less well-studied taxa in the context of urban affinity, for example, amphibians (Liu et al., 2021) and insects (Callaghan, Bowler, et al., 2021).

The terminology used to describe urban wildlife is not always consistent in the literature (e.g. Callaghan, Bowler, et al., 2021; Ferenc et al., 2018), with terms such as 'urban tolerance' and 'urban affinity' sometimes used synonymously. Clearly defining the terminology is therefore important (e.g. Callaghan, Bowler, et al., 2021). Thus, we define and hereafter use the term 'urban affinity' in the sense of a continuous spectrum from a weak to a strong tendency to live in urban areas, and regard other terms, such as 'urban avoiders', 'urban tolerators' or 'urban exploiters' as groupings of species representing different positions along this urban affinity spectrum.

Many studies also investigated which traits characterize species that thrive in, tolerate or avoid urban areas (e.g. Callaghan et al., 2019; Jung & Threlfall, 2018; Knapp et al., 2010; Santini et al., 2019; Sayol et al., 2020; Wolf et al., 2020). Identifying these traits is crucial to understand how biodiversity responds to urbanization and thus guide the conservation of endangered species and urban planning. According to the 'ideal urban dweller hypothesis' (Croci et al., 2008; Sol et al., 2020), species that tolerate or even benefit from urban conditions tend to have a small body size (Magura et al., 2006; Santini et al., 2019), a broad dietary breadth (Slatyer et al., 2013), a higher reproductive output (Santini et al., 2019), are more likely pre-adapted to urban conditions (McDonnell & Hahs, 2015), show behavioural flexibility (Santini et al., 2019) and tend to be less specialized in general (Concepción et al., 2015; Sorace & Gustin, 2009). Species capable of powered flight are additionally characterized by enhanced mobility (Santini et al., 2019). However, studies of 'urban traits' have mostly been conducted at small spatial scales.

Large-scale studies allow to generalize patterns and provide insights that go beyond the impact of local conditions. For such studies, the ever-growing amount of data in biodiversity networks, such as the Global Biodiversity Information Facility (GBIF), provides a promising source for comparative studies. In comparison to the data used in meta-analyses, geo-referenced occurrence data provide a consistent and reproducible basis to uncover biogeographical patterns. In addition, a further increase in observations will most probably also strengthen the informative value of future studies (Wisz et al., 2008). However, biodiversity data from GBIF or similar sources are known to be biased due to several reasons (Zizka et al., 2021): heterogeneity of data entry sources, underrepresentation of certain taxa ('taxonomic bias'), over-sampling in specific time periods ('temporal bias') and overrepresentation of certain regions ('geographic bias'). Since urban areas represent centres of human activity, they are particularly prone to over-sampling (Zizka et al., 2021) Therefore, such data need to be thoroughly evaluated and results must be discussed accordingly.

Meta-analyses are another way of determining the relative urban affinity of several species by jointly evaluating the results of a large number of studies on individual species (e.g. Jung & Threlfall, 2018). Although meta-analyses are powerful to reveal ecological patterns that cannot be typically captured by single studies, they depend on the availability of studies on their focal taxa and often suffer from the heterogeneity of the input data.

The main objective of our study was to collate and modify traditional approaches (see above) to establish relatively simple and reproducible indices to determine the urban affinity of species on a continuous scale. Using a case study with bat data, we tested if each of these indices, as well as the scores from a recent meta-analysis on the same topic (Jung & Threlfall, 2018), resulted in convergent urban affinity rankings of species and in similar trait associations with urban areas. Ideally, this should be the case. However, due to the different complexities and information that is compiled in each index, we expected subtle deviations.

Bats (Chiroptera) are relatively sensitive to environmental changes (Jones et al., 2009) and some species may occur in human settlements (Russo & Ancillotto, 2015). Factors that influence the presence of bat species in urban environments include the prevalence of adequate roosting sites (Kunz, 1982; Kunz & Lumsden, 2003; Russo & Ancillotto, 2015), availability of foraging habitats (Fukui et al., 2006; Nakamoto et al., 2007; Rowse et al., 2016; Threlfall et al., 2011), morphology (Norberg & Rayner, 1987) and echolocation characteristics (Denzinger & Schnitzler, 2013; Neuweiler, 1984; Norberg & Rayner, 1987; Schnitzler & Kalko, 2001). While many studies investigated the differences in species-specific responses towards urban environments, based on the abundance, occurrence or activity of bats in more urbanized compared to more natural areas at a regional scale (e.g. Avila-Flores & Fenton, 2005; Gehrt & Chelsvig, 2003; Mehr et al., 2011; Shapiro & Bordignon, 2014), the meta-analysis by Jung and Threlfall (2018) is the only study we are aware of that attempted to investigate these patterns at a large scale—taxonomically and geographically.

More urban affine bat species are generally expected to be characterized by traits that better adapted them to open and edge habitats (sites at transition from open landscape to landscapes with pronounced vertical and dense structure, e.g. forest edges), as such are prevalent in cities. Hence, we tested whether eight different urban affinity indices reflect the following hypotheses on bat adaptation to urban environments, in accordance with previous findings (Avila-Flores & Fenton, 2005; Duchamp & Swihart, 2008; Jung & Kalko, 2011; Jung & Threlfall, 2018; Threlfall et al., 2011): (1) Bats with lower peak echolocation call frequency, longer call duration and species of the edge-aerial and open-aerial guilds tend to be more urban-affine than bats with short calls of high frequency and bats belonging to one of the narrow-space foraging guilds. (2) Bats with adaptations to rapid and directed flight should exhibit higher urban affinity. Thus, we expected positive correlations of both aspect ratio and wing loading with urban affinity. (3) Consistent with the ideal urban dweller hypothesis (Croci et al., 2008), which states that generalists and small species do better in urban environments, we hypothesized that small body size (here represented by body mass and forearm length) and a less specialized roosting strategy relate to higher urban affinity.

2 | MATERIALS AND METHODS

2.1 | Urban affinity indices

Partially based on concepts of previous studies (Callaghan et al., 2019; Ferenc et al., 2018; Hill et al., 2002; Knapp et al., 2009; Sol et al., 2014), we developed a set of eight indices to quantify the urban affinity of species using georeferenced occurrence records and a proxy for the level of urbanization. As we intended the indices to be applicable to any species, independently of its global distribution, it was mandatory to use a proxy for the level of urbanization that is available on a global scale. Nevertheless, depending on the focal species and research question, the indices can also be calculated with data for a smaller spatial extent. Here, we took a grid-based approach to define spatial units but are aware that other types of spatial units also exist for which the introduced indices might still be applicable. For example, instead of using a grid-based land cover map, one could use a polygon-based map that might reflect urban areas in more detail. In that case, the concepts behind the indices would remain the same, but the exact ways of calculating them might differ from those presented here. Furthermore, it is assumed that occurrence data have been cleaned, are reliable and available in sufficient quantity for the species in question. The number of occurrence points that can be considered sufficient to detect a species habitat affinities depends strongly on the characteristics of the species itself, the size of the study area and the species' prevalence (van Proosdij et al., 2016). For comparison and evaluation purposes, we extracted the scores obtained by the global meta-analysis (Jung & Threlfall, 2018) from their supplementary material and included them as an additional urban affinity index here. In Table 1, we introduce the main conceptual and technical characteristics of each index. We provide more detailed descriptions and illustrative figures for all the indices in the Supplementary Material (S1), and the R code for calculating each of them in the electronic supplement (ES1; Wolf et al., 2022).

2.2 | Occurrence data

We obtained species occurrences from the GBIF, the largest network for open-access distribution records (Beck et al., 2014). We downloaded all available occurrence records with coordinates for all accepted species listed in the order Chiroptera (GBIF.org, 2020). This resulted in a dataset with more than 2 million records from a total of 1221 species. After we corrected for erroneous entries, extinct species, bat parasite species and synonyms by comparing the data to a species list provided by the Integrated Taxonomic Information System (ITIS, 2021) and the taxonomy following Wilson

TABLE 1 Conceptual and technical characteristics of each urban affinity index

#	Index	Short description	Variations	Feature of variation	Urban proxy	References
1	*iPoints*	Share of urban occurrences			ESA CCI Land Cover Map 2015 (ESA, 2017)	Hill et al. (2002)
2	*iBuffer*	Proportion of urban land cover within circular buffers of different radii (*r*) around occurrence records	$iBuffer_{01}$	$r = 1$ km		
			$iBuffer_{05}$	$r = 5$ km		
			$iBuffer_{10}$	$r = 10$ km		
3	$iBuffer_{FD}$	Proportion of urban land cover within the species-specific used area around occurrence records		$r =$ foraging distance		
4	$iSDM_{COR}$	Correlation between urban land cover and occurrence probability				Knapp et al. (2009)
5	$iSDM_{CON}$	Contrast between occurrence probability in urban areas and surrounding rural areas				
6	$iCon_{UrbRur}$	Difference in number of occurrences between urban and surrounding rural areas				Sayol et al. (2020)
7a	*iVIIRS*	Average radiance of artificial night light in 5 km buffers around occurrence records	$iVIIRS_{MEDIAN}$	unmodified VIIRS data; median	VIIRS radiance of artificial night lights (Elvidge et al., 2017)	Callaghan et al. (2019)
7b			$iVIIRS_{MEAN}$	modified VIIRS data; mean		
8	*iDist*	Average distance of occurrence records from urban areas			ESA CCI Land Cover Map 2015 (ESA, 2017)	
meta	*iMeta*	Urban affinity scores obtained from meta-analysis by Jung and Threlfall (2018)				Jung and Threlfall (2018)

Note: More detailed descriptions and illustrative figures for all indices are found in the Supplementary Material (S1). First column refers to the index numbering as used in the R code (electronic Supplementary Material ES1).

and Mittermeier (2019), the number of species was narrowed down to 1185. If possible, we assigned the affected records to the accepted names of the respective species. A complete overview on our approach can be found in in the electronic Supplementary Material (ES2).

Although data publication in GBIF requires compliance with certain data standards, many entries are still erroneous or incomplete. The use of this data therefore requires careful cleaning beforehand. In accordance with current standards (Zizka et al., 2019), we carried out a thorough data cleaning. Detailed information on the steps we have taken can be found in the Supplementary Material (S2).

After the cleaning, the data consisted of 817,846 observations from 889 species. To ensure that all further steps were based on robust data, we retained only data from species for which at least 50 observations were available after cleaning. This was the case for 356 species. We should note, however, that the choice of this threshold was arbitrary and that it possibly excluded rare species. Therefore, the applied analyses might be biased in this respect. To keep the computational requirements manageable, we randomly selected 10,000 observations for estimation of the indices for species that had more than 10,000 remaining occurrences after cleaning ($N = 31$). To determine the distribution range of each species, we used distribution polygons obtained from the International Union for Conservation of Nature and Natural Resources (IUCN, 2019).

2.3 | Assessing the influence of range size, availability of urban area and sampling bias

We performed three types of sensitivity tests. First, we assessed the impact of the species' distribution range size on their urban affinity, as the former may be related to the availability of urban areas (Callaghan, Benedetti, et al., 2020). To test whether this is an issue in our dataset, we divided the species into deciles according to the size of their distribution range and assessed for each index whether urban affinity correlates with range size (Figure S4.1).

Second, we tested whether the proportion of urban area within the range of a species is related to the urban affinity scores calculated by the different indices. We correlated for each index the calculated urban affinity scores with the proportion of urban area that is present within the concave hull around the occurrence points of each species, respectively. A high correlation coefficient (either negative or positive) would indicate that our scores are biased by this factor (Table S4.2).

In the third test, we assessed the degree of sampling bias towards urban areas. Here, we applied the 'sampbias' algorithm (Zizka et al., 2021) for each species. This Bayesian framework provides a posterior weight for a biased factor, which can be interpreted as the strength of the bias. However, it was primarily designed for the analysis of multi-species datasets rather than single species, since results for single species might reflect species-specific habitat preferences (appendix 2 in Zizka et al., 2021). We addressed this discrepancy by comparing and assessing the deviation of the urban bias of a focal species (Figure S4.3.1) from the general urban bias (of all bat species in our study) within the concave hull polygon (created with R package concaveman; Gombin et al., 2020) of the focal species' occurrence records. A more positive deviation indicates a stronger species preference for urban areas, while a more negative deviation indicates a stronger sampling bias (Figure 4.3.1). For details, see the Supplementary Material (S4.3).

2.4 | Proxies for the level of urbanization

As the first proxy for the level of urbanization, we used the 2015 land cover map (v2.0.7) provided by the Climate Change Initiative (CCI) of the European Space Agency (ESA) for all indices except *iVIIRS*. It has a spatial resolution of *c*. 300 × 300 m and comprises 37 different land cover classes, including one for urban areas (ESA, 2017). As the second proxy, for both variations of *iVIIRS*, we used the annual night-light radiance map of the year 2016 obtained from data collected by the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band on a satellite jointly operated by NASA and NOAA (https://www.ngdc.noaa.gov/eog/download.html). Most of these artificial lights are associated with human settlements and hence, their emitted radiance provides a suitable continuous measure for the degree of urbanization. The product we used had already filtered out background noise, unrelated light sources such as fires and volcanoes and other data degradation (Elvidge et al., 2017).

2.5 | Foraging distance data

As home range data were not available for most species, we used the foraging distance (FD) as the radius of the circular buffers as an approximation to account for the species-specific spatial use in the calculation for $iBuffer_{FD}$. The foraging distance is the average maximum distance a species commutes from its roost to the foraging grounds. We obtained data on the foraging distance from the literature for 106 species (Table ES3 in electronic supplement).

2.6 | Species distribution models

The calculation of $iSDM_{COR}$ and $iSDM_{CON}$ is preceded by fitting species distribution models (SDMs) to obtain grids with the occurrence probability for each species for at least the extent of the respective distribution range. To ensure reasonably robust outcomes, we fitted SDMs only for species for which the cleaned records were located in at least 20 discrete grid cells (Wisz et al., 2008). As model predictors, we applied a set of bioclimatic (Fick & Hijmans, 2017) and land cover (ESA, 2017) variables. We used five different modelling algorithms that are commonly used in studies that employ SDMs (Merow et al., 2014) and conducted 10 runs per algorithm per species. To gain a final occurrence probability map for each species, we combined the models produced by the five algorithms into one ensemble

model (Marmion et al., 2009). More details on the parameterization of the SDMs are provided in the Supplementary Material (S3).

2.7 | Comparing urban affinity indices

To compare the urban affinity indices, we determined the Spearman correlation coefficient (ρ) between each of them (Figure 1). This allowed us to assess how similarly the indices rank the species in our dataset in terms of their association with urban areas. We distinguish between weak ($\rho < .4$), moderate ($.4 \leq \rho < .7$) and strong ($\rho > .7$) correlations. The correlation diagram was created with the R package corrgram (Wright, 2021). To assess the average rank and variation of each species across all eight indices, we present a boxplot chart with the distribution of ranks per species. This allows to evaluate which species are constantly ranked high or low, which are ranked inconsistently across indices and if species within a focal genus are ranked closely to each other (Figure 2).

2.8 | Trait data

We selected eight traits that are associated with habitat and foraging ecology of bats in general and with factors we considered crucial for an urban bat life in particular: forearm length, body mass, aspect ratio, wing loading, echolocation frequency, echolocation call duration, roosting specialization and the functional guild (Table 2). Most of the trait data were compiled and published by Jung and Threlfall (2018; for more details on the original sources, see there). Supplementary trait values were retrieved from several different sources, often from specific studies on single species. In total, complete trait data were available for 130 species and we were able to calculate at least one of our indices for 109 species. Details on the exact source per trait and species are shown in the electronic Supplementary Material (ES4). To ensure comparable effect sizes and better interpretation of the models, we standardized the continuous trait variables (centred to mean = 0 and scaled to standard deviation = 1) using the scale function in R.

2.9 | Phylogenetic data

The phylogenetic tree was obtained from Amador et al. (2016). It included a total of 812 bat species and covered 731 of the total 889 species for which any clean occurrence data were available and 296 out of 356 species that had at least 50 remaining occurrences after cleaning. For the 109 species that we included in the analysis, only 16 were missing in the phylogeny. We incorporated these missing species by adding them next to species of the same genus and treating them as polytomies, or if no species of the same genus was already in the tree, by adding them next to the closest related genus according to Wilson and Mittermeier (2019). To assess the phylogenetic signal (Revell et al., 2008) among the continuous predictor traits and all the urban affinity indices, we

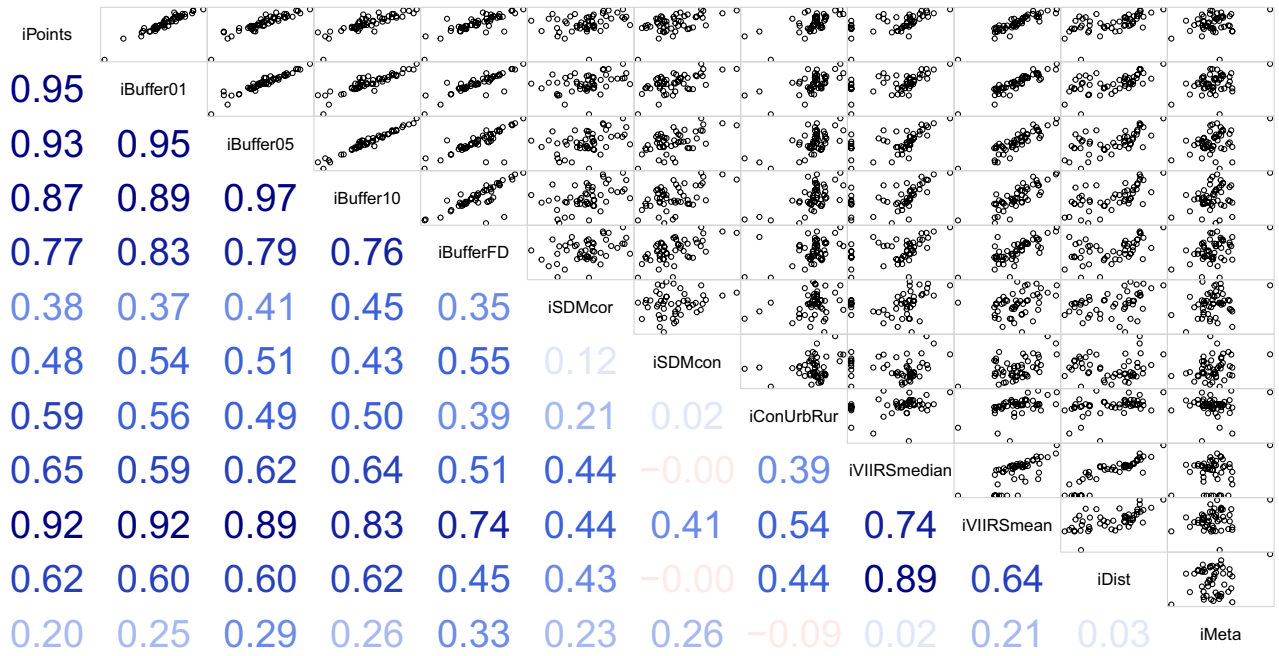

FIGURE 1 Comparison of the indices based on how they rank the species in terms of their urban affinity. The upper half of the correlation diagram shows the scatter plots from the correlation of the urban affinity scores between two indices or variations, respectively. The lower half shows the resulting spearman correlation coefficient ρ for each of these correlations. A very similar ranking of the indices is indicated when ρ approaches 1, whereas a low value indicates a rather different ranking when comparing two indices. Included are those bat species for which all indices could be calculated and complete trait data were available ($n = 50$). For details on the individual indices, see Supplementary Material (S1).

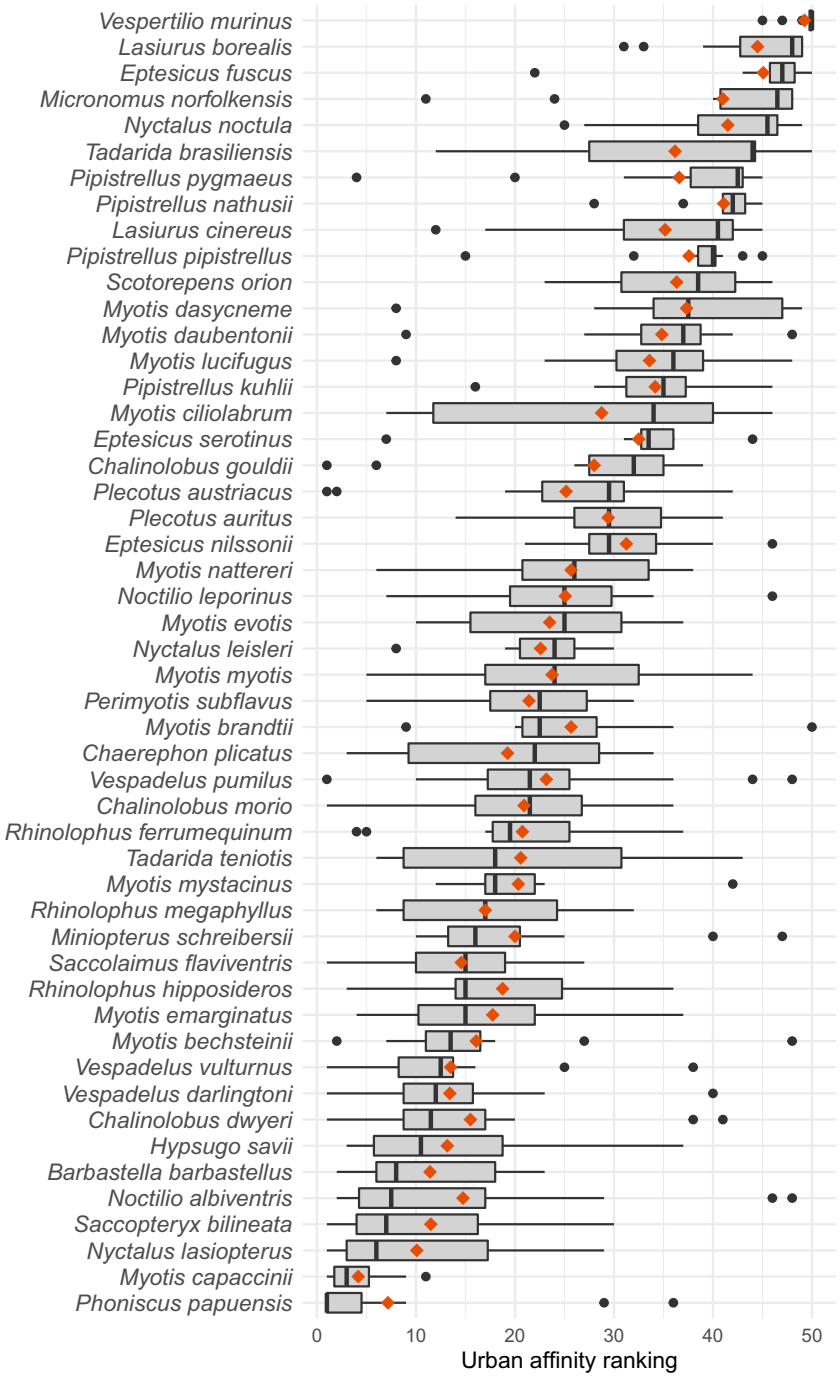

FIGURE 2 Average urban affinity ranking of bat species included in the case study. For each species ($n = 50$), the distribution of ranks for urban affinity across all indices is shown. A higher average rank indicates species with consistently higher urban affinity across all indices. The size of the boxplots indicates the variation in the ranking across all indices. Boxplots depict medians (black bar), interquartile ranges (boxes), full ranges (whiskers), outliers (black points) and means (red diamonds).

estimated Pagel's Lambda (λ) with the phylosignal R package (Keck et al., 2016). More details are shown in the Supplementary Material (S6).

2.10 | Modelling

Before fitting the models, we assessed the collinearity between the continuous traits via variance inflation factors (VIF), using the function vifstep from the R package usdm (Naimi et al., 2014). We excluded predictors with a VIF > 2 from further analysis. This was the case for body mass and wing loading.

To implement them as response variables in the respective models, we normalized the scores of the urban affinity indices to min = 0 and max = 1 and in some cases log-transformed them to stabilize the variance and to improve the normality of the residuals.

We applied Phylogenetic Generalized Least Square Models (PGLS), which account for the potential influence of the shared evolutionary history on the association between the selected traits and the urban affinity (Felsenstein, 1985). Phylogenetically informed models were fitted with the function pgls from the R package caper (Freckleton et al., 2002), which considers evolutionary processes under a Brownian motion model, identically to OLS regression of phylogenetically independent contrasts (PICs; Blomberg et al., 2012). We

TABLE 2 Overview of the traits included in the analysis

Trait	Abbreviation	Unit/levels	Description
Forearm length	FL	mm	Species' average forearm length
Body mass	BM	g	Species' average body mass
Aspect ratio	AR	cm^2/cm^2	Squared wingspan divided by wing area
Wing loading	WL	g/cm^2	Body mass divided by wing area
Echolocation frequency	EF	kHz	Peak or characteristic call frequency
Echolocation call duration	ED	ms	Average echolocation call duration
Roosting specialization	RS	f—flexible	Species using more than one roost type
		s—specialized	Species exclusively using one roost type
Functional guild	FG	NG—narrow gleaning	Gleaning off prey from surfaces
		NF—narrow flutter detection	Detecting fluttering prey
		ET—edge trawling	Catching prey by trawling water surfaces
		EA—edge aerial	Catching prey close to vegetation
		OA—open aerial	Catching prey in open airspace

Note: Shown are the abbreviations used for the respective traits, the unit for continuous traits and the levels of the categorical variables as well as a short description.

fixed transformation parameters δ and κ to 1 and set λ to 'ML', allowing a maximum likelihood estimation for this parameter. The estimation for λ can be interpreted as the phylogenetic signal in the residuals of the model, where $\lambda = 0$ indicates no signal and $\lambda = 1$ indicates phylogenetic covariance expected under a Brownian model.

Models included those species for which we could obtain scores of all urban affinity indices, scores from the meta-analysis (Jung & Threlfall, 2018) and the trait data ($n = 50$; see Table 3). The global models included all predictors that remained after the collinearity check. To obtain the candidate set of models, we 'dredged' all possible submodels with the R package MuMIn (Barton, 2020) and included those models with a $\Delta_{AICc} < 2$ plus the model with the next lowest AICc (Akaike's Information Criterion corrected for small sample sizes; Sugiura, 1978).

Models with $\Delta_{AICc} < 2$ are assumed to be equally supported. To interpret these models and to compare the frequency in which each model occurred in the candidate set of the different indices, we present a comprehensive summary table (Table 4). This table shows the sign of the effect sizes of the respective predictors. The actual effect sizes may vary between the same models of the individual indices. The exact effect sizes and other details of the individual models are found in the Supplementary Material (Table S5 and as spread sheet in the electronic Supplementary Material ES5).

3 | RESULTS

3.1 | Comparing the urban affinity indices

The number of species for which a score could be calculated or was available from the meta-analysis by Jung and Threlfall (2018) varied across indices (Table 3). Ultimately, we were able to obtain scores of all urban affinity indices (ours and the meta-analysis) for 51 species. For 50 of them, we also had the complete trait dataset.

With the exceptions of $iSDM_{COR}$ and $iSDM_{CON}$, both of which included an SDM component, all indices showed at least a moderate conformity in the ranking of the bat species' urban affinity (Figure 1). The strongest correlations were observed between *iPoints*, all variations of *iBuffer*, $iBuffer_{FD}$ and $iVIIRS_{MEAN}$. While $iVIIRS_{MEDIAN}$ and *iDist* showed a moderate to strong similarity to these indices as well, they were much more similar to each other. The other indices, $iSDM_{COR}$, $iSDM_{CON}$ and $iCon_{UrbRur}$, showed at best a weak to moderate similarity to some of the other indices. The scores provided by the meta-analysis were at best only very weakly correlated with any of the scores from our indices.

Only some species were ranked consistently on the urban affinity spectrum across all indices (Figure 2). Consistent with the weak phylogenetic signal of the individual indices (Table S6.2), the ranking of species compared to their congeners (e.g. *Myotis*, *Nyctalus*) also appeared to be highly variable, further indicating a weak ancestral effect (Figure 2). The size of species distribution was only weakly correlated with the urban affinity indices and has not had a major impact on the results (see Supplementary Material S4.1). In addition, we found that for none of the indices was the proportion of urban area within a species' range related to the values of urban affinity (Table S4.2). The analysis of sampling bias towards urban areas revealed that only few species whose urban affinity ranking was high showed a stronger bias of their sampling towards urban areas than that of the sampling of all bats in their distribution range (e.g. *Myotis lucifugus*), which indicated that the ranking of most highly urban species likely stems from true preference rather than sampling bias for urban areas (see Supplementary Material S4.3).

TABLE 3 Overview of the number of species in the analysis

Step	Number of species	Note	Number of species with available trait data
Download	1221	Listed in the order Chiroptera on GBIF in August 2020	
Taxonomic cleaning	1185	Remaining after taxonomic cleaning	
Cleaning	889	Remaining after general cleaning	130
Final	356	Remaining species with ≥50 clean records	109
Index	**Number of species**	**Reason for reduced number**	**Number of species with available trait data**
iPoints	356		109
$iBuffer_{01}$	356		109
$iBuffer_{05}$	356		109
$iBuffer_{10}$	356		109
$iBuffer_{FD}$	106	Limited data available for foraging distance	61
$iSDM_{COR}$	289	Preconditions for the SDMs (≥20 occupied grid cells)	105
$iSDM_{CON}$	284	Preconditions for the SDMs (≥20 occupied grid cells) and no rural–urban pair enclosed in distribution range	105
$iCon_{UrbRur}$	356		109
$iVIIRS_{MEDIAN}$	356		109
$iVIIRS_{MEAN}$	356		109
iDist	356		109
iMeta	115	Number of matched species for which a score was provided	84
Overlap	51		50

Note: Given are the number of species after downloading, each cleaning step, the number of species for which a score was available per index and the number of species with available trait data per index.

3.2 | Association of bat traits to urban environments

None of the urban affinity indices, except $iSDM_{CON}$, showed a significant phylogenetic signal based on the scores for the 50 species with complete trait data and scores for all indices. Each of the predictor variables (i.e. traits) showed a moderate to strong phylogenetic signal. It usually was weaker than Brownian motion ($\lambda < 1$), but statistically significant (Table S6.2, Supplementary Material).

Excluding the one model per index with $\Delta_{AICc} > 2$, the candidate model set for all 12 indices consisted of 22 different models (Table 4). The single most frequently emerging model (in 8 out of the 12 indices) indicated that species with shorter forearms, lower echolocation frequencies, a longer call duration and a less specialized roosting strategy tend to have a stronger urban affinity. The trend signs (i.e. positive or negative association between traits and urban affinity) were consistent across most candidate models, regardless of the urban affinity index. Two other models were each supported by four of the indices. One of them is the only other model that is supported by *iPoints*, $iBuffer_{01}$ and $iBuffer_{05}$ and additionally suggests a positive effect of aspect ratio. The second one (supported by $iBuffer_{FD}$, $iSDM_{COR}$, *iDist* and *iMeta*) suggests a negative correlation with roosting specialization. Two models were supported by three of the indices, respectively. The first one, supported by $iBuffer_{FD}$, $iSDM_{COR}$ and *iDist*, indicates a positive correlation with echolocation call duration and a negative correlation with roosting specialization. The second one (supported by $iVIIRS_{MEDIAN}$, $iVIIRS_{MEAN}$ and *iDist*) additionally suggests a negative correlation with echolocation frequency. All other models only appeared in the selected model set of one or two of the indices. Here, a few things in particular stood out: (1) two out of three models that were supported by $iVIIRS_{MEDIAN}$ were at the same time supported by $iVIIRS_{MEAN}$; (2) two out of four models supported by the index from the meta-analysis were not among the candidate models of any of the other indices; (3) *iDist* was the only index including foraging guild in one of its candidate models; (4) $iSDM_{COR}$ was the only index that revealed opposite sign of the effects of aspect ratio. Apart from that, the direction of the effect sizes was uniform for all models of all indices.

3.3 | Model results in relation to index similarity

Although in some cases similar patterns can be observed, the models of indices that revealed a similar urban affinity ranking of

TABLE 4 Summary table of the trait analysis

Forearm length	Aspect ratio	Echolocation frequency	Echolocation call duration	Roosting specialization	Functional guild		Indices
−		−	+	−			*iPoints*, $iBuffer_{01}$, $iBuffer_{05}$, $iBuffer_{10}$, $iSDM_{COR}$, $iCon_{UrbRur}$, $iVIIRS_{MEDIAN}$, $iVIIRS_{MEAN}$
−	+	−	+	−			*iPoints*, $iBuffer_{01}$, $iBuffer_{05}$, $iVIIRS_{MEAN}$
				−			$iBuffer_{FD}$, $iSDM_{COR}$, *iDist*, *iMeta*
		−	+	−			$iVIIRS_{MEDIAN}$, $iVIIRS_{MEAN}$, *iDist*
			+	−			$iBuffer_{FD}$, $iSDM_{COR}$, *iDist*
−		−					$iSDM_{CON}$, $iCon_{UrbRur}$
−		−	+				$iSDM_{CON}$, $iCon_{UrbRur}$
	+						*iDist*, *iMeta*
		−		−			$iBuffer_{FD}$
−				−			$iSDM_{COR}$
−							$iSDM_{COR}$
−			+	−			$iSDM_{COR}$
	−			−			$iSDM_{COR}$
	−		+	−			$iSDM_{COR}$
−	+	−					$iSDM_{CON}$
	+	−	+	−			$iVIIRS_{MEDIAN}$
−			+		ET	+	*iDist*
					NG	−	
					NF	+	
					OA	+	
			+				*iDist*
		−	+				*iDist*
		−					*iDist*
	+			−			*iMeta*
	+		+	−			*iMeta*

Note: Included are models with $\Delta_{AICc} < 2$ for each index. Given are the signs (+/−) of the effect size of the trait responses to urban affinity: Four standardized continuous predictors (forearm length, aspect ratio, echolocation frequency and echolocation call duration) and two nominal scaled predictors (roosting specialization, comparing specialized relatively to flexible roost type selection); functional guild, comparing the edge trawling (ET), narrow flutter (NF), narrow gleaning (NG) and open aerial (OA) relatively to the edge aerial (EA) guild. The last column indicates for which indices the model was among the candidate models.

species (Figure 1) did not necessarily yield similar trait responses (Table 4). For example, *iPoints*, all variations of *iBuffer* and $iVIIRS_{MEAN}$ showed great similarities in the ranking and largely the same candidate models. However, although $iBuffer_{FD}$ was also similar to these indices in the ranking, it did not share the same set of selected models. In addition, the high similarity of $iVIIRS_{MEDIAN}$ with *iDist* was not as clearly reflected in the set of selected trait models. In contrast, while the urban affinity ranking of species by $iSDM_{COR}$, $iSDM_{CON}$ and $iCon_{UrbRur}$ was each unique, their set of selected models of these three indices still contained at least partially matching predictors, in some cases even the same models. As for the index from the meta-analysis, the different ranking of species' urban affinity compared to all other indices was also reflected in the selected set of trait models which was mostly distinct from those of all other indices.

4 | DISCUSSION

To our knowledge, this is the first study that collates and compares a variety of approaches to quantify species-specific urban affinity based on publicly available occurrence data for bats. The eight indices that we used can be divided into two groups (Table 5): one set of indices determining urban affinity is based on the share of urban area present in proximity to the species' occurrence (*iPoints*, *iBuffer*, *iVIIRS*, *iDist*) and the other set is based on the assumption that species with different urban affinities also vary in their number of occurrences or occurrence probability in urban compared to surrounding rural areas ($iSDM_{COR}$, $iSDM_{CON}$, $iCon_{UrbRur}$). Interestingly, indices of the same group did not necessarily rank the urban affinity of bat species consistently. The three variations of *iBuffer*, differing in the radius used to create buffers around observations, were largely

TABLE 5 Overview on indices groups and respective data properties

Type of urban affinity index	Index	Urban proxy	Resolution	Source of occurrence data
Share of urban area in proximity to species occurrence	*iPoints*	Land cover map	ca. 300×300 m	GBIF
	iBuffer			
	$iBuffer_{FD}$			
	iDist			
	$iVIIRS_{MEDIAN}$	VIIRS artificial night lights data	ca. 460×460 m	
	$iVIIRS_{MEAN}$			
Differences in abundance/occurrence probability between urban and rural areas	$iSDM_{COR}$	Land cover map	ca. 10′×10′	
	$iSDM_{CON}$			
	$iCon_{UrbRur}$		ca. 300×300 m	
Meta-analysis	*iMeta*	Inconsistent, as dependent on primary studies		

similar to each other, revealing that considering larger areas around the observation points has little influence on the relative ranking and is redundant in this context. Thus, it seems that a small buffer suffices to account for movements of individuals and potential georeferencing inaccuracies.

Our attempt to account for species-specific differences in the use of space by employing the foraging distance as the buffer radius ($iBuffer_{FD}$) proved futile. Likely, using foraging distances as radius allocates far more area than species actually use, as doubling the radius increases the buffer area by a factor of four. This overcompensation is especially true for species that travel long distances between roost and hunting grounds. While choosing a fixed buffer size for all species seems arbitrary and neglects biological differences between species, it overcomes problems such as the heterogeneous nature of reported data on aspects such as foraging distances and home range which can impact biological inference (Slavenko et al., 2016) and the lack of available space-use information for many species. Therefore, $iBuffer_{FD}$ can only be used to a limited extent in large-scale analyses.

Since they are based on different urban proxies, we did not necessarily expect the great similarity in species ranking between *iPoints*, *iBuffer*, $iBuffer_{FD}$ and $iVIIRS_{MEAN}$. However, this probably reflects the correlation between the radiance of artificial light sources and the proportion of urban area (not shown). Why using the median (as in $iVIIRS_{MEDIAN}$) instead of mean (as in $iVIIRS_{MEAN}$) to average radiance across species observation localities produces a less similar ranking to that of *iPoints* and *iBuffer* remains more difficult to explain. By applying the median, many species received a score of 0, which affected the ranking, but for taxa that are better-sampled or more urban-affine, this effect would be reduced (Callaghan et al., 2019). Interestingly, *iDist* to $iVIIRS_{MEDIAN}$, which use a median score, show both high similarity of species ranking and an almost identical similarity pattern with the other indices. Most likely, this reflects that both urban land cover and the distance to the closest urban area are strongly correlated with radiance of artificial light sources (Callaghan et al., 2019).

The consistently observed sharp deviation of all indices from the urban affinity scores provided by the study of Jung and Threlfall (2018) can be explained by the input data of the meta-analysis (Senior et al., 2016). As mentioned by the authors themselves, the environments representing the urban and non-urban components in the data collated from multiple studies were highly heterogeneous due to various sampling designs. In contrast, within each of our indices, the definition of what is urban and rural is consistent. Admittedly, applying *iMeta* as response variable for the model types we use is questionable. The analysis of data from different individual studies usually requires dedicated methods (Harrison, 2011) that, for example, account for heterogeneity in these data (as done in Jung & Threlfall, 2018). Nevertheless, this was the only study we are aware of that provided continuous effect sizes for the urban affinity of a large number of bat species and also applied them to investigate trait responses to urbanization. Therefore, it called for testing to what extent the results of our models correspond to these results.

Overall, it remains difficult to judge which indices provide the most useful scores. As all of them provide largely the same patterns in the trait analysis, which are also largely consistent with previous findings (see case study), all indices seem to reflect urban affinity to some extent. The simpler indices (*iPoints*, *iBuffer*, $iBuffer_{FD}$ and $iVIIRS_{MEAN}$) are easier and faster to work with and clearer to follow. In addition, employing them revealed fewer different model variants and stronger predictions overall. Since more complex methods, for example those using SDMs, are time-consuming and require special expertise, we advise against using them in studies with a large number of species, especially if occurrence data are scarce (Wisz et al., 2008). An absolute limit for the minimum number of occurrence data is difficult to define and often arbitrarily chosen. However, some studies attempted to estimate this threshold (Callaghan et al., 2019; Callaghan, Bowler, et al., 2021; Liu et al., 2021; van Proosdij et al., 2016). Although scientists in this field should be aware of this limitation and assess it for specific cases, given the significant increase in occurrence data availability (Heberling et al., 2021), this point could become a less limiting factor for some taxa in the future. For species with a sufficient number of reliable records, it may be possible to optimize the results of the SDMs by tailoring the model for a particular focal species even more

precisely to its specific ecology. However, this would require both in-depth ecological expertise on each of the species under study and advanced methodological skills in niche modelling. Furthermore, the extent to which the results are then comparable across species remains unclear. Other approaches to determine urban affinity based on SDMs are also conceivable. For example, unlike the two SDM-based indices we show here, urban land cover could be included as a variable in the SDMs and the corresponding coefficient then used as a value for urban affinity. However, this is only readily possible with certain model algorithms (e.g. GLM).

Another potential shortcoming when using occurrence records from global databases like GBIF is their susceptibility to several types of biases (Zizka et al., 2021). If the aim of a study is to identify species-specific preferences towards certain habitat types, sampling biases due to different accessibility should always be considered. For our purposes, especially a sampling bias towards urban areas was a main concern. Using a sensitivity test, we found that this bias was not affecting our indices significantly. The comparison of species with different range sizes, and thus potentially different compositions of available habitats, is subject to the assumption that they all have the same probability of colonizing one of these habitat types, regardless of interspecific competition. However, we could not detect a clear impact of the size of the distribution range or of the proportion of available urban area on our indices, potentially because for bats interspecific competition is often weak (Bell, 1980; Fenton, 1990; Roeleke et al., 2018). However, we would like to stress that this should be considered on a case-by-case basis. Recently, an adjustment of urban affinity indices that aims to account for the potential effects of range size, sampling biases and interspecific competition has been published and provides a potential solution for biased data (Callaghan, Cornwell, et al., 2021; Callaghan, Major, et al., 2020). In any case, the scores of the indices we present should not be interpreted as absolute but as relative values of urban affinity that allow comparing different indices and species with each other but do not necessarily reflect the actual urban affinity.

To conserve species in urban environments, it is essential to understand the characteristics that determine their ability to persist under prevailing novel conditions (Sol et al., 2014). Studying trait responses to urbanization can elucidate general patterns in this respect (Webb et al., 2010). Apart from the study by Jung and Threlfall (2018), our study is the only one we are aware of investigating the responses exclusively of bat species to urban environments globally. Regardless of the urban affinity index used as response variable, our results support the hypothesis that urban areas act as filters favouring species with certain traits (Table 4).

Echolocation is considered as one of the most prominent features of bats, largely determining how they interact with their environment (Denzinger & Schnitzler, 2013; Neuweiler, 1984) and showing highly habitat-related variation across species (Simmons et al., 1975). Indeed, we found that echolocation characteristics were important for predicting urban affinity: bats calling with lower peak frequency and longer duration were more urban-affine. These results are consistent with previous findings on the echolocation characteristics best adapted to urban environments (Avila-Flores & Fenton, 2005; Jung & Kalko, 2011; Jung & Threlfall, 2018; Threlfall et al., 2011, 2012).

Body size, indicated here by forearm length, showed an inverse correlation with affinity to cities, which is in line with earlier studies (Croci et al., 2008; Jung & Threlfall, 2018; Santini et al., 2019; Sol et al., 2014). This is likely because small species can hide or roost better than large species in small urban green spaces, underground cavities, crevices or small patches of vegetation (Santini et al., 2019). In contrast to earlier findings (Jung & Threlfall, 2018), aspect ratio was rarely a significant predictor of urban affinity, in the models including the indices we developed as response variables. However, when using the meta-analysis affinity scores as a response variable, aspect ratio appeared to be positively correlated with urban affinity and the most common predictor in the selected models. Higher aspect ratios are associated with a fast and less manoeuvrable flight (Norberg & Rayner, 1987), which again is associated with both foraging in open areas (Neuweiler, 1984) and the ability to commute over larger distances (Dietz et al., 2016:30; Jung & Kalko, 2011). While the former is partially already reflected by echolocation characteristics, the aspect of higher mobility seemingly had no further sufficient impact in most models. We suspect that species foraging in urban habitats may also find suitable roosting sites within cities, making long-distance commutes unnecessary.

We also found that roost-type flexibility was associated with stronger urban affinity. This is consistent with the general perception that generalists are better at dealing with unknown or novel environments (e.g. Callaghan et al., 2019; Concepción et al., 2015; Sorace & Gustin, 2009). This is usually attributed to the ability to opportunistically adapt to the available resources. It has been argued that cities offer conditions that are preferably exploited by species with a wide habitat breadth that are also common in other artificial habitats like rural gardens or agricultural land (Ducatez et al., 2018). Nevertheless, the heterogeneous structure of cities seems to provide bats with a variety of suitable roosting sites that resemble the conditions of natural roosts (Kunz, 1982; Russo & Ancillotto, 2015).

5 | CONCLUSIONS

We compared a variety of approaches to quantify species' urban affinity. In contrast to the majority of previous studies that were restricted to a limited spatial extent or used a discrete classification of species in terms of their urban affinity (Evans et al., 2011), all indices introduced here reveal continuous scores, are generalizable to all kinds of taxa and applicable on a global scale, depending only on the availability of occurrence data. We conclude that simple indices give at least as useful indications as the more complex ones and are easier to apply and follow. Comparable scores of a previously published meta-analysis (Jung & Threlfall, 2018), which were based on inconsistent definitions of urbanity level, showed clear differences from our indices in the relative urban affinity of

bat species. We conclude that some of the introduced indices have potential to outperform meta-analyses in terms of the taxonomic and geographic scope, are easy to reproduce and reveal more accurate results. However, apart from this one study to our knowledge there are no comparable data available for bats, making a precise evaluation of the indices difficult. To more comprehensively examine their general value, it would be useful to apply the indices to more extensively studied taxa such as birds and plants (e.g. Callaghan et al., 2019; Hill et al., 2002). Another interesting possibility to extend the application of the indices would be to add a temporal component, that is, to track changes in the urban affinity in the course of a year (Callaghan, Cornwell, et al., 2021) or over longer time periods. The latter could help to detect long-term effects of urbanization. Identifying the traits that characterize successful urban dwellers is useful for recognizing and prioritizing species that suffer greater threats by the rapidly intensifying process of urbanization worldwide and adapt conservation measures for their needs.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R-Code supporting or complementing the findings of this study are available in OSF at https://doi.org/10.17605/OSF.IO/N4QHJ.

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