RESEARCH ARTICLE

Bird lineages colonizing urban habitats have diversified at high rates across deep time

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Abstract

Aim: Urbanization exposes species to novel ecological conditions. Some species thrive in urban areas, whereas many others are excluded from these human-made environments. Previous analyses suggest that the ability to cope with rapid environmental change is associated with long-term patterns of diversification, but whether the suite of traits associated with the ability to colonize urban environments is linked to this process remains poorly understood.

Location: World.

Time period: Current.

Major taxa studied: Passerine birds.

Methods: We applied macroevolutionary models to a large dataset of passerine birds to compare the evolutionary history of urban-tolerant species with that of urban-avoidant species. Specifically, we examined models of state-dependent speciation and extinction to assess the macroevolution of urban tolerance as a binary trait, in addition to models of quantitative trait-dependent diversification based on relative urban abundance. We also ran simulation-based model assessments to explore potential sources of bias.

Results: We provide evidence that historically, species with traits promoting urban colonization have undergone faster diversification than urban-avoidant species, indicating that urbanization favours clades with a historical tendency towards rapid speciation or reduced extinction. In addition, we find that past transitions towards states that currently impede urban colonization by passerines have been more frequent than in the opposite direction. Furthermore, we find a portion of urban-avoidant passerines to be recent and to undergo fast diversification. All highly supported models give this result consistently.

Main conclusions: Urbanization is mainly associated with the loss of lineages that are inherently more vulnerable to extinction over deep time, whereas cities tend to be colonized by less vulnerable lineages, for which urbanization might be neutral or positive in terms of longer-term diversification. Urban avoidance is associated with high rates of recent diversification for some clades occurring in regions with relatively intact natural ecosystems and low current levels of urbanization.

KEYWORDS
anthropic habitats, land-use change, macroevolution, passerines, trait-dependent diversification, urban biodiversity

1 | INTRODUCTION

Urbanization is a rapid anthropogenic change to the environment that can have a dramatic impact on local communities. Urban environments create new ecological opportunities for a few species (hereafter "urban tolerants"), whereas a much larger number of species tend to be excluded from this habitat transformation (hereafter "urban avoidants"), with urbanization therefore leading to declines in biodiversity and the homogenization of ecological communities (Ibáñez-Álamo et al., 2017; McKinney, 2002; Sol et al., 2017). To predict the long-term impact of urban areas on biodiversity, it is important to understand the macroevolutionary persistence of species attributes linked to the recent colonization of urban areas. One possibility is that urban-tolerant species are similar to those that have been successful in the face of habitat change and disturbance more generally, in which case current urban tolerance might be detectable across deep evolutionary time-scales (Bennett & Owens, 1997; Cardillo et al., 2005; Fritz & Purvis, 2010; Greenberg et al., 2021). However, it remains unclear whether the characteristics of modern city-dwelling species have been shaping their macroevolutionary history long before the Anthropocene.

A long-term macroevolutionary effect of urban tolerance might not seem likely given that urban habitats are a relatively recent phenomenon. Nor is the ability to colonize cities easily conceptualized as a heritable trait. However, the underlying combination of traits associated with urban tolerance is likely to be heritable and to have evolved through time, even in the case of cognitive abilities (e.g., Branch et al., 2022). A similar argument is made for other composite indices, such as the International Union for Conservation of Nature (IUCN) red list categories describing extinction risk. Although these categories are not directly heritable, they are, nonetheless, closely associated with sets of heritable traits that are often explored in a macroevolutionary framework (Bennett & Owens, 1997; Cardillo et al., 2005; Fritz & Purvis, 2010).

The traits most clearly associated with urban tolerance are related to ecological plasticity or adaptability. A growing body of evidence suggests that organisms can evolve rapidly in response to urbanization (Johnson & Munshi-South, 2017; Kern & Langerhans, 2018), perhaps because lineages thriving in cityscapes are inherently adaptable, with high ecological niche lability. Evidence of this comes from the fact that urban birds are often characterized by having high dispersal ability, broad environmental tolerance, behavioural flexibility and generalist habits (e.g., feeding generalists) (Bonier et al., 2007; Evans et al., 2011; Sol et al., 2013). This suite of traits can also increase the success of invasion into a wide range of other habitats, which, in turn, might increase exposure to environmental fluctuations, further selecting for traits that maximize fitness in a broad variety of conditions (Devictor et al., 2008; Waldron, 2010).

If urban-tolerant species are therefore inherently invasive and adaptable, their characteristics might shape diversification in the long term, either through effects on diversification rates or on available genetic variation (Cooney et al., 2016; Phillimore et al., 2006; Tebbich et al., 2010). In some cases, traits associated with greater adaptability are associated with increased rates of diversification (Fernández-Mazuecos et al., 2013; Qiao et al., 2016; Wang

et al., 2017), in line with evidence that environmental change can promote diversification through increasing ecological opportunity or genetic isolation (Ezard et al., 2011; Kozak & Wiens, 2010). In other cases, indices of adaptability, such as broad niches and ecological generalism, have been associated with lower net diversification rates, probably because population abundance and flexibility can increase connectivity and gene flow between subpopulations, impeding allopatric speciation (Rolland & Salamin, 2016; Weeks & Claramunt, 2014). The extent to which urban tolerance is positively or negatively associated with diversification is therefore uncertain.

Although urban environments might tend to be colonized by generalist species and other recurrently successful invaders, they can simultaneously act as filters for less adaptable lineages that tend to experience higher rates of extinction over time (Lavergne et al., 2013). The strong similarities between urban environments around the world mean that only a limited number of species have the combination of traits that allow urban colonization, often leading to remarkable similarities in communities across cities (Olden & Rooney, 2006). Conversely, evolutionarily distinct species rarely thrive in urban environments (Sol et al., 2017), suggesting that lineages with low net diversification are more sensitive to the environmental changes created by urbanization. It is likely that many of these species belong to clades that, owing in part to their specialist habits (Devictor et al., 2008) and low rates of niche evolution (Lavergne et al., 2013), have historically been unsuccessful at coping with disturbances to their environment.

In this study, we compared the macroevolutionary history of urban-tolerant passerine bird species with that of urban-avoidant species. Passerines are a suitable system for exploring this question because they are widely surveyed in both urban and non-urban environments. Using a dataset of 925 passerine species from four continents, we tested whether urban tolerants have a tendency to diversify comparatively successfully, and thus act as reservoirs of novel diversity over longer time frames; and whether urban-avoidant species have frequently been doomed throughout history to undergo high levels of extinction. We used likelihood-based tests to assess the macroevolution of urban tolerance as a binary trait state (presence/absence) or continuous trait (relative abundance), modelling its relationship with rates of speciation and extinction, in addition to the rate at which it appears or disappears across evolutionary time (i.e., rate of "transition" among traits) (Maddison, 2006). We also ran a simulation-based assessment of models of state-dependent diversification to explore the probability that observed data would emerge under the models examined. The results provided insight into the historical success of current urban-tolerant versus urban-avoidant species.

2 | METHODS

2.1 | Data collection

To explore the macroevolutionary dynamics of urban tolerance, we gathered information about urban presence and absence across a sample of passerine bird species in 319 assemblages distributed

across 50 regions in Africa, Australia, Europe and North/South America (Sol et al., 2020). Studies were excluded if they did not sample the entire passerine assemblage in both urban and non-urban environments. Urban tolerance was estimated through matched comparisons between urban habitats and nearby non-urban areas (Sol et al., 2020) to focus on species that have either invaded cities already or have the potential to do so because they inhabit adjacent natural habitats. Conversely, species living far from cities and therefore unlikely to encounter urban environments were excluded. Based on the data presented by Sol et al. (2020), we classified species as "absent" from urban areas if they were not found in urban categories (varying from highly to little-urbanized habitats) and appeared only in nearby non-urban environments. We considered a species to be "present" if it was found in any of the urban categories, independently of its presence or absence in the nearby non-urban environment. These data scored urban presence/absence for 925 passerine bird species (15.6% of all passerine species), of which 590 were present in urban areas and 335 species were absent. In addition, we included the relative abundance data (number of individuals of a species in assemblage i / sum of individuals of all the species present in assemblage i) in the urban assemblages from the original study (Sol et al., 2020), averaging the values for each species across all the cities in which they occur. As with the binary measure of urban tolerance and avoidance, the continuous metric of relative urban abundance was taken as a measure of the affinity of species for urban areas. Relative urban abundance data were available for 849 species.

2.2 | Statistical analysis

To compare the macroevolutionary trajectories among urban-tolerant and urban-avoidant species, we first estimated the maximum clade credibility (MCC) phylogenetic tree of a random sample of 1000 time-calibrated trees containing every species of birds (Jetz et al., 2012). This estimate focused on the sample of trees based on the backbone tree from the study by Hackett et al. (2008). The complete MCC tree was pruned to contain the 925 species of passerine birds, and then used for subsequent analyses. Using this phylogenetic estimate, we tested weather urban-tolerant and urban-avoidant species differ in their rates of speciation or extinction and in the rates of transition between the two states.

We assessed the statistical support for eight alternative models of diversification in explaining the macroevolution of urban-tolerant versus urban-avoidant species. These models started with simple models of binary state speciation and extinction (BiSSE; Maddison et al., 2007; FitzJohn et al., 2009). In the simplest (*i*), urban-tolerant and urban-avoidant species have identical rates of speciation, extinction and transition among states. In two further models, we allowed variation in either (*ii*) speciation and extinction, or (*iii*) transition rates among urban-tolerant and urban-avoidant species. The most complex BiSSE model allowed for (*iv*) variation in speciation, extinction and transition among the two states. None of the models

assumed any directionality of the effect a priori (e.g., higher extinction in avoidant species or the reverse). For example, in models allowing different rates of speciation, the faster rate might occur in either the tolerant or the avoidant state.

Owing to the limitations of BiSSE models (Rabosky & Goldberg, 2015), we ran two additional hidden-state speciation and extinction (HiSSE) models, which are less prone to identifying trait-dependent diversification falsely (Beaulieu & O'Meara, 2016). The HiSSE models allow us to assess the influence of other factors on diversification dynamics, beyond any differences between urban-tolerant versus urban-avoidant taxa (models *v* and *vi*; Beaulieu & O'Meara, 2016). The models include a hidden-trait model that allowed us to examine whether hidden factors dominate diversification rates and the extent to which they are associated with urban traits in passerines. Both models included diversification parameters for each of the four combinations of the two observed states (urban tolerant versus urban avoidant) and two hidden states (A and B), implemented as four parameters of turnover. A simple HiSSE model (*v*) included a single rate of transition in each direction between urban-tolerant and urban-avoidant species, regardless of the hidden state, and a single parameter of transitions among hidden states. The more complex model (*vi*) included five parameters of transitions among states, involving each of the combinations of observed and hidden states (0A → 1A, 1A → 0A, 0B → 1B and 1B → 0B).

Last, we examined two character-independent hidden-state diversification models, (*vii*) and (*viii*). These represent the null hypothesis that trait states are dissociated from any of a set of multiple diversification rates across the phylogeny, even while traits undergo transitions during the diversification process (Beaulieu & O'Meara, 2016; Rabosky & Goldberg, 2015). These two null character-independent diversification models differed in the number of diversification rate parameters included. Model (*vii*) included four diversification rate parameters (called CID-2), to resemble a BiSSE model. The last model (*viii*) included eight diversification rate parameters (called CID-4), resembling a HiSSE model. Parameter estimation for each BiSSE and HiSSE model was performed while correcting for the fraction of sampled passerine species (925/5966 = 15.6%, but see Section 2.3). To avoid reaching local maxima, each analysis was repeated 10 times using different starting parameters, and the run with the maximum likelihood was selected for interpretation. All analyses were performed using the *hisse* R package (Beaulieu & O'Meara, 2016). We report the full results of the best-fitting of the eight state-dependent diversification models, as well as model-averaged ancestral reconstructions using Akaike information criterion weights (AICw).

The macroevolution of urban tolerance was also examined using the continuous variable of mean relative urban abundance, under a series of quantitative trait-dependent diversification models (QuaSSE; FitzJohn, 2010). In the models examined, speciation and extinction were either constant across lineages, and therefore independent from urban abundance, or followed a linear association with the metric (two treatments for each of speciation or extinction). The model with the greatest support was assessed with a parameter accounting for a possible directional tendency of the metric across evolutionary time,

called the drift parameter. Parameter estimation in each of the QuaSSE models was performed in *diversitree* (FitzJohn, 2012), while accounting for the proportion of sampled passerine species.

2.3 | Assessment of limited sample size and SSE model adequacy

Some of the known limitations of BiSSE (Davis et al., 2013; Simpson et al., 2018) are unlikely to have a substantial impact on our analyses, given that our sample is large (>300 tips), balanced across states and shows no substantial decline in diversification rate over time. Nonetheless, the portion of the complete passerine tree sampled was small (15.6% sampling), which can be problematic for parameter inference (Chang et al., 2020; Rabosky & Goldberg, 2015), particularly when sampling is non-random across the phylogeny (Lynch, 2009). We used three approaches to ameliorate these potential limitations.

First, we compared the phylogenetic distribution of our samples across the complete MCC passerine tree against simulations, using Fritz and Purvis's *D*-statistic to test for phylogenetic randomness in the sample (Fritz & Purvis, 2010). We found that our sample was not purely random ($D = 0.826$; $p < .001$), which could be associated with a phylogenetically clustered or biased sample. However, the sample was also not significantly phylogenetically clustered to resemble a Brownian motion process ($p < .001$). Although this suggests that clustering is minimal and will have only a minor impact on methods of accounting for missing data based on sampling proportion, we repeated all analyses with a randomized subsample. To do this, we subsampled the species 1000 times using 12.5% of all passerine species (randomly removing 151 species from the original sample) and took the subsampled dataset that maximized phylogenetic randomness (including 497 tolerant species and 277 avoidant species; $D = 0.877$; $p = .031$). Although this subsampling technique provides only an approximate estimate of the impact of non-random sampling, it should expose datasets where non-random sampling is severe and likely to bias the results.

These initial analyses were focused only on a pruned tree, and therefore branches with data on urban avoidance and tolerance, with *c*. 5000 passerine species missing from the dataset. To assess the influence of missing phylogenetic information, we re-ran all analyses using a tree containing the full set of 5966 species of passerines available, including branches with missing data (scored as "NA" for urban tolerance). This approach focuses on including additional phylogenetic information while rendering missing species as uninformative in the analyses.

Lastly, we verified whether the model was a plausible description of the dataset and taxon-sampling regime using simulations from the model and parameter estimates and comparing these with the empirical data (e.g., Bromham et al., 2016; Greenberg et al., 2021). If the model used describes the data adequately, the simulated data should resemble the observed data (Brown & Thomson, 2018). This type of assessment can also reveal any major inadequacies in the models examined. We performed a simulation-based assessment of the adequacy (or plausibility) of each of the four BiSSE candidate models. We compared

the empirical data with simulations under each of the models examined using two test statistics as proposed by Bromham et al. (2016). The first statistic measures the number of urban-tolerant species that emerged per origin of the trait (number of tips per origin statistic; NoTO), and the second statistic measures the disparity in numbers of urban-tolerant species across pairs of sister clades across the phylogeny (sum of sister clade differences statistic; SSCD). Tests of model adequacy were performed by accounting for the fraction of sampled passeriform species, using the R package *phylometrics* (Hua & Bromham, 2016). The analyses accounted for the sampling fraction of the data and were repeated assuming that different fractions of all passerine birds were urban tolerants. This included the value of 20% of all bird species being urban tolerants, as suggested in previous work (Aronson et al., 2014), plus three other possible values (40, 60 and 80%).

3 | RESULTS

Of eight BiSSE, HiSSE and character-independent diversification models, the strongest statistical support was obtained with the most complex character-dependent HiSSE model (*vi*, Akaike information criterion with a correction for sample size AICc = 7339.6), rather than the character-independent diversification models (*vii*, CID-2, AICc = 7509.9; or *viii*, CID-4, AICc = 7427.6). When averaging the results of the full BiSSE and all HiSSE models together (Figure 1), the models of character-independent diversification (CID-2 and CID-4) received negligible AIC weights (Table 1).
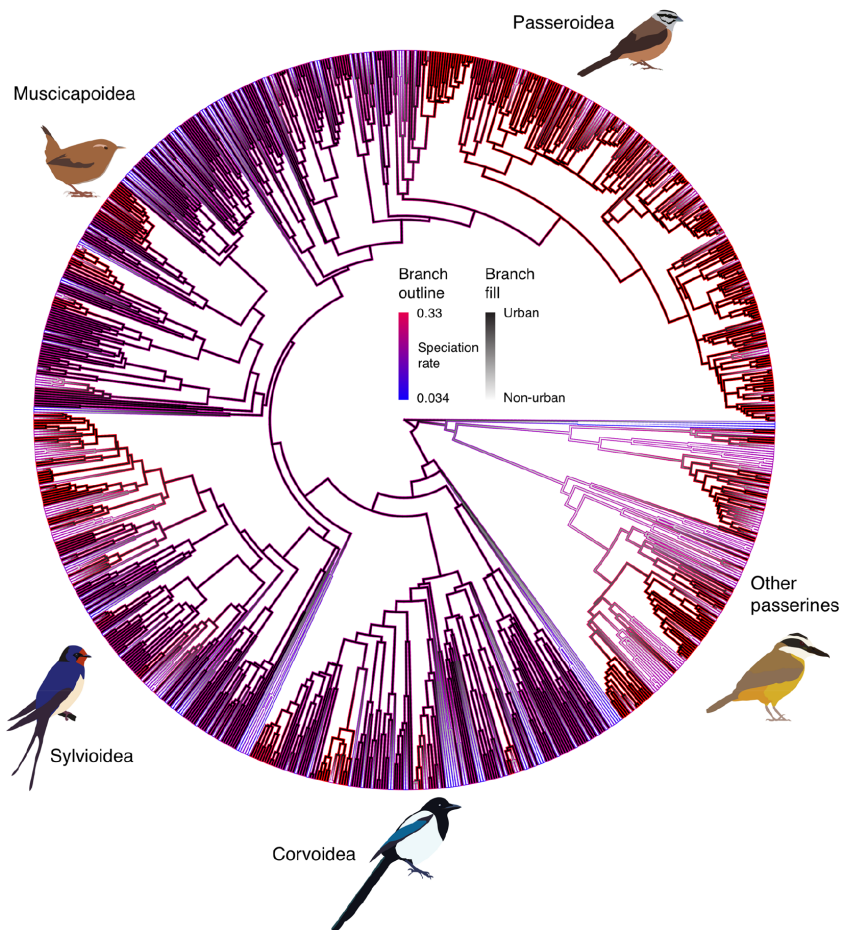
Parameter estimates for the complex HiSSE model, which received the best statistical support, consistently separated diversification rates by urban-tolerant and urban-avoidant taxa and by a hidden trait with states A and B. The models support a scenario wherein rates of transition towards urban avoidance are several times greater than in the opposite direction, and in which diversification rates are several times greater in urban-tolerant taxa (Figures 1 and 2a).

Analyses of QuaSSE models supported a positive association between speciation rates and the continuous variable of mean relative urban abundance (Table 2; slope = 1.6, intercept = 0.06), suggesting that diversification rates are faster in urban-tolerant lineages, in agreement with the best HiSSE models. However, there was limited support for an association between extinction rates and mean relative urban abundance. In addition, we found significant support for a directional tendency (drift model) of mean relative urban abundance to decrease across lineages ($p < .001$; drift parameter = −0.006; Table 2). The superior drift model indicates an evolutionary tendency towards urban-avoidant species, potentially driven by some young and rapidly diversifying urban-avoidant lineages (Figure 2b).

3.1 | Results of the assessment of limited sample size and SSE models

All results were nearly identical when using the complete dataset (925 species), the dataset subsampled to maximize phylogenetic

FIGURE 1 Phylogenetic tree of the passerine species sampled, showing the positioning of urban-tolerant (black) and urban-avoidant (white) species, with the fill of branches as a continuous grey scale reconstructed from the model-averaged results shown in Table 1. The outline of branches ranges from low diversification rates in blue to high in red. The label "Other passerines" includes a mix of oscine and suboscine passerine clades, including superfamilies Menuroidea and Meliphagoidea and suborders Tyranii and Acanthisitti.

TABLE 1 Parameter estimates and statistical support for the best-performing binary state speciation and extinction (BiSSE) and all hidden-state speciation and extinction (HiSSE) models examined using the original dataset with 925 species.

| Model	Number of diversification rate parameters	Log maximum likelihood (lnL)	AICc	AICw
i. BiSSE null	1	−3825.95	7657.93	1.08×10^{-63}
ii. BiSSE transition	1	−3820.69	7649.42	7.69×10^{-62}
iii. BiSSE diversification	2	−3767.70	7543.45	7.90×10^{-39}
iv. BiSSE full	2	−3751.54	7513.14	3.04×10^{-32}
v. HiSSE simple	4	−3682.31	7380.77	0.002
***vi*. HiSSE full**	**4**	**−3673.97**	**7368.18**	**0.998**
vii. HiSSE CID-2	2	−3748.91	7509.91	1.55×10^{-31}
viii. HiSSE CID-4	4	−3705.75	7427.65	1.17×10^{-13}

Note: Metrics of statistical support include the Akaike information criterion with a correction for sample size (AICc) and AIC model weights (AICw). Bold denotes the best-performing model.

randomness (774 species; see Table S1) and the full tree of 5966 species (Table S2). However, the full tree analyses revealed an additional signal in one hidden state, where transition rates were higher in the direction from urban-avoidant towards urban-tolerant taxa, and diversification rates were several times higher in urban-avoidant taxa (Figure S1). The evidence from this hidden state in the full tree analyses suggests that urban-avoidant taxa tend to be distributed towards either end of the age spectrum. In other words, urban avoidants tend to arise from more recent

or more ancient nodes, whereas urban-tolerant taxa have more intermediate ages.

Consistent with the results of likelihood-based model testing, simulation-based assessment of model adequacy supported the most complex model as plausible under the most likely proportions of urban tolerance (Table 3). Specifically, model *iv*, which allowed different diversification and transition rates among urban-tolerant and urban-avoidant taxa, provided an adequate description of the data when the percentage of urban-tolerant species was >20 and <80%.
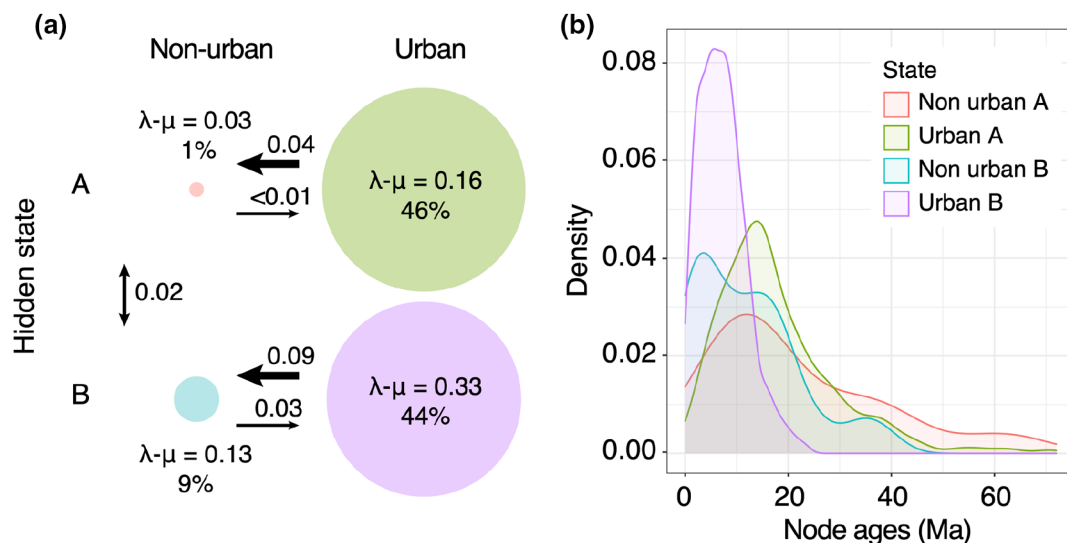
FIGURE 2 (a) Rates of diversification and transition, and proportions of nodes per trait state; and (b) node ages per trait state inferred from the best hidden-state speciation and extinction (HiSSE) models. The proportion of nodes per state is given below net diversification rates (λ – μ). Values above arrows denote transition rates. Data were obtained for 925 of 5966 passerine species in the full tree; analyses accounted for missing data using the proportion of species sampled.

TABLE 2 Estimated rates of speciation and extinction in passerine birds based on relative urban abundance, assessed under quantitative state speciation and extinction (QuaSSE) models.

Speciation link	Extinction link	Speciation m	Speciation c	Extinction m	Extinction c	Diffusion	Drift	d.f.	lnLik	AIC	χ^2	Pr(>|χ|)
Constant	Constant	–	0.316	–	0.193	<0.001	–	3	−1466.675	2939.350	–	–
Linear	Constant	1.595	0.060	–	<0.001	<0.001	–	4	−1348.724	2705.447	235.902	<0.001
Constant	Linear	–	0.270	0.470	−0.160	0.001	–	4	−1397.281	2802.563	138.787	<0.001
Linear	Linear	0.814	0.049	−0.302	−0.210	<0.001	–	5	−1348.765	2707.529	235.821	<0.001
Linear	**Constant**	**1.803**	**−0.031**	**–**	**0.020**	**<0.001**	**−0.006**	**5**	**−1331.399**	**2672.797**	**270.552**	**<0.001**

Note: Parameter m indicates the correlation slope between relative urban abundance and diversification parameters; parameter c indicates the y-intercept or constant. Bold denotes the best-performing model.

Abbreviation: AIC, akaike information criterion.

Bold denotes the best-performing model.

TABLE 3 Results from the binary state speciation and extinction (BiSSE) model-adequacy assessment using simulations.

Percentage of passerines with the set of traits allowing urban tolerance	20%		40%		60%		80%	
Test statistic for assessment of model adequacy	SSCD	NoTO	SSCD	NoTO	SSCD	NoTO	SSCD	NoTO
i. Similar rates among states	<0.001	0.336	<0.001	0.430	0.001	0.363	<0.001	0.508
ii. Different rates of speciation and extinction	0.304	0.001	0.060	<0.001	0.145	<0.001	0.377	0.003
iii. Different rates of transition	0.177	0.002	**0.171**	**0.063**	**0.229**	**0.018**	**0.069**	**0.015**
iv. Different rates of diversification and transition among states	0.001	0.239	**0.292**	**0.011**	**0.121**	**0.019**	0.004	0.197

Note: Values indicate the minimum proportion of simulations that fall either above or below the empirical value (*p*-values). Significant results (*p* ≤ .01) indicate that the model does not accurately describe the observed distribution of urban-tolerant taxa across the phylogeny (model not adequate). Values in bold indicate scenarios in which both test statistics retained the model as plausible (*p* > .01). According to the two tests [sum of sister clade differences statistic (SSCD) and number of tips per origin statistic (NoTO)], model *iii* is plausible when urban tolerants are 40, 60 and 80% of passerine species, whereas model *iv* is plausible when urban tolerants are 40 and 60% of passerine species.
Bold indicates scenarios retained by both test statistics used.

Model *iii* (allowing different transition rates) was also identified as plausible across the various portions of urban-tolerant and urban-avoidant species across passerines, and particularly when urban

tolerants were assumed to be a small (20%) proportion of passerines. Models *i* (assuming no differences in rates) and *ii* (allowing differ-ent diversification rates) were rejected by at least one test statistic

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regardless of the proportion of passerines that were assumed to be urban tolerant (Table 3).

4 | DISCUSSION

Our study shows that urban environments provide an appropriate habitat for lineages that tend to diversify consistently over deep time-scales, while detrimentally affecting species with a long history of reduced diversification. All models with the best support show that urban avoidance (including as a binary trait state or as lower relative abundance in urban areas) is associated with lower net rates of diversification compared with urban tolerance. These results, combined with a previously observed loss of avian phylogenetic diversity in urban areas (Sol et al., 2017), suggests that low diversification rates might be related to the susceptibility of these lineages to habitat disturbance in general, including disturbances that occurred long before the recent emergence of urbanization.

Speciation and extinction are difficult (and in some conditions impossible) to disentangle using phylogenetic data (Louca & Pennell, 2020; Rabosky, 2010); therefore, we tested our hypotheses using a range of complementary modelling approaches, data types and sampling regimes. All these analyses support our main result, with the dominant dynamic suggesting that many urban-avoidant species are not only susceptible to extinction and thus ancient and slow-diversifying over deeper time-scales, but also rarely transition to become urban tolerants. These results suggest that urban avoidants have had a limited tendency to respond to environmental changes, such as those caused in recent years by urbanization, and are consistent with previous evidence showing a link between low rates of niche evolution and current population declines in birds (Lavergne et al., 2013). Slow diversification and limited chances of transition to more successful forms are likely to provide a general explanation for why unique lineages, with low numbers of extant species and a long evolutionary history, tend to be lost from human-made environments (Emer et al., 2019; Greenberg et al., 2018).

Although our findings indicate that the suite of traits associated with urban-avoidant species is often associated with less successful macroevolutionary strategies compared with the traits that occur in urban species, the patterns we describe also suggest that urban areas serve as reservoirs of clades with long-term high diversification rates and frequent transition towards non-urban states. Previous analyses show evidence that ecological generalism is associated with high diversification rates (Fernández-Mazuecos et al., 2013; Phillimore et al., 2006), but also with high rates of transition from generalist to specialist forms (Goldberg et al., 2010; Laenen et al., 2016; Tripp & Manos, 2008). Therefore, our results might be explained by a link between urban tolerance and generalist strategies, such as wide ecological niches (Evans et al., 2011), behavioural flexibility (Ducatez et al., 2020) and broad environmental tolerance (Bonier et al., 2007). The generalist nature of urban tolerants has been suggested by multiple previous studies (Evans et al., 2011; Ishitani et al., 2003;

McKinney, 2006) and is consistent with the hypothesis that generalist strategies are key for invasion success and for allowing species to thrive in multiple habitats (Clavel et al., 2011; Richards et al., 2006). Given the possible link between urban tolerance and generalist strategies, our results are consistent with a process whereby originally generalist species can develop specialized strategies more suited to life in urban environments.

Similar processes have been documented in the biological invasion literature. One example is that of amphibious blenniid fishes, in which dietary generalism and behavioural plasticity are key during the invasion of the terrestrial habitat, but more specialized strategies are necessary for the successful establishment in the novel environment (Ord & Hundt, 2020). Although there is currently no evidence that urban adaptation can drive speciation in birds, minor or incipient divergence of populations in urban areas is increasingly reported (Thompson et al., 2018; Zuñiga-Palacios et al., 2020). Thus, it is possible that the emergence of specialized forms adapted to urban environments might, in the future, contribute to urban populations becoming reproductively isolated.

The analysis performed with the full tree showed an additional signal whereby some young, rapidly diversifying lineages are mostly urban avoidant. These recent radiations might be driven by factors such as high sexual selection or low dispersal ability, particularly in tropical taxa (Tobias et al., 2020). It is unclear why these recent bursts of diversification do not translate into high rates of diversification over a longer span of evolutionary history in urban-avoidant lineages, although one explanation is that such cases are relatively infrequent overall. In addition, radiations of taxa restricted to non-urban habitats often involve incipient species (e.g., ecologically similar geographical isolates), which might be relatively ephemeral because they tend to hybridize with their ancestors after secondary contact (McEntee et al., 2018). In any case, this pattern of recent diversification in urban-avoidant lineages emerged in only one analysis, suggesting that it is outweighed overall by the tendency for rapid diversification to occur in urban-tolerant lineages.

This link between urban tolerance and diversification rate highlights the threats posed by fast-growing urban habitats for urban-avoidant species, many of which appear to be intrinsically sensitive to environmental change. Strategic management of cities should include wildlife conservation as an important goal, with a focus on improving habitat quality in ways likely to favour currently excluded taxa (see examples provided by Apfelbeck et al., 2020). In general, this involves increasing the proportion of vegetated land cover, including urban parks and improving connectivity among patches of native or semi-native habitats (Sol et al., 2020). An encouraging outcome of this study is that the best-fitting macroevolutionary models based on comparisons with our simulated data suggest that urban tolerance is more widespread in passerines than currently estimated. Specifically, the extent of urban tolerance might span 40% of passerine species, rather than the 20% estimated by Aronson et al. (2014), perhaps indicating that the number of bird species colonizing cities will increase over time.

5 | CONCLUSIONS

As urban areas continue to expand, it is crucial to understand and predict which species will succeed or fail in colonizing these novel habitats. A macroevolutionary perspective on species tolerance to novel habitats can help to shed light on the long-term responses of animals to anthropogenic impacts, in addition to appropriate strategies for sustainable urban development. The results of our macroevolutionary analyses suggest that cities can add an additional negative stressor to species that are already liable to be unsuccessful over deep time, whereas over the same long time frames species currently classified as urban tolerant are associated with successful diversification, perhaps because of their greater adaptability. On the one hand, if urban tolerants tend to thrive because of their generalist and opportunistic attributes, they might act as a continuous source for the evolution of specialist urban and non-urban forms. On the other hand, the expansion of cities will exacerbate threats for the majority of passerine species, which have one or more traits associated with urban avoidance. Future studies should explore these patterns in greater detail across a wider sample of avian diversity, in addition to other taxonomic groups once relevant datasets are available.

AUTHOR CONTRIBUTIONS

Maider Iglesias-Carrasco and David A. Duchêne conceived the idea; Maider Iglesias-Carrasco, Joseph A. Tobias and David A. Duchêne designed the analysis; Maider Iglesias-Carrasco and David A. Duchêne collected and analysed the data; all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data used in this project are available at Figshare doi. org/10.6084/m9.figshare.19891219.v1.

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BIOSKETCHES

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