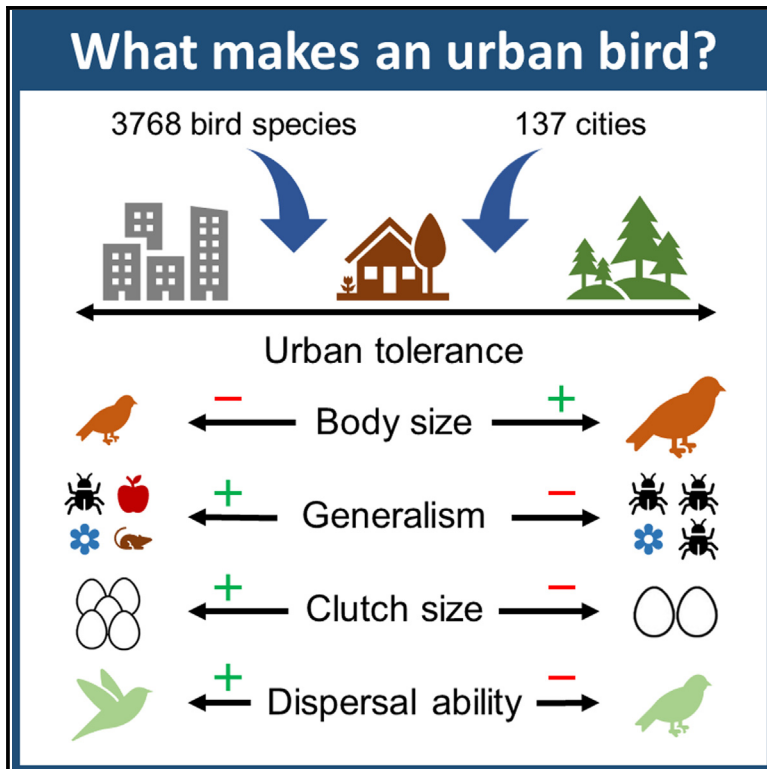# Traits shaping urban tolerance in birds differ around the world

Graphical abstract

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In brief

Neate-Clegg et al. evaluate functional traits underlying the urban tolerance of 3,768 bird species across the world's urban areas. They find urban-tolerant species are smaller, less territorial, longer-lived generalists with higher dispersal ability and larger clutches, but the strength of these relationships varies with latitude and human density.

Highlights

- Globally, urban tolerance in birds relates to life history and functional traits

- Important traits include body size, ecological generalism, and dispersal ability

- Strengths of trait relationships vary globally with latitude and human population

- What makes an urban-associated bird shows strong consistency across the world

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Traits shaping urban tolerance in birds differ around the world

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SUMMARY

As human density increases, biodiversity must increasingly co-exist with urbanization or face local extinction. Tolerance of urban areas has been linked to numerous functional traits, yet few globally consistent patterns have emerged to explain variation in urban tolerance, which stymies attempts at a generalizable predictive framework. Here, we calculate an Urban Association Index (UAI) for 3,768 bird species in 137 cities across all permanently inhabited continents. We then assess how this UAI varies as a function of ten species-specific traits and further test whether the strength of trait relationships vary as a function of three city-specific variables. Of the ten species traits, nine were significantly associated with urban tolerance. Urban-associated species tend to be smaller, less territorial, have greater dispersal ability, broader dietary and habitat niches, larger clutch sizes, greater longevity, and lower elevational limits. Only bill shape showed no global association with urban tolerance. Additionally, the strength of several trait relationships varied across cities as a function of latitude and/or human population density. For example, the associations of body mass and diet breadth were more pronounced at higher latitudes, while the associations of territoriality and longevity were reduced in cities with higher population density. Thus, the importance of trait filters in birds varies predictably across cities, indicating biogeographic variation in selection for urban tolerance that could explain prior challenges in the search for global patterns. A globally informed framework that predicts urban tolerance will be integral to conservation as increasing proportions of the world's biodiversity are impacted by urbanization.

INTRODUCTION

Urbanization erases natural habitats and decimates species richness.[1–3] By 2030, an expected 5.2 billion people will live in urban areas[4] and urban land cover is predicted to exceed 1.2 million km[2] globally.[5] Urbanization is accompanied by a consistent loss of biodiversity,[6–8] including reduced phylogenetic[9,10] and functional diversity,[6,11,12] resulting in more homogenized wildlife communities. Despite these overall losses, cities can still harbor substantial biodiversity,[13] including threatened species,[14] and several factors can contribute to higher species richness within urban areas. For example, biodiversity can be bolstered by green space,[15–17] greater habitat heterogeneity,[18,19] higher tree cover,[20–22] or reduced housing density.[15,23] Within these species pools, some species—often termed urban adapters, urban exploiters, or synanthropes—generally succeed in cities where others do not.[13] The relative tolerance of species to urbanization can result from shared evolutionary history[24] and is often linked to functional traits. For example, in Australian birds, urban adapters show diet generalization, bigger brains, and larger clutch sizes.[25] Although many such traits have been suggested or regionally

evaluated, what remains untested is whether the traits that confer urban tolerance in species differ across the cities and biogeographic contexts of the world. With recently available global data on occurrence[26] and species traits (e.g., AVONET[27]), birds are an ideal system to explore this question.

Several ecological traits have been linked to urban association in birds[25,28,29] (Table 1). For example, urban tolerance is often positively associated with niche breadth,[30,31] including dietary[11,25,32] and habitat generalism.[25,33,34,35] The degree of sociality also plays a role, with urban-tolerant species tending to be more social,[29,32,36] although they also tend to be behaviorally dominant over other species.[37] In addition, nest placement is important, with ground nesters often avoiding urban areas[29,38,39,30,40] while tree nesters tend to persist in cities.[38,40] Yet despite some general trends, the importance of certain traits often varies between studies. For example, although urban-associated species tend to have larger clutch sizes,[11,25,41] this pattern is not always supported.[36,42] Similarly, the role of body size has received mixed support, with urban tolerance positively associated with body mass in Australia,[25] negatively associated in raptors,[33] and showing no relationship globally.[9] Longevity or

Table 1. Ten functional traits tested in relation to the Urban Association Index

Trait	Description	Data sources	Hypothesized effect	In support	Lacking support
Body mass	log-transformed	AVONET[27]	negative	Cooper et al.[33]	Callaghan et al.,[25] Sol et al.,[29] and Conole and Kirkpatrick[38]
Bill shape	second PC from a PCA of four bill measurements	AVONET[27]	negative	–	–
Hand-wing index	the ratio of wing length to Kipp's distance	AVONET[27]	positive	Møller[41]	–
Diet breadth	number of major food groups, 1–9	BirdBase,[44] Birds of the World[45]	positive	Evans et al.,[6] Lizée et al.,[11] Callaghan et al.,[25] Conole and Kirkpatrick,[38] Croci et al.,[32] Fidino et al.,[46] and Jokimäki et al.[43]	Sol et al.[29]
Habitat breadth	number of major habitats, 1–11	BirdBase,[44] Birds of the World[45]	positive	Callaghan et al.,[25] Sol et al.,[29] and Sayol et al.[34]	–
Lower elevational limit	lower limit of elevational range reported in the literature	BirdBase,[44] Birds of the World[45]	negative	–	–
Territoriality	a scale from 1 (low) to 3 (high)	Tobias et al.[47]	negative	–	Kark et al.[36]
Longevity	log-transformed	Bird et al.[48]	positive	Møller[41] and Croci et al.[32]	Guetté et al.[39]
Clutch size	log-transformed	Myhrvold et al.,[49] BirdBase,[44] and Birds of the World[45]	positive	Lizée et al.,[11] Callaghan et al.,[25] and Møller[41]	Kark et al.[36] and Chamberlain et al.[42]
Nest type	categorical: ground, cavity, open, and enclosed	BirdBase,[44] Birds of the World[45]	enclosed, positive; ground, negative	Evans et al.,[6] Sol et al.,[29] Conole and Kirkpatrick,[38] Croci et al.,[32] and Jokimäki et al.[43]	Callaghan et al.[25]

For each trait, we list a description, the data sources used, the hypothesized effect (e.g., smaller body size for species with higher urban association), and examples of literature, either in support of the hypothesis or with no support/contradictory support.

lifespan has seldom received strong support in models,[32,39] while cavity nesters show mixed responses to urban areas.[6,11,38,40,43] Finally, although dispersal ability has been linked to urban tolerance,[41] migratory strategy is rarely associated with urban tolerance.[6,25,34,39,30,40,43]

The lack of generality in previous work may arise for multiple reasons. Many studies sample only a subset of biogeographic regions and/or species. Variation in the importance of traits may be driven by differences in species pools or by context-dependent differences in filters between different landscapes.[19,50] It thus seems likely that results should differ between biomes due to the differences in climate and biogeographic history.[10,51,52] Yet even studies that have taken a global perspective have been biased in their sampling toward North America, Europe, and Australia, with a distinct lack of data from the tropics.[29,34,53] Moreover, the number of species in global trait studies has also been limited, with the largest sample size (629 species by Sayol et al.[34]) representing only ∼6% of bird species found globally. Previous studies have been restricted by the lack of bird occurrence data across urbanization gradients, particularly in the tropics,[53] but also by access to global trait datasets that have only recently become available.

Here, we combine global data on occurrence (>125 million records) from the citizen science project, eBird,[26] with a continuous measure of urbanization (night-time lights) to calculate an Urban Association Index (UAI) for 3,768 bird species (∼35% of extant bird species) in 137 cities across six continents and 11 biomes. We chose ten species-specific functional traits with globally available data and hypothesized links to urban tolerance (Table 1), and modeled UAI values as a function of these traits. We further chose three city-specific landscape variables that we predicted would influence the importance of our traits for urban tolerance,[19] assessing whether the relationships with each trait varied as a function of latitude, human population density, and landscape greenness (NDVI, Normalized Difference Vegetation Index). We present the first evidence that the importance of different traits for urban tolerance varies predictably across the planet.

RESULTS

Our analysis included 16,455 UAI estimates representing data from >125 million eBird records across 137 cities (Figure 1A). This list comprised cities from 62 countries, including 39 in North

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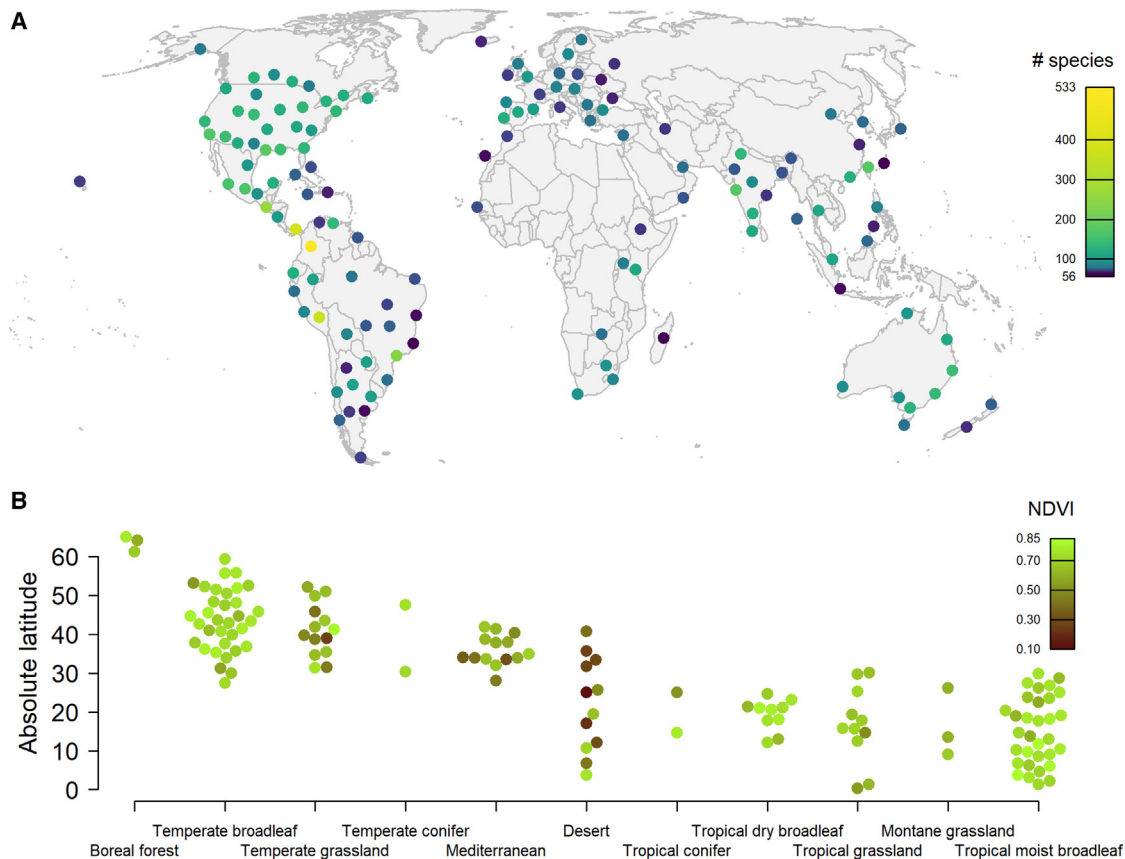
Figure 1. Geographical coverage of 137 cities included in the analysis

(A) Cities (points) were distributed across 62 countries, including 39 in North America, 28 in South America, 27 in Asia, 23 in Europe, 10 in Africa, and 10 in Australasia. Each of these cities was initially selected to have a population of ≥100,000 people and be ≥500 km apart. Cities were then retained that had ≥50 species each with ≥100 eBird records within a 100-km radius circles over 20 years (2002–2021). Cities are colored by the (log) number of species that met the criteria from 56 (dark purple) to 533 (yellow).

(B) Cities were representative of 11 of the world's biomes.[54] Biomes are ordered by the mean absolute latitude of the cities included, and cities are colored by the NDVI of the greenest month, from the greenest city (lime green) to the least green city (dark brown).

America, 28 in South America, 27 in Asia, 10 in Africa, and 10 in Australasia. Together, these cities span 11 of the world's 14 terrestrial biomes.[54] The number of avian species meeting the inclusion criteria in each city ranged from 56 in Naha (Japan) to 533 in Bogotá (Colombia).

Of the 3,768 species for which we calculated UAI, the five species present in the most urban areas were Feral (Rock) Pigeon (*Columba livia*), House Sparrow (*Passer domesticus*), Barn Swallow (*Hirundo rustica*), Osprey (*Pandion haliaetus*), and Peregrine Falcon (*Falco peregrinus*). Across species, UAI values ranged from 0 (for 46 species) to 3.97 (Yellow-crested Cockatoo—*Cacatua sulphurea*—a species introduced to Hong Kong) with a mean of 1.14 and standard deviation of 0.91. Of species present in at least ten cities, the top-five species with the highest UAI were Monk Parakeet (*Myiopsitta monachus*), Rose-ringed Parakeet (*Psittacula krameri*), Yellow-chevroned Parakeet (*Brotogeris chiriri*), Feral Pigeon, and Sayaca Tanager (*Thraupis sayaca*).

There was considerable phylogenetic signal in UAI across species (Figure 2; $\lambda = 0.61$, CI = 0.56–0.65). Notable families with high average UAI values, indicating broad urban associations, included Sturnidae (starlings; 1.75 ± 0.13 SE, $n_{species} = 40$), Apodidae

(swifts; 1.61 ± 0.12, $n_{species} = 44$), Hirundinidae (swallows; 1.55 ± 0.09, $n_{species} = 52$), Psittacidae (parrots; 1.55 ± 0.11, $n_{species} = 86$), and Icteridae (New World orioles and blackbirds; 1.47 ± 0.08, $n_{species} = 80$). Notable families with a low average UAI included Pipridae (manakins; 0.33 ± 0.07, $n_{species} = 21$), Petroicidae (Australasian robins; 0.38 ± 0.09, $n_{species} = 20$), Trogonidae (trogons; 0.45 ± 0.07, $n_{species} = 24$), Thamnophilidae (antbirds; 0.55 ± 0.06, $n_{species} = 72$), and Tinamidae (tinamous; 0.58 ± 0.09, $n_{species} = 22$).

Of the ten species-specific traits considered, all except bill shape were significantly associated with UAI (Figures 3 and 4). Body mass (Figure 3A), lower elevational limit (Figure 3E), territoriality (Figure 3F), and ground nesting (Figure 3I) were negatively associated with UAI, while hand-wing index (HWI; Figure 3B), diet breadth (Figure 3C), habitat breadth (Figure 3D), longevity (Figure 3G), and clutch size (Figure 3H) were positively associated with UAI. In other words, more urban-tolerant species are smaller, tree- or building-nesting species with higher dispersal ability, wider diet and habitat breadths, lower elevational limits, lower territoriality, longer lifespan, and greater clutch size. Of the eight significant numerical traits, those with the largest effect sizes—and therefore the
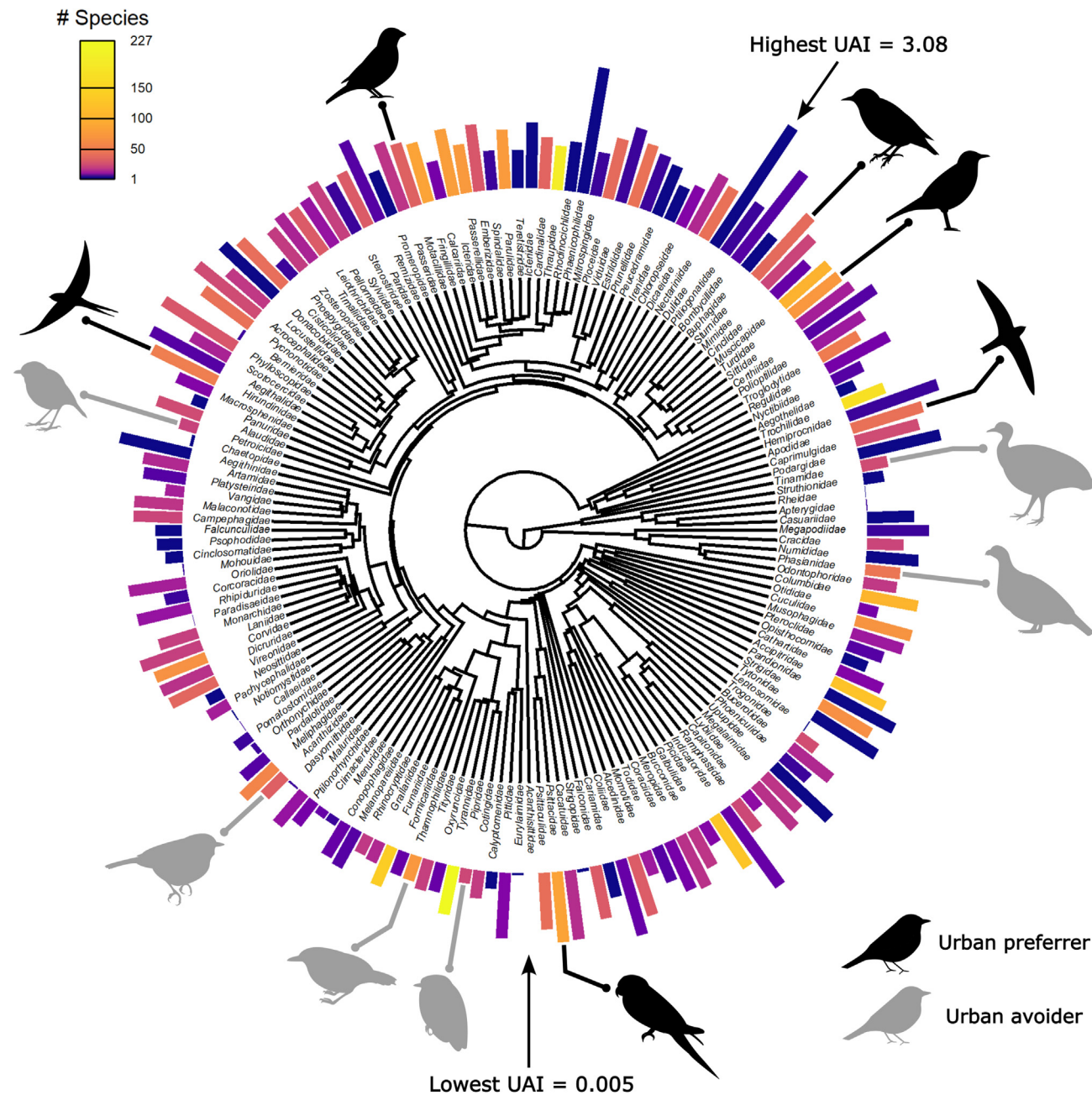
Figure 2. The phylogeny of Urban Association Index (UAI) across 3,768 species by family
For visualization, UAI values were averaged across species and then across taxonomic families. The height of the bar indicates the UAI, with taller bars indicating higher urban tolerance. The color indicates the (log) number of species in the family from 1 (dark purple) to 231 (Tyrannidae, yellow). Icons represent speciose families averaging high (black) and low (gray) UAI, respectively.

strongest relationships—were body mass and lower elevational limit, while diet breadth and HWI had the smallest effect sizes (Figure 4A). These traits were largely robust to phylogenetic non-independence, although it is possible—based on a more simplified phylogenetic model—that the effects of some traits, such as body mass and territoriality, are more phylogenetically constrained (supplemental information).

Seven of the trait relationships varied significantly as a function of city-level covariates (Figures 4 and 5). In terms of latitude

(Figure 4B), the negative association with body mass (Figure 5A) and the positive associations with diet breadth (Figure 5B) and longevity (Figure 5D) became more pronounced in cities at higher latitudes. Contrastingly, the positive association with habitat breadth (Figure 5E) and the negative association with lower elevational range limit (Figure 5G) became more pronounced in tropical cities. The association between bill shape and UAI—which showed no globally consistent relationship—varied with latitude (Figure 5H), such that species with longer, pointier bills were
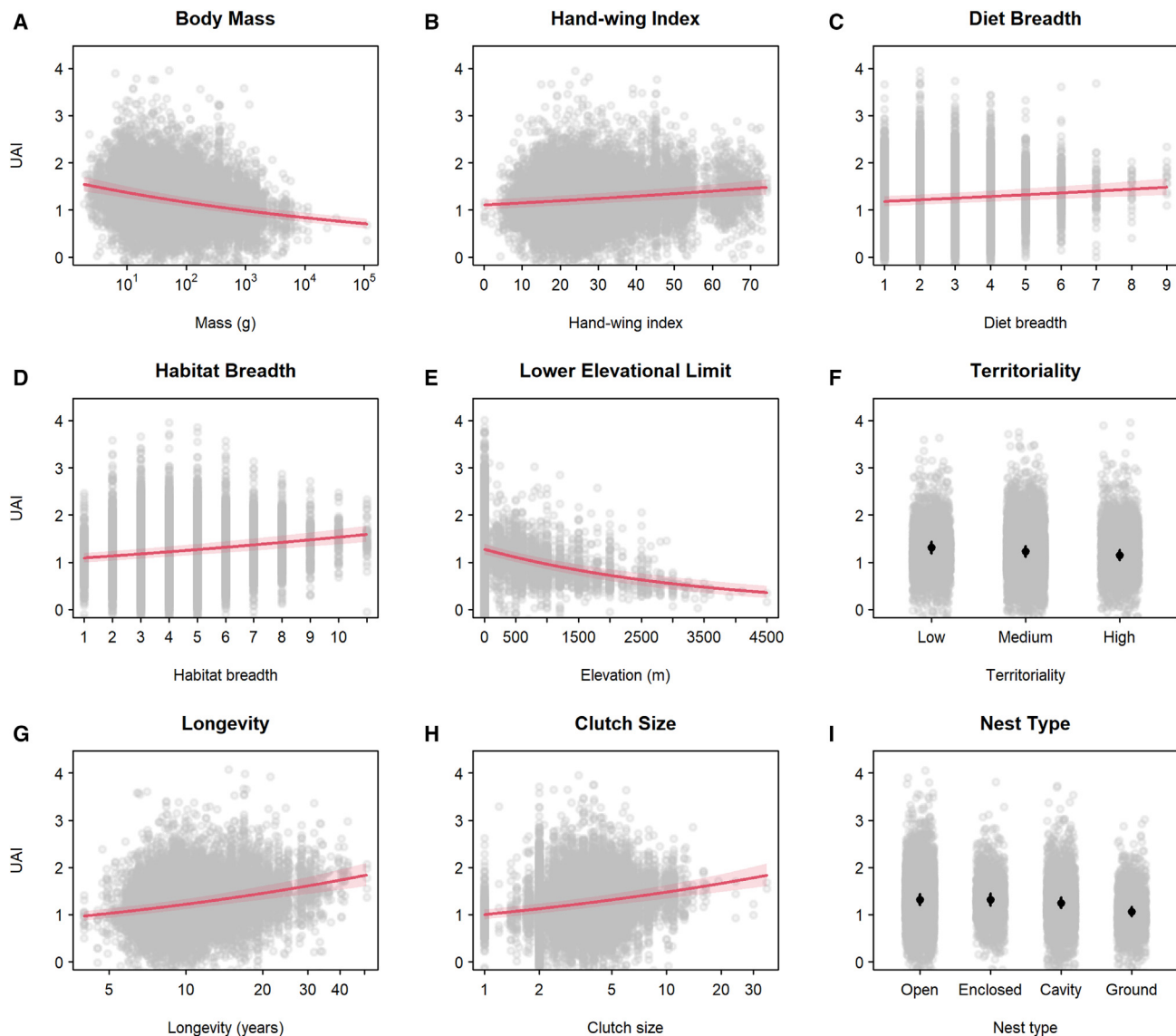
Figure 3. The global mean relationships of nine species traits with the Urban Association Index (UAI) of 3,768 bird species across 137 cities

There were significant relationships between UAI and (A) body mass, (B) hand-wing index, (C) diet breadth, (D) habitat breadth, (E) lower elevational limit, (F) territoriality, (G) longevity, (H) clutch size, and (I) nest type. Gray points show the partial residuals of each data point. Trend lines for numerical traits are shown along with the 95% credible intervals. Territoriality is treated as numerical in the model, but here we summarize the data for the three levels of territoriality (low, medium, high). Nest type is treated as categorical in the model (open, enclosed, cavity, or ground). For territoriality and nest type, black points show the mean and bars show the 95% credible intervals.

more urban tolerant at higher latitudes while species with shorter, thicker bills were more urban tolerant at lower latitudes. In terms of population density (Figure 4D), the negative association with territoriality (Figure 5C) and the positive associations with diet breadth (Figure 5F) and longevity (Figure 5I) became more pronounced in cities with a lower population density. Finally, none of the nine numerical trait relationships varied significantly as a function of landscape greenness (Figure 4C).

DISCUSSION

Many studies have linked species-specific functional traits to urban tolerance,[25,29,41,34] but none have tested for interactions between traits and geographic factors, especially not at the global taxonomic and spatial scale that we employ here. For 35% of the world's bird species across 137 cities and 11 biomes—including regions of the world underrepresented in ecological studies (i.e., Asia, Africa, South America[53,55])—we find that nine different functional traits are significantly related to urban association. Furthermore, we find that two geographic variables—latitude and human population density—significantly modulate the associations of seven of these traits, meaning that the strength of trait-based filters in urban environments varies systematically across the planet.[19,50] Our study is the first at a global scale to demonstrate the relationships between urban association and body size, HWI, diet breadth, lower elevational
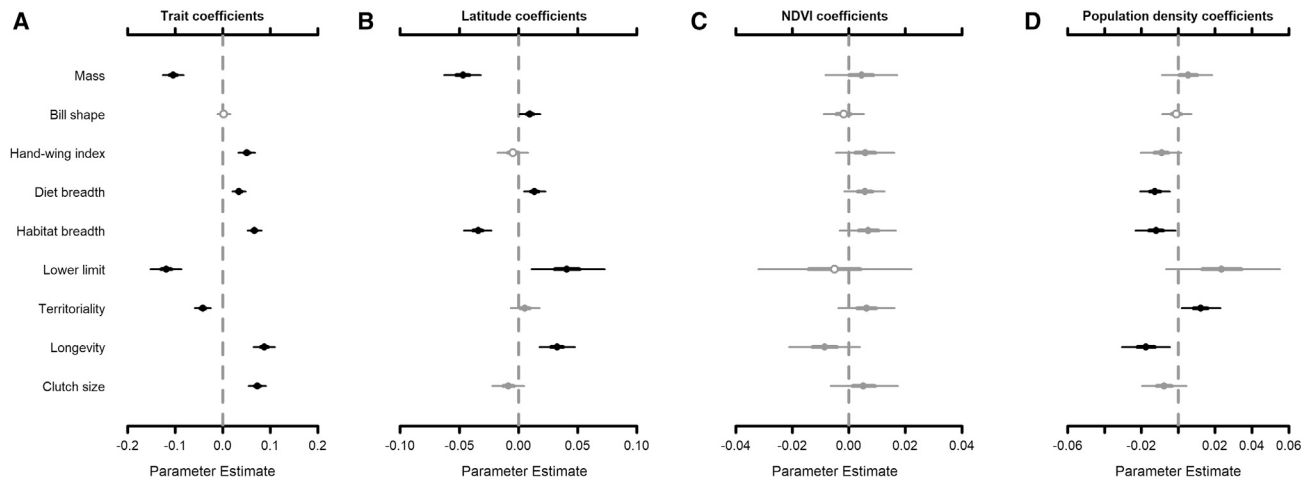
Figure 4. The relationship between Urban Association Index (UAI), species traits, and city variables for 3,768 birds species across 137 cities
(A) Covariate coefficients (β) show how UAI varies as a function of nine numerical trait covariates.
(B–D) In turn, these trait coefficients vary across cities as a function of three city-level variables with corresponding coefficients (θ): (B) latitude, (C) NDVI, and (D) human population density. Points show the posterior mean covariate coefficient estimates with corresponding interquartile range (thick lines) and 95% credible intervals (thin lines). Points are open when the interquartile range overlaps 0. Points and lines are gray when the 95% credible intervals overlap 0 and black when they do not.

limit, territoriality, longevity, and clutch size, and confirms the positive association of habitat breadth and the negative association of ground nesting.[29,35] Although our study includes introduced species for which traits are important in successful establishment,[56,57] such species comprise <4% of the dataset. Our results, therefore, pertain generally to the filtering of native species. Of the nine numerical traits, lower elevational limit was the strongest predictor (i.e., largest effect size) of UAI. In general, cities are located in lowland areas—e.g., 80% of our focal cities are <500 m in elevation—so it makes sense that cities would tend to favor species whose lower range limits encompass lowlands.

In our study, urban-associated species tended to have wider diet and habitat breadths (Figures 3C and 3D), confirming the role of ecological generalism in urban tolerance.[25,46,31,35] These traits have also been shown to predict invasion success,[56] which is pertinent for the ~3% of exotic species in our dataset. Although the effect size for diet breadth was relatively small compared with the other traits (Figure 4A), an increase in UAI from 1 to 1.5 with increasing diet breadth (Figure 3C) would still take a species from being relatively urban avoiding (34th percentile of UAIs) to being relatively urban tolerant (60th percentile). As cities erase or erode most native habitats,[2] ecological specialists are less able to survive while more versatile species persist. However, we found that the importance of diet and habitat breadth had opposing patterns across latitude (Figures 5B and 5E). Habitat breadth was more important in tropical urban areas, possibly because most tropical land birds have high forest dependency[58] and thus are more likely to experience a stronger filter in urban areas.[59] But with fewer habitats to specialize on toward the poles, habitat breadth becomes less important at higher latitudes. By contrast, diet breadth was more important in temperate areas. Many urban-associated tropical birds are dietary specialists, particularly nectarivores and frugivores, where they take advantage of plentiful year-round fruiting and flowering

ornamental trees.[60] Temperate cities, with seasonal resource pulses and troughs, favor omnivores that can make use of a wide variety of food sources.[6,11,32,43]

Related to diet, the relationship between beak shape and urban association changed sign with latitude (Figure 5H). In the tropics, species with short, thick bills were favored in urban areas, a result that may be explained by the abundance of specialist frugivores in fruit-plentiful tropical cities, exemplified by urban-tolerant parrots (Cacatuidae, Psittaculidae, Psittacidae). At more temperate latitudes, species with short, stubby bills tend to be granivores and also tend to avoid urban areas where grasses are cut short. Although the occasional short, stubby bill does well in temperate urban environments (e.g., House Sparrow or House Finch, *Haemorhous mexicanus*), many temperate granivores such as game birds (Phasianidae), longspurs (Calcariidae), and grassland sparrows (Passerellidae) require suitable habitat far from development.[25,32] Meanwhile, the hummingbirds (Trochilidae)—long-billed species with high data leverage—present an interesting outlier. In the Neotropics, where their diversity peaks, only a fraction of species are found in urban areas,[61] such as Panama City, while in North America, most hummingbird species frequent urban feeders.[62,63] Variation in the importance of bill shape is clearly complex, underscoring the diverse responses of different feeding guilds to urbanization.[6,25,36,43]

Previous studies have suggested that migratory strategy was not associated with urban tolerance,[6,25,34,39,40,43] while only one study has found dispersal ability per se to be related to urban association.[41] We found, however, that species with higher HWI (i.e., longer, more pointed wings, associated with greater dispersal ability[64]) have higher UAI values (Figure 3B), albeit with a lower effect size than other traits. Although dispersal ability is positively associated with migratory capacity,[64] previous studies focusing on temperate cities may not have found a role

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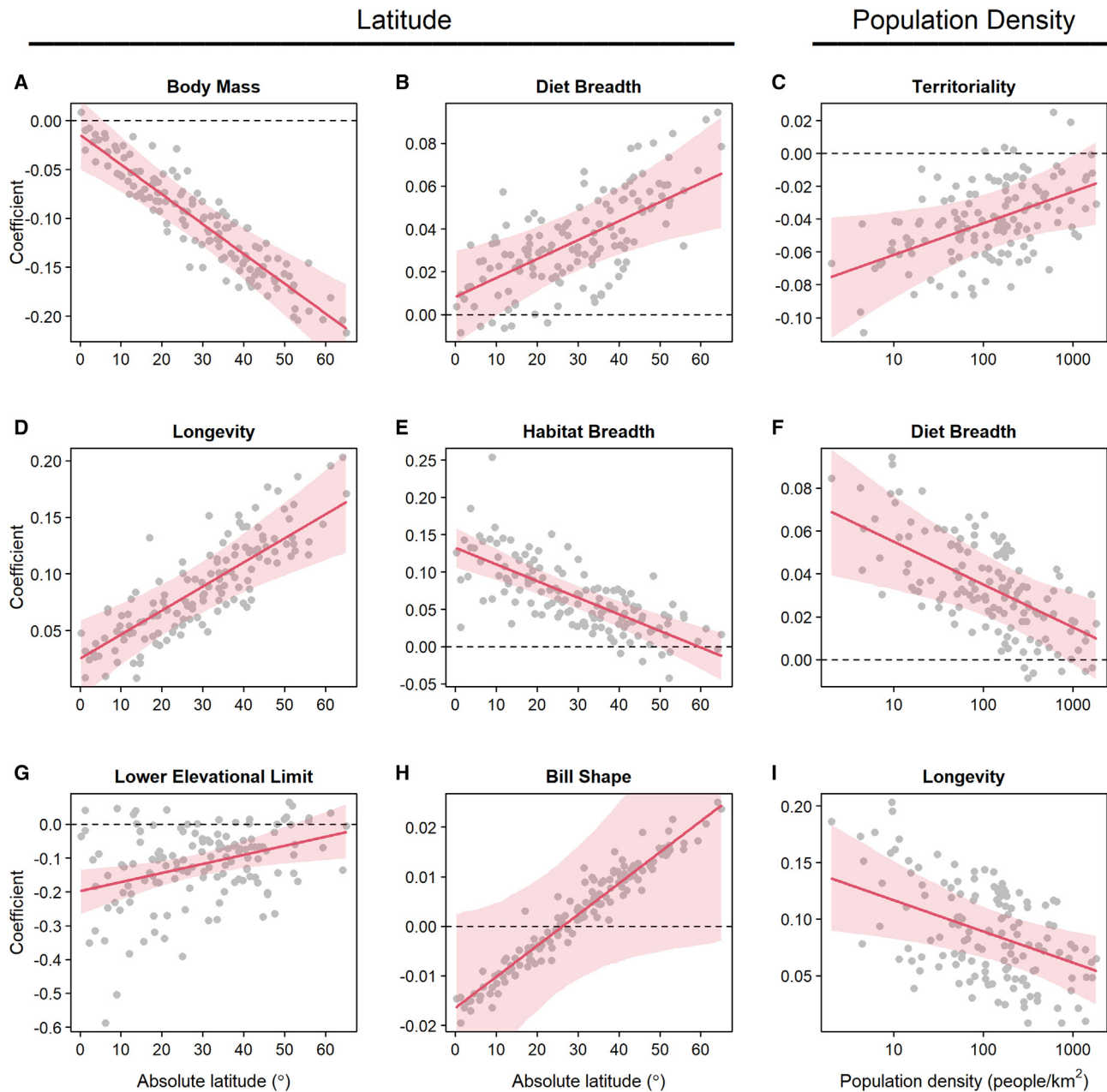
Figure 5. Variation in UAI-trait associations by city as a function of latitude and human population density

(A, B, D, E, G, and H) Latitude was significantly associated with the city-level trait coefficients for (A) body mass, (B) diet breadth, (D) longevity, (E) habitat breadth, (G) lower elevational limit, and (H) bill shape.

(C, F, and I) Human population density was significantly associated with the city-level trait coefficients for (C) territoriality, (F) diet breadth, and (I) longevity. Points represent the model-estimated trait coefficients for each city (n = 137). Trend lines and 95% credible intervals show how these coefficients vary as a function of the city-level covariates.

for migratory capacity as migrants tend to broaden their habitat use to include cities on migration routes and in their tropical wintering grounds.[65] Thus, urban tolerance within a continent does vary across the annual cycle,[66] and future studies focusing on migrants could test explicitly how urban tolerance varies between breeding, migratory, and wintering ranges. Overall, our observed relationship of HWI to UAI could be driven by a number of factors, including the sensitivity of low-dispersal species to

anthropogenic change[67] and the association between HWI and specific foraging modes, such as flycatching, aerial insectivory, frugivory, and nectarivory (as opposed to gleaning, terrestrial insectivory, etc.) that would be favored in urban environments.[64,68]

The role of body size in urban tolerance has mixed support, including a positive association in Australia[25] and a negative association for raptors,[33] but no effect globally across 358 species.[29] Here, body mass had one of the largest effect sizes, and

we found that urban-tolerant species are significantly smaller, a relationship (Figure 3A) that strengthens toward the poles (Figure 5A). Many families of large species, such as bustards (Otididae), tinamous, and pheasants, appear to avoid urban areas (Figure 2). These species tend also to be cursorial, which could put them at elevated risk of urban-associated predators (e.g., domestic cats[69]) and nest predators (e.g., rats[70]). In the tropics, these families of large species might be balanced out by urban-tolerant arboreal-nesting large hornbills (Bucerotidae), turacos (Musophagidae), parrots, and cockatoos.[38] In temperate regions, game birds are likely selected against in urban areas due to habitat requirements, the history of hunting, or pressure from meso-predators.[71]

Supporting results from other studies,[11,25,41] we found that species with larger clutches were more urban tolerant (Figure 3H). Species with larger clutch sizes tend to live at the faster end of the life-history continuum and may be able to adapt faster to novel environments.[41] Conversely, however, we found that species with longer lifespans were also more urban tolerant (Figure 3G), corroborating the findings that urban-tolerant species also have higher annual survival rates[41] and longer lifespans.[32] One possibility is that living longer allows more reproductive attempts given the uncertainties of the urban environment—a factor that also facilitates invasion success.[57] Alternatively, long-lived species are also more intelligent species.[72] The role of brain size in urban tolerance appears linked to other life-history strategies, with big brains important for species with high brood value (i.e., fewer broods over a lifetime), whereas small brains predominate in species with low brood value.[34] Although we lacked the data to test this hypothesis globally across our full species set, our results suggest a similar trade-off—that it helps to either have large clutch sizes or live longer in order to learn to exploit urban environments. The importance of longevity also increases in temperate cities (Figure 5D), suggesting that living longer and, perhaps, being smarter are more beneficial closer to the poles, where having more experience surviving the winter is often critical.

Certain aspects of breeding biology were also tied to urban tolerance. Although we did not test sociality per se (a trait which is not available broadly), we did find a significant negative association with territoriality (Figure 3F). Urban-tolerant species tend to be more social or gregarious[29,32,36] and therefore less territorial. Being strongly territorial year-round (level 3 on the scale) is usually tied to defense of resources,[47] and in resource-poor cities it makes less sense to be territorial and more sense to follow resources more plastically. Where species nest also matters, and we confirm the results of other studies that ground-nesting species tend to be less urban-tolerant.[29,38,39,30,40] Species that nest above the ground with open or enclosed nests have the highest urban tolerance (Figure 3I), probably due to safety from predators,[73,74] with evidence that urbanized populations switch to nesting above ground.[75] Some studies have suggested that cavity nesters have higher urban tolerance,[38,32,73] while others have suggested the opposite.[6] We found intermediate UAI values for cavity nesters, perhaps reflecting the contrast of relative success of cavity nesters with lower availability of nest cavities in urban areas.[76]

The associations between UAI and territoriality, diet breadth, and longevity were all reduced in cities with higher population density (Figures 5C, 5F, and 5I). As population density is calculated across the whole 100-km radius circle, it is possible that the most densely populated cities are more homogenous with less non-urban habitat for urban avoiders. For example, Anchorage (USA) and Reykjavík (Iceland) are small cities surrounded by wilderness, where habitats strongly differ between urban and non-urban areas. In contrast, cities like Bangkok (Thailand) and İstanbul (Turkey) are vast sprawling metropolises with abundant feral predators such as cats and where there is little room for specialized, territorial urban avoiders. Finally, we did not find that any trait relationships varied as a function of landscape greenness, indicating that ecological filters in urban areas are similar for cities at the same latitude that differ in greenness, a measure driven in large part by habitat (Figure 1B). Further studies could investigate additional covariates that might explain these spatial nuances.

In summary, we found that numerous species-specific functional traits (smaller body size, lower territoriality, greater dispersal ability, broader dietary and habitat niches, larger clutch sizes, greater longevity) predict urban tolerance across the planet. However, many of these trait relationships are modulated by landscape-level properties, most notably latitude. That is, some degree of spatial non-stationarity[77] exists in the urbanization-trait relationships. Where previous studies have demonstrated the importance of certain traits in certain parts of the world, we demonstrate the importance of geography in determining trait-based urbanization filters[50–52,78] at an unprecedented taxonomic and spatial scale. Moreover, much of the region-specific variation in previous trait-seeking studies could be due to the predictable geographic variation in trait strength that varies with latitude and human population density. Studying how traits filter diversity across the globe moves us toward a more predictable framework that will better allow us to understand future biodiversity loss—and how we might mitigate it—given the expected future expansion of urban areas.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Data filtering
  - City selection
  - Urbanization association index (UAI)
  - The effect of spatial mismatch between VIIRS and eBird checklists
  - The effect of uneven eBird sampling
  - Comparison of UAI to logistic regression of presence/absence

Current Biology
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- ○ Comparison of UAI to an index based on relative abundance
- ○ Species traits
- ○ City variables
- ● QUANTIFICATION AND STATISTICAL ANALYSIS
  - ○ Modeling
  - ○ Phylogenetic non-independence

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
UAI and city-level data	This paper	https://doi.org/10.6084/m9.figshare.21779150
eBird data	eBird	https://science.ebird.org/en/use-ebird-data/download-ebird-data-products
City dataset	OpenDataSoft	https://public.opendatasoft.com/explore/dataset/geonames-all-cities-with-a-population-1000/table/?disjunctive.cou_name_en&sort=name
VIIRS night-time lights	Elvidge et al.[79]	https://doi.org/10.1080/01431161.2017.1342050
AVONET trait data	Tobias et al.[27]	https://doi.org/10.1111/ele.13898
BirdBase trait data	Şekercioğlu et al.[44]	https://doi.org/10.1073/pnas.0408049101
Clutch size data	Myhrvold et al.[49]	https://doi.org/10.1890/15-0846R.1
Longevity data	Bird et al.[48]	https://doi.org/10.1111/cobi.13486
Global bird species accounts	Birds of the World	https://birdsoftheworld.org/bow/home
NDVI data	USGS	https://lpdaac.usgs.gov/products/mod13a3v061/
Human population density data	NASA	https://sedac.ciesin.columbia.edu/data/collection/gpw-v4

RESOURCE AVAILABILITY

Lead contact
Requests for further information should be directed to and will be fulfilled by the lead contact, Montague Neate-Clegg (monteneateclegg@gmail.com).

Materials availability
This study did not generate new materials.

Data and code availability

- All UAI estimates and city-level data have been deposited on FigShare and are publicly available as of the date of publication. Trait data can be accessed/requested from the cited sources. DOIs and websites are listed in the key resources table.
- The code specifying the model is available on FigShare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The full eBird dataset was downloaded from eBird.[26] The city dataset came from OpenDataSoft.[80] Trait data were extracted mainly from AVONET[27] and BirdBase[44] (see also Table 1). Territoriality data came from Tobias et al.,[47] Longevity data from Bird et al.,[48] and clutch size data were augmented from Myhrvold et al.[49] Remaining trait gaps were filled with information from Birds of the World.[45] Finally, NDVI data were extracted from USGS,[81] while human population density data came from NASA.[82]

METHOD DETAILS

Data filtering
eBird is a semi-structured citizen science platform that is increasingly being used to reliably estimate bird occurrence.[83–87] We downloaded the global eBird basic dataset[26] including all records up until February, 2022 (v1.14). We restricted the dataset to the years 2002–2021 – the 20 complete years before present. We then limited eBird protocol types to "traveling", "stationary", and "area". We removed incomplete checklists – where a species may have been observed but not recorded. Following eBird best practices,[86] we removed checklists with >10 observers, with durations >5 hr, with distances >5 km (for "traveling" protocol), and with areas >500 ha (for "area" protocol). For group checklists involving duplicate records, we randomly retained one checklist per group. Finally, we

removed records that were not identified to species level, including all hybrids, intergrades, "slashes" (e.g., "Greater/Lesser Yellowlegs"), indefinite species (e.g., "hummingbird sp."), and domestics. We made a single exception to these exclusions, retaining the widespread, ubiquitous, and domesticated Feral (Rock) Pigeon (*Columba livia*), as it is a key avian species in many cities. Although some species in our dataset are introduced in some cities, they are native in others (e.g., *Passer domesticus*, *Sturnus vulgaris*). Introduced species on average comprised <3% of species per city. We therefore chose not to remove or classify species based on being exotic, in part because we wanted to explain their urban tolerance based on their intrinsic traits, not their extrinsic history which also depends on traits.[56,57] Finally, we restricted our dataset to exclude water birds (∼15% of the species set) since they have substantially different natural histories and traits compared to land birds.[25]

City selection

We define a "city" as a municipal center with a population of at least 100,000 people. We chose this relatively low population cut-off to include smaller, remote cities in ecologically distinct regions – including Darwin (Australia), Punta Arenas (Chile), and Reykjavík (Iceland). To select cities for use in our study, we downloaded the dataset "Geonames – All Cities with a population > 1000" from the data repository OpenDataSoft,[80] and reduced the dataset down to cities with a population >100,000, yielding 4643 cities. We then calculated the pairwise distance between every city using the package *geodist*.[88] Starting with the cities with the largest populations, we sequentially removed all smaller cities within 500 km of the larger city in order to produce a set of non-overlapping, spatially independent cities. This algorithm retained 289 cities separated by at least 500 km. After identification of these target urban areas around the world, we filtered the eBird dataset to checklists within a 100 km radius of each city center. This radius was chosen to include the whole metropolitan area as well as surrounding habitats that might supplement the species pool, although varying the radius led to qualitatively similar results in another study.[89] For each city dataset (hereafter "city"), we removed species with <100 records, as well as species that comprised <0.01% of all occurrences per city. The first filter ensured a minimum data requirement while the second filter was a threshold intended to filter out vagrant species while retaining scarce but expected species. As some cities lacked 100 records for even one species, we removed any city with <50 species remaining after restricting species to ≥100 records, such that all remaining cities had ≥5000 bird records. This 50-species threshold was chosen in order to remove cities that contained only a handful of species that would tend to be more urban associated (high UAIs), but to retain cities in environments with low species richness (e.g., boreal regions) that would have been removed if the threshold was 100 species. Our final dataset contained 127,046,578 eBird occurrence records of 3768 species across 137 cities (Figure 1A).

Urbanization association index (UAI)

To quantify species' relationships with urban areas, we aimed to create a globally applicable continuous metric of urban association that would avoid the assumptions of using arbitrary thresholds to categorize species based on urban tolerance.[25,90] Following Callaghan et al.,[25] we downloaded the VIIRS night-time lights imagery (Annual VNL V1[79]), a composite global image of night-time lights for the year 2016 with 15-arc-second resolution. Although 2016 is not the mid-point of the eBird data (2012), it is close to the mean year of all checklists (2017). We chose light radiance as a proxy for urbanization because we wanted a globally available continuous measure that reflected human development in built-up areas, as opposed to human population density *per se*.[79,91,92] For example, industrial zones can be highly urbanized but low in population density. Metrics based on night-time lights that use eBird data are correlated with other measures of urban tolerance based on relative abundance data.[89,90] From this imagery, we extracted the radiance value for every eBird checklist locality (i.e., the unique latitude/longitude coordinates associated with a checklist).

As radiance values start at 0 (total darkness) and increase exponentially, we added 1 then log-transformed all radiance values to reduce the leverage of extremely bright buildings. Then, for every species within each city, we calculated the mean radiance value of all occurrence records, including multiple presences from the same location but on different checklists. Given this incidence data, the mean radiance value of a species indicates its tendency toward relatively more or less urban areas, as compared to other species in the city. We chose to use the mean radiance instead of the median[25] because we found that many species had a median radiance of 0, as they occurred predominantly in non-urban areas. Moreover, the distribution of mean radiance values of species within cities was fairly normal (Figure S1), while the distribution of median radiance values was heavily right skewed. We then took additional steps to validate our metric by comparing it with other formulations of urban association (see below). Ultimately, since our metric was highly correlated with all these other metrics (Figures S2–S4), we decided to retain our metric for the primary analysis as it is the simplest to implement while using all the data. Thus, our Urban Association Index (UAI) for each species is the mean of the transformed radiance values across eBird records, where the radiance value of each record is taken from a single pixel of night-time lights.

Cities vary greatly in their baseline brightness – i.e., size and level of development – and so the expected UAI of species will also differ between cities, with the same species potentially having very different UAIs depending on the brightness of the city. However, what matters for our analysis is that the UAIs for different species are compared relative to one another within cities. For example, in a relatively "dark" city, all species will tend to have low UAIs, but the most urban-associated species will still have the highest UAI within that city. Our hierarchical modeling approach (see below) accounts for these differences in city-level brightness through the use of city-specific intercepts for UAI.

The effect of spatial mismatch between VIIRS and eBird checklists

The VIIRS night-time lights imagery has a spatial resolution of ∼500 m, much finer than the 5 km filter applied to eBird checklists, and so a single point value may not be representative of the landscape sampled during a specific checklist. To check whether this

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affected our index, we experimented on six example cities, one from each continent (Los Angeles, Buenos Aires, London, Nairobi, Mumbai, Sydney). For every checklist locality within each city, we sampled 100 points from a bivariate normal distribution of latitude and longitude centered on the checklist locality, with a standard deviation of 1 km, truncating values >5 km from the locality. This sampling approach created a scatter of points around the locality, from which a mean radiance value can be calculated. From these mean estimates, we then calculated the mean radiance values for each species across localities. We found that these species-level estimates based on the sampled points were highly correlated with the estimates based on single radiance values per locality (r = 0.97–0.98; Figure S2A). Thus, our Urban Association Index (UAI) for each species is the mean radiance value across records where the radiance value of each record is taken from a single pixel of radiance.

The effect of uneven eBird sampling
Birdwatchers do not visit all levels of urbanization with equal effort, biased often towards greener spaces within urban environments. We tested whether this uneven effort affected our index for the same six cities as above. We classified the night-time lights level of every eBird locality into four categories from 1 to 4 by rounding up the radiance value of each locality. All radiance values above 4 (of which there are few) were also categorized as level 4. We then calculated which category had the fewest checklists and randomly subsampled the other categories without replacement so that they had the same number of checklists. Thus, each night-time lights level received the same number of checklists. We then calculated the UAI of each species as before. We repeated this process 100 times and took the mean UAI for each species. We found that these estimates based on equal sampling of light levels were highly correlated (r = 0.88–1; Figure S2B). Thus, our UAI is robust to uneven sampling of light levels.

Comparison of UAI to logistic regression of presence/absence
An alternative way to estimate urban tolerance is to model presence/absence, which we did for the six example cities. As we only use complete checklists, we can assume that a species not present on a checklist is absent. For each species we used a binomial GLM to model its presence/absence across all checklists (binary 0 or 1) as a function of the radiance value of each checklist. We then extracted the slope coefficient, i.e., the effect of radiance on the probability of occurrence. We found that these coefficients were highly correlated with our UAI estimates (r = 0.89–0.99; Figure S3). The relationships were somewhat curvilinear, which is to be expected due to the link function in the GLM. Thus, our UAI is a good predictor of the effect of urbanization on presence/absence. In fact, our metric is arguably better, as the logistic regression method causes species at the tails of urban tolerance to have more spread-out estimates.

Comparison of UAI to an index based on relative abundance
Intensive survey effort can be used to calculate the relative abundance of bird species in different habitats. Sayol et al.[34] used survey data from 27 cities to calculate the abundance of bird species in urban and wild habitats and then calculated the difference between the two – log(urban abundance)-log(wild abundance) – to produce an index of urban tolerance. Of these cities, seven are shared with our analysis: Barcelona (Spain), Fukuoka (Japan), La Paz (Bolivia), Las Palmas (Spain), Madrid (Spain), Melbourne (Australia), and Saskatoon (Canada). In addition, Palo Alto (USA) in their dataset was close enough to San Francisco to warrant comparison. For each city, we compared our UAI with their urban tolerance index. In general, we found that these indices were highly correlated (r = 0.70–0.81; Figure S4). La Paz had a low coefficient (0.31), perhaps due to the low sample size of nine species.

Melbourne had an even lower correlation coefficient (0.22). To check whether this was a local artefact, we made an additional comparison between our UAIs for Sydney and their estimates for Newcastle, two cities in New South Wales, Australia. These estimates were fairly well-correlated (r = 0.62). For Melbourne, differences in the indices could arise based on the very low abundances recorded in Sayol et al.'s dataset (mean across species = 3.6). We further investigated one of the biggest discrepancies in Melbourne, the Australian Raven (*Corvus coronoides*). This species had the lowest UAI but second-highest urban tolerance index which was based on an urban abundance of 2 and a wild abundance of 0. By inspecting its eBird records:

(https://ebird.org/map/ausrav1?neg=true&env.minX=106.09015916480298&env.minY=-41.48680020779488&env.maxX=160.933909164803&env.maxY=-12.82630044231655&zh=true&gp=false&ev=Z&excludeEx=&mr=1-12&bmo=1&emo=12&yr=cur) we could see that Australian Ravens do appear to be largely absent from the city itself and so we believe our UAI better captures that relationship than an index based on very low abundance levels. Thus, in general, our UAI appears to be a good predictor of the relative abundance of birds in urban versus wild habitats, except when that abundance data is low.

Species traits
We chose species-specific functional traits that have been linked to urban tolerance in the past and/or traits that we hypothesized would predict urban tolerance that have not been tested globally. We chose traits that were available for the entire species set and, where possible, we chose numerical (rather than categorical) traits in order to reduce the number of parameters estimated. We therefore did not use traits such as residual brain size or competitive ability where the data does not exist for all species[34,37] and excluded categorical traits with many levels, such as primary diet. Traits for every species were then extracted from several datasets, as follows (Table 1).

From the publicly available AVONET[27] we extracted body mass, four bill measurements (length from culmen, length from nares, width, and depth), and hand-wing index (HWI). These data were complete for all species. To reduce the four bill measurements

down to a single axis, we conducted a PCA on the variables and extracted the second principal component, ignoring the first principal component, which is highly correlated with body size.[93] This second principal component – which we refer to as "bill shape" – represents a spectrum from long, thin, pointy bills (e.g., *Ensifera ensifera*) to short, thick bills (e.g., *Callocephalon fimbriatum*), a spectrum associated with foraging specializations.[93] HWI is a proxy for dispersal ability,[64] essentially capturing the "pointiness" of a wing by measuring the ratio between wing length and Kipp's distance (the distance between the longest primary feather and first secondary feather). HWI has not been tested as a global predictor of urban tolerance but is highly correlated with several ecological factors, including primary diet and habitat type.[64]

From the dataset BirdBase[44,94] we extracted diet breadth, habitat breadth, lower elevational limit, clutch size, and nest shape/substrate. Diet breadth is the number of major food groups (1–9) that a species eats (e.g., invertebrates, fruit, seeds) while habitat breadth (1–11) is the number of major habitats where a species is found (e.g., forest, grasslands, desert). Lower elevational limit was included because we hypothesized that cities – which tend to be found non-randomly at lower elevations[95] – would favor species that occur at lower elevations. Nest shape and nest substrate were originally sourced as two separate data columns, but we collapsed these into one. As there was no way to define these nests numerically by shape and substrate, we instead defined four categories: ground (nests of any form located on the ground), cavity (nests above ground in cavities or crevices), open (nests above ground with open tops such as cups, saucers, and platforms), and enclosed (nests above ground with entrance holes such as spheres, pendants, and domes). Clutch size data were augmented with data from an existing published dataset,[49] while further gaps in BirdBase variables were filled using the online database Birds of the World.[45] Where information was lacking for a species, missing values were inferred from close extant relatives with complete data. Finally, longevity (a measure of lifespan) and territoriality (a scale from 1 to 3 where 3 is more territorial) were extracted from published datasets.[47,48] Once assembled, we had complete data for ten functional traits: body mass, bill shape, HWI, diet breadth, habitat breadth, lower elevational limit, territoriality, longevity, clutch size, and nest type (Table 1).

Trait variables were transformed, as necessary, prior to analysis. Given expected non-linear relationships, we took the log of body mass, longevity, and clutch size. We then scaled and centered all numerical traits (Table 1) to have a mean of 0 and a standard deviation of 1. Correlation between traits was generally low (Table S1), except between body mass and longevity, but all variance inflation factors were low (<3).[96]

City variables

For each 100 km-radius city circle we gathered data on three covariates that we hypothesized would alter the importance of traits: latitude, greenness, and population density. We chose numerical covariates in order to reduce the number of parameters, as each new city covariate adds nine parameters (one for each numerical trait) to the model. However, combined, latitude and greenness cover much of the variation among biomes (Figure 1B).

Many factors vary with latitude including climate, species richness, and human development, so there are many possible avenues through which latitude could affect urban tolerance. For example, the stability of tropical climate and ecosystems[97] may mean stronger filters in urban areas against ecological specialists in the tropics compared to temperate regions.[59] We extracted the latitude of each city from the same Geonames dataset as the city populations.

The amount of greenness in a city – whether tree cover or vegetation diversity – is an important predictor of bird diversity in cities.[16–18,20–22] Moreover, overall greenness of the landscape depends on the primary habitat. For example, desert cities such as Phoenix (USA) and Dubai (UAE) are greener than the surrounding landscape while forest cities such as Iquitos (Peru) and Nashville (USA) are less green than the surroundings. We thus hypothesized that the amount of greenery in the city radius would also alter trait filters.[19] For example, less green landscapes with fewer resources may select for habitat generalists or more mobile species in non-urban habitats. We used NDVI (Normalized Difference Vegetation Index) as a measure of the greenness within 100 km of each city center, derived from the MOD13A3 product.[81] This product provides 1 km monthly NDVI values globally, excluding water bodies. We calculated the mean NDVI values within the 100 km buffer of each city for each month for the year 2021 and retained the maximum NDVI value. We used the maximum NDVI value as each city has a different seasonal cycle over which greenness is likely to vary (i.e., greenness peaks in some cities in August, while in January in others).

Human population density has been linked to taxonomic and functional diversity in cities.[19,23] We hypothesized that cities with higher population densities may present strong selection pressures against species that are, for example, larger with narrower diets. To obtain population density (number of people/cell), we downloaded Gridded Population of the World data from the Center for International Earth Science Information Network.[82] The data are available on 5-year intervals between 2000–2020. We used 30 arc-second resolution population size for the year 2015 as the year closest to the VIIRS imagery and the mean year of eBird records. We buffered city midpoints by 100 km and extracted the mean value of the gridded density data within each buffer.

We calculated the absolute value of latitude and the log of population density. All three city covariates were then scaled and centered.

QUANTIFICATION AND STATISTICAL ANALYSIS

Modeling

We modeled UAI values as a function of traits and city variables in a Bayesian hierarchical framework that accounted for the random effects of city and species. We modeled the effect of the ten species traits on UAI with the following structure:

Current Biology
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$$y_{ij} \sim Gamma\left(\zeta_j, \frac{\zeta_j}{e^{\mu_{ij}}}\right)$$

$$\mu_{ij} = \alpha_{ij} + \delta_1 \cdot enclosed_i + \delta_2 \cdot cavity_i + \delta_3 \cdot ground_i +$$

$$\beta_{1j} \cdot mass_i + \beta_{2j} \cdot beak_i + \beta_{3j} \cdot HWI_i + \beta_{4j} \cdot DB_i + \beta_{5j} \cdot HB_i +$$

$$\beta_{6j} \cdot elevation_i + \beta_{7j} \cdot territory_i + \beta_{8j} \cdot longevity_i + \beta_{9j} \cdot clutch_i,$$

where the estimated mean UAI, y_{ij}, for species i in city j was modeled as a gamma-distributed random variable with a city-specific shape parameter ζ_j and a rate parameter equal to $\frac{\zeta_j}{e^{\mu_{ij}}}$. We chose a gamma distribution to reflect the fact that our response variable was bounded by 0 on the lower end and right skewed. The shape of the distribution was allowed to vary among cities to accommodate variation in the data. In turn, μ_{ij} was modeled as a linear combination of an intercept for open nesters, α_{ij}, three differences in intercepts (δ_1 to δ_3) and nine covariates with corresponding parameters (β_{1j} to β_{9j}). The parameters δ_1 to δ_3 represent the difference in UAI for three dummy variables (*enclosed*, *cavity*, and *ground*) that together encode the three other nest types, where all three covariates are binary (1 = species' nest type, 0 = otherwise) and mutually exclusive. The parameters β_{1j} to β_{9j} represent the slopes of the effects of nine numerical traits on μ_{ij}.

The intercept α_{ij} can be further decomposed,

$$\alpha_{ij} = \gamma + \eta_i + \omega_j,$$

into a global intercept, γ, and the random effects of species, η_i, and city, ω_j. The random effect of species accounts for species being represented across multiple cities that differ in their light levels. Critically, the random effect of city allows species in different cities to have different expected UAIs based on unmodeled factors such as differences in brightness, development, and birdwatching effort. For example, species from brighter cities will tend to have higher UAIs while species from darker cities will have lower UAIs. UAIs are thus modeled relative to city-specific mean intercepts such that a high UAI in a dark city and a low UAI in a bright city are not equivalent even if they share the same value.

The random effects of species identity,

$$\eta_i \sim t(0, \sigma_\eta, \kappa),$$

were drawn from a t-distribution with a mean 0, standard deviation σ_η, and degrees of freedom κ (which controls the degree to which the distribution resembles a normal, as κ approaches infinity, or a Cauchy, as κ approaches 1). The choice of t-distribution allowed for fatter tails in the distribution of intercepts across species. The random effects of city,

$$\omega_j \sim Normal(0, \sigma_\omega),$$

were drawn from normal distributions with mean 0 and standard deviation and σ_ω.

In order to integrate the city covariates with the functional traits, every β_j parameter for trait k was drawn from a normal distribution

$$\beta_{kj} \sim Normal(\nu_{kj}, \sigma_{\beta_k}),$$

with a mean ν_{kj} and a standard deviation σ_{β_k} such that each β_{kj} had its own process error, to accommodate variation in the data. The mean was then modeled as a linear combination of city covariates

$$\nu_{kj} = \varphi_k + \theta_{1,k} \cdot latitude_j + \theta_{2,k} \cdot density_j + \theta_{3,k} \cdot greenness_j,$$

such that the effect of each numerical trait on UAI varied as a function of the city-level covariates. Importantly, this allowed urban tolerance to be predicted differently by different traits in different geographical contexts.

We ran this Bayesian model using the program JAGS[98] via the R package *R2jags*.[99] We used vague priors (mean of 0, standard deviation of 100) and we ran three chains, each with 40,000 iterations, beginning with a burn-in of 10,000 followed by a thinning of 30, retaining 1000 posteriors per chain. We verified that the model had successfully converged (Rhat $\leq$ 1.01 and n.eff > 400). We performed posterior predictive checks to ensure that data generated by the model were similar to data used to fit the model.[100] We found that 49.4% of the means of the posteriors were less than the observed mean UAI, indicating that our model could successfully reproduce the mean UAI. From the parameter posteriors we calculated the means and 95% credible intervals for each parameter.

Phylogenetic non-independence
In order to test for phylogenetic signal in the UAI values, we aligned the eBird (Clements) taxonomy with the taxonomy of BirdTree.org[101] and downloaded 100 phylogenetic trees with the Hackett backbone. We averaged UAI values across the tips of the phylogeny. For each tree, we calculated Pagel's λ as a measure of phylogenetic signal using the package *phytools*.[102] We then calculated the mean λ across trees, with associated 95% quantiles. We then took additional steps to assess whether

phylogenetic non-independence would affect our results (see below). Ultimately, we determined that further accounting for phylogeny would not substantially alter the observed trait relationships.

Directly incorporating phylogenetic information into our Bayesian model was not practical due to the extensive computational time (over a year) required for an analysis that includes so many species (model run times scale exponentially with additional species due to the covariance matrix required for the multivariate normal portion of phylogenetic models). Instead, we tested whether model residuals, averaged at the species level, contained a phylogenetic signal.[103] This test would tell us whether there was unexplained variation in the model associated with phylogeny. Model residuals contained relatively low phylogenetic signal ($\lambda = 0.37$, CI = 0.33–0.43). Moreover, most of this signal resulted from species with few data points – i.e., those represented in 1–4 cities – as the model was less able to estimate suitable species-specific intercepts due to the shrinkage of intercept parameters towards the cross-species mean. We therefore fit a second, identically structured model using a dataset where species represented in <5 cities were excluded, and checked for consistency of model results (i.e., βs) as compared to the original, full dataset model. Removing these 2848 species (76% of the species set) and re-running the model produced qualitatively similar trait coefficients (Figure S5) and greatly reduced the phylogenetic signal in the residuals ($\lambda = 0.15$, CI = 0.09–0.22). Thus, phylogenetic signal in the residuals was likely driven more by issues of intercept estimation than by phylogenetic non-independence.

To further test for phylogenetic non-independence, we conducted a phylogenetic generalized least-squares (PGLS) analysis of reduced complexity. For each of the 100 trees we ran a PGLS (package ape[104]) that included all ten traits. We then averaged the coefficients and confidence intervals (1.96*standard error) from the models. Comparing these coefficients with our main results is somewhat problematic as the PGLS necessarily lacked the desired complexity of our full Bayesian model including gamma-distributed UAIs, multiple city-specific UAIs for some species, and city-level covariates (no doubt resulting in some degree of model misspecification). However, the coefficients from this approach were consistent in sign with our main results (Figure S6). As one final check, we also conducted a linear model with a structure identical to the PGLS but without the phylogeny. We found the coefficients from this model (Figure S6) to be very similar to the PGLS results (albeit with wider confidence intervals and shrinkage towards 0 on some covariates), suggesting that similar trait relationships still emerge when accounting for phylogeny. Furthermore, the credible intervals in our main results are so tight that accounting for phylogeny in the full model would be unlikely to qualitatively change our results. We conclude that our estimates of trait relationships with UAI are robust to potential phylogenetic or sample-based biases.