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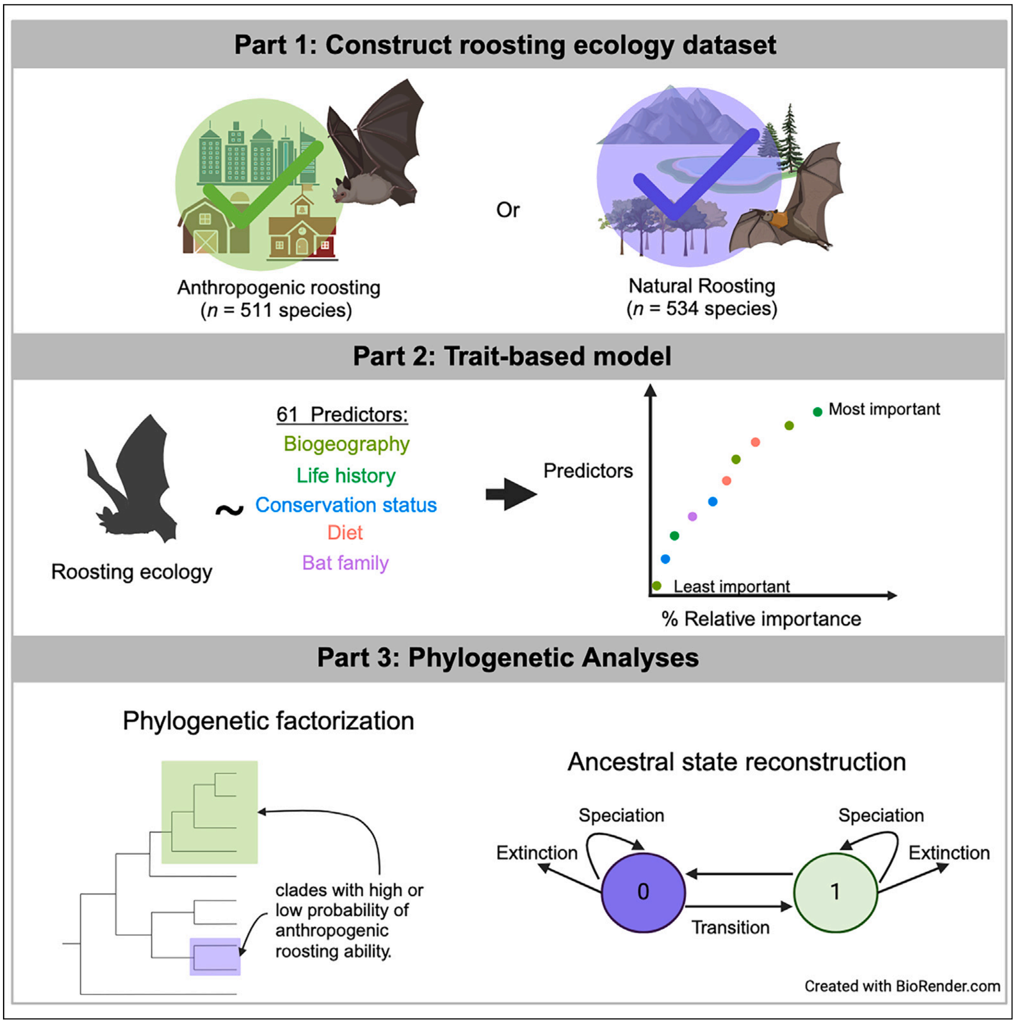

Briana A. Betke, Nicole L. Gottdenker, Lauren Ancel Meyers, Daniel J. Becker

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Highlights

Globally, around 40% of extant bat species can roost in anthropogenic structures

Anthropogenic roosting ability is predicted by geography, life history, and diet

Such traits include geographic range, habitat breadth, body size, and insectivory

Phylogenetic analysis found two frugivorous taxa less likely to have this ability

Betke et al., iScience 27, 110369
July 19, 2024 © 2024 The Authors. Published by Elsevier Inc.
https://doi.org/10.1016/j.isci.2024.110369

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Ecological and evolutionary characteristics of anthropogenic roosting ability in bats of the world

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SUMMARY

Although the global conversion of wildlife habitat to built environments often has negative impacts on biodiversity, some wildlife species have the ability to cope by living in human-made structures. However, the determinants of this adaptation on a global scale are not well understood and may signify species with unique conservation needs at the human–wildlife interface. Here, we identify the trait profile associated with anthropogenic roosting in bats globally and characterize the evolution of this phenotype using an original dataset of roosting behavior developed across 1,279 extant species. Trait-based analyses showed that anthropogenic roosting is predictable across bats and is associated with larger geographic ranges, habitat generalism, temperate zone distributions, small litter and body size, and insectivory. We identified moderate phylogenetic signal in this complex trait profile, which has undergone both gains and losses across bat evolution and for which speciation rates are lower compared to natural roosting bats.

INTRODUCTION

Human influences on environmental conditions (e.g., climate change, urbanization, deforestation, agriculture) impact wildlife by altering community composition, resource availability, and available habitat.[1–4] As a result, wildlife health can suffer through exposure to toxins and pathogens,[5] vehicle collisions,[6] predation by domestic animals,[7,8] and competition with invasive species.[7] Despite these risks, some wildlife species thrive in the midst of human disturbance, benefiting from anthropogenic resources such as shelter, supplementary food, and protection from predation.[9,10] For example, urban environments provide the coyote (*Canis latrans*) with an ample diet of small-to medium-sized mammals (e.g., rabbits, squirrels, domestic cats) and vegetation (e.g., ornamental fruits), as well as protection from apex predators.[11,12] Researchers have associated various functional traits that facilitate the observed tolerance of some wildlife species to human disturbance.[13–21] However, most studies do not consider the propensity to occupy anthropogenic structures (e.g., buildings, bridges, houses) when measuring urban tolerance, often categorizing species broadly by urban presence (i.e., defined as dwellers, avoiders, or visitors) or dichotomizing species as urban or non-urban.[16,22] Such structures serve as an increasingly critical frontier where human–wildlife conflict can occur.[23,24] Identifying the species that inhabit anthropogenic structures and their functional traits that facilitate usage can inform more effective wildlife conservation through conflict mitigation efforts.

Wildlife use a variety of anthropogenic structures as habitat including roofs,[25–29] crawl spaces and under floorboards,[25,30] chimneys,[31,32] bridges,[33–35] road culverts,[33,34] dumpsters,[36] and power line pylons.[37,38] Some species live in these structures occasionally while others rely on them as primary habitation. For instance, European stone martens (*Martes foina*) live almost exclusively in buildings, and large-spotted genets (*Genetta tigrina*) roost in roofs of houses with increasing occurrence in South African suburbs, whereas Madagascar free-tailed bats (*Otomops madagascariensis*) are obligate cave-dwellers.[28,39,40] Wildlife that inhabit anthropogenic structures may be threatened by extirpation originating from human-wildlife conflict.[23] Such threats include the potential transmission of zoonotic pathogens and parasites that cause disease in humans and companion animals (e.g., rabies, tuberculosis, roundworm, leptospirosis, salmonellosis).[41,42] Additionally, wildlife species may be perceived as pests due to property damage,[23,43] attacks on humans and companion animals,[44,45] the off-putting odors of excreta near or in homes.[46,47] Identifying structures and the species that commonly use them can help tailor conservation efforts. For example, such actions could include preserving existing structures for vulnerable wildlife, developing structures that would be more suitable for dwelling, and targeting efforts that reduce conflict with humans.

While there are many reports of wildlife use of anthropogenic structures, global patterns of this behavior are largely unknown. Most studies typically make intraspecific rather than interspecific comparisons, focus on a local or regional scale which limit data available for global biogeographic comparisons, and do not consider underlying determinants of habitat choice beyond microclimatic conditions. Although

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https://doi.org/10.1016/j.isci.2024.110369

mass data collection remains cost prohibitive, comparative analysis of existing global data can help to overcome some of these limitations and robustly identify the foundational biological principles that determine anthropogenic habitat usage.

Bats are an ideal model for studying functional traits associated with living in anthropogenic structures, given their high species diversity, global geographic distribution, and the substantial research investment to understand and address conservation and public health risks associated with various bat species. The order Chiroptera constitutes approximately 20% of all mammalian species and includes a high diversity of physical characteristics, life history, and ecology.[48] They roost in a variety of structures owing to wide interspecific variation in roosting requirements ranging from natural (e.g., caves, foliage, rock crevices, banana leaves, tree canopy, and crevices) to anthropogenic (e.g., buildings, bridges, and mines).[49,50] Human-made structures provide similar conditions to natural roosts that have been lost to rapid land use changes, offering protection from predation, shelter from extreme weather, and stable temperatures for improved reproductive success.[50,51] However, some bat species suffer adverse effects when moving from natural to anthropogenic habitats, such as increased vulnerability to predation, and unstable roost microclimates,[26,52,53] and extermination by humans who perceive them as nuisance wildlife and reservoirs of zoonotic pathogens.[54–57] Due to these negative perceptions, bats' ability to provide essential ecosystem services (e.g., pollination, seed dispersal, maintenance of insect populations) and bioindicator status is often overlooked.[58] On a local scale, there is evidence that identifying anthropogenic roosts can prioritize important bat conservation sites and reduce bat–human conflict.[59–61] Identifying global trends in this behavior may allow for the application of conflict mitigation on a global scale.

Here, we compiled a novel and comprehensive dataset documenting roosting structure type of 1,279 bat species, based on historical records. We first describe geographic and taxonomic patterns in anthropogenic roosting ability. Next, we use a machine learning algorithm, boosted regression trees (BRTs), to identify ecological and evolutionary characteristics (i.e., the trait profile) of anthropogenic roosting across bats globally, leveraging data from PanTHERIA,[62] COalesced Mammal dataBase of INtrinsic and Extrinsic traits (COMBINE),[63] and the International Union for the Conservation of Nature (IUCN).[64,65] BRTs side-step many challenges associated with analyzing such ecological datasets, including nonindependent data, non-randomly missing covariates, nonlinear patterns, and complex interactions, and demonstrate improved classifier ability than traditional regression methods.[66] Rather than explicitly test hypotheses about the role that specific species traits play in shaping anthropogenic roosting ability, this approach allows us to identify an overall trait profile as well as patterns that could generate more formal predictions to guide future research.[67] Finally, we characterize the phylogenetic distribution and evolution of the traits that underlie anthropogenic roosting ability. This dataset provides a new window into global trends of anthropogenic roosting and traits underlying anthropogenic dwelling that may not be apparent in data reflecting only the presence/absence of bats in human dominated landscapes.

RESULTS

Dataset description

Of most of the known diversity of bats (over 1,470 species to date),[68] we examined 1,279 extant bat species included in the most recent mammal phylogeny.[69] Our systematic dataset included the presence or absence of anthropogenic roosting across 80% of this order (n = 1,045). We find that approximately 40% (511 of 1,279 species) of extant bat species are capable of roosting in anthropogenic structures, although the occurrence of anthropogenic roosting varies markedly across bat families, biogeographic regions, and conservation status (Figure 1). Anthropogenic roosting structures included bridges, attics, mines, and overhangs of buildings. The proportion of anthropogenic roosting species per family ranged from 0% to 100% (Figure 1A). Several small families have 100% coverage with all species labeled as anthropogenic (i.e., Rhinopomatidae, Noctilionidae, and Megadermatidae). Nycteridae, Molossidae, and Furipteridae contain 75%, 57%, and 50% anthropogenic roosting bat species, respectively. Three families (i.e., Thyropteridae, Myzopodidae, and Craseonycteridae) have no known anthropogenic roosting species. Of the biogeographical regions (Figure 1B), the proportion of anthropogenic bats recorded was lowest in the Oceanian region (9%) and highest in the Nearctic region (81%). Fifty-two percent of bat species with a IUCN conservation status of Least Concern were found to roost in anthropogenic structures, followed by 39% of Near Threatened species (Figure 1C); the Critically Endangered species had the lowest proportion of anthropogenic roosting bats (14%).

Trait profile of anthropogenic roosting ability

To identify the trait profile of an anthropogenic roosting bat species, we evaluated 61 features of bat life history, geography, diet, phylogeny, and conservation status (Figure 2) with a BRT model. Our model distinguished anthropogenic and natural roosting species with high accuracy and specificity, and moderate sensitivity (AUC = 0.95, specificity = 0.88, sensitivity = 0.83). The top features for classifying anthropogenic roosting species included geography (i.e., geographic range size, habitat breadth, mean monthly precipitation, mean monthly actual evapotranspiration rate (AET), mean monthly potential evapotranspiration rate (PET), maximum latitude, mean human population density), life history (i.e., litter size, adult body length, adult body mass, adult forearm length), diet (i.e., percentage of plants, fruit), and IUCN conservation status (Figure 2). In contrast, taxonomic predictors had lower relative importance, with family-level traits each having less than 1% relative importance when accounting for all other traits. Importantly, citation count also had low importance, suggesting that anthropogenic roosting status is not simply a function of high study effort.

Partial dependence plots (Figure 3) described anthropogenic roosting species as being habitat generalists that occupy larger geographic ranges with low monthly AET and precipitation. Anthropogenic roosting bats were also located further from the equator, showing presence at both extremes of latitude, especially in the northern hemisphere. This phenotype was further described by smaller litter sizes and smaller body size overall, as measured by adult body mass, forearm length, and body length. Additionally, the diet of an anthropogenic roosting bat

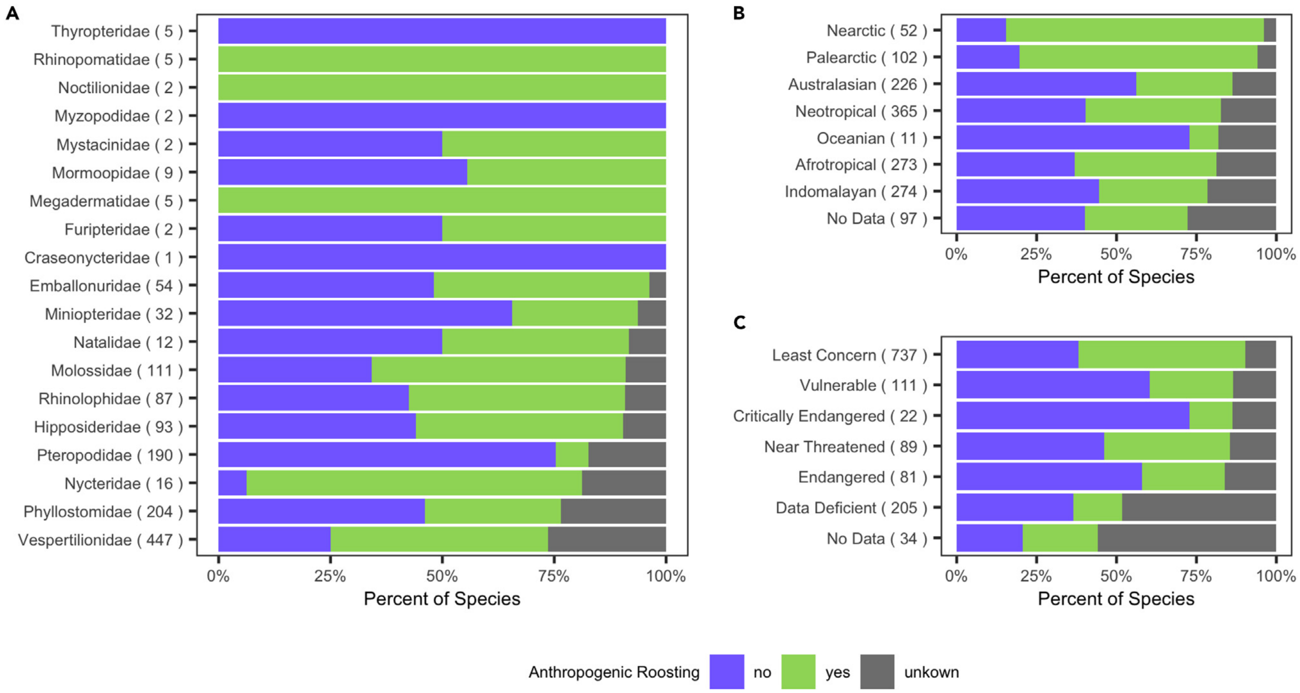

Figure 1. Coverage of roosting ecology data across bat families, biogeographic regions, and conservation categories

Proportion of species by roosting type across bat families (A), biogeographic regions (B), and IUCN conservation statuses (C). The colors indicate the proportion of bats that are natural roosting (purple), anthropogenic roosting (green), and have no roosting data available (gray). The numbers located at the end of the bars show the total number of species in each category.

consisted of a low percentage of plants, low percentage of fruit, and a high percentage of invertebrates. Of all IUCN conservation status categories, species listed as Least Concern were the most likely to be classified as anthropogenic roosting, followed by endangered species.

We assessed the sensitivity of these results to pseudoabsences, species for which adequate information on roosting status does not exist (n = 234). The BRT model containing pseudoabsences (n = 1,279 species) performed similarly to the above BRT model (n = 1045 species) but had lower sensitivity and higher specificity (AUC = 0.95, sensitivity = 0.80, specificity = 0.92). With the exception of citation count, variable importance between models was similar (Figure S1A) and displayed strong correlation ($\rho = 0.95$, $p < 0.001$; Figure S1B). Partial dependence plots for the pseudoabsence model revealed a similar trait profile of anthropogenic roosting ability compared to the initial model (Figure S2), suggesting the inclusion of pseudoabsences did not qualitatively influence results.

Evolution of the trait profile underlying anthropogenic roosting

As our BRT model demonstrated, anthropogenic roosting was a predictable trait on the basis of bat geography, life history, and diet, we next quantified the phylogenetic signal in this multifaceted phenotype and tested how it has evolved. Anthropogenic roosting showed low-to-moderate phylogenetic signal across bats ($D = 0.64$) and departed from both Brownian motion and phylogenetically independent models of evolutionary processes ($p < 0.001$). We also used a graph-partitioning algorithm, phylogenetic factorization, to flexibly identify clades with different propensity to roost in anthropogenic structures at various taxonomic depths.[70] Phylogenetic factorization identified two clades of bats with markedly lower propensities to harbor anthropogenic roosting phenotypes compared to the rest of the bat phylogeny, after adjusting for differential sampling effort: the family Pteropodidae (9%) and the phyllostomid subfamily Stenodermatinae (25%; Figure 4). Results were consistent when including pseudoabsences for the 234 understudied bat species, with similar estimates of phylogenetic signal ($D = 0.69$) and equivalent identification of both the Pteropodidae and Stenodermatinae as less likely to roost in anthropogenic structures (Table S1).

We compared among multiple binary state speciation and extinction (BiSSE) models to assess whether the phenotypes that enable anthropogenic roosting have facilitated bat diversification.[71] Of eight candidate models where speciation, extinction, and transition rates could vary between natural and anthropogenic roosting states, we found the most support for a constrained model with trait-dependent speciation and transitions but not extinction ($\lambda_0 \neq \lambda_1$, $\mu_0 = \mu_1$, $q_{01} \neq q_{10}$; $w_i = 0.59$). Models with trait-dependent extinction and irreversible models (i.e., $q_{10} = 0$) consistently received little information theoretic support (Table 1). MCMC sampling of the top BiSSE model demonstrated that speciation rates were greater in natural roosting bats than in anthropogenic roosting bats, as 95% credible intervals did not overlap (Figure 4). Transitions from natural to anthropogenic roosting were slightly more frequent than transitions from anthropogenic to natural roosting, with less posterior support. Ancestral state reconstruction using the estimated posterior mean transition rates and stochastic character mapping further emphasized relatively more gains of natural roosting lineages across bat evolution (Figure 4).

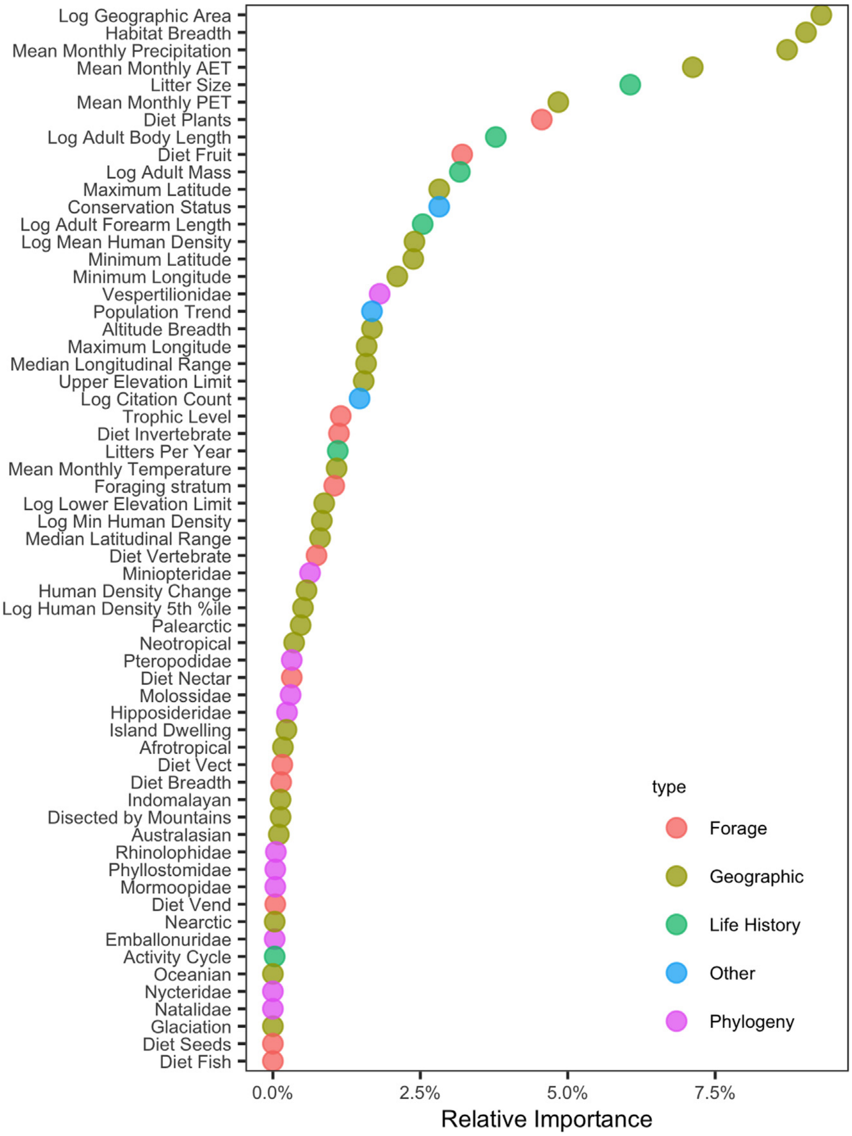

Figure 2. Relative importance of trait covariates from the boosted regression tree model of roosting status

Traits are ordered by ranking, with the highest at the top, and colors in the legend correspond to variable type. AET is the actual evapotranspiration rate and PET is the potential evapotranspiration rate.

The inclusion of anthropogenic roosting pseudoabsences did not affect the selection of the top BiSSE model, with similar support for trait-dependent speciation and transition rates but not extinction and no support for irreversible models (Table S2). MCMC sampling suggested similarly strong differences in speciation rates between anthropogenic and natural roosting bats, with again weak posterior support for differences in transition rates (although this analysis suggested more frequent losses of anthropogenic roosting than gains of this trait; Figure S3).

DISCUSSION

As built environments expand with human population growth,[72] the risks of human–wildlife conflict increase. In this study, we characterize the trait profile of anthropogenic roosting bats to support the detection of bat species at the human–wildlife interface and potentially mitigate associated risks to bats and/or humans. We compiled the largest curated database of anthropogenic roosting across all bat families, biogeographical realms, and conservation status to date, and then we used these data to assess the determinants of anthropogenic roosting with fundamental ecological and evolutionary characteristics. These data are standardized to integrate seamlessly with the COMBINE, PanTHERIA, and IUCN mammal trait databases.

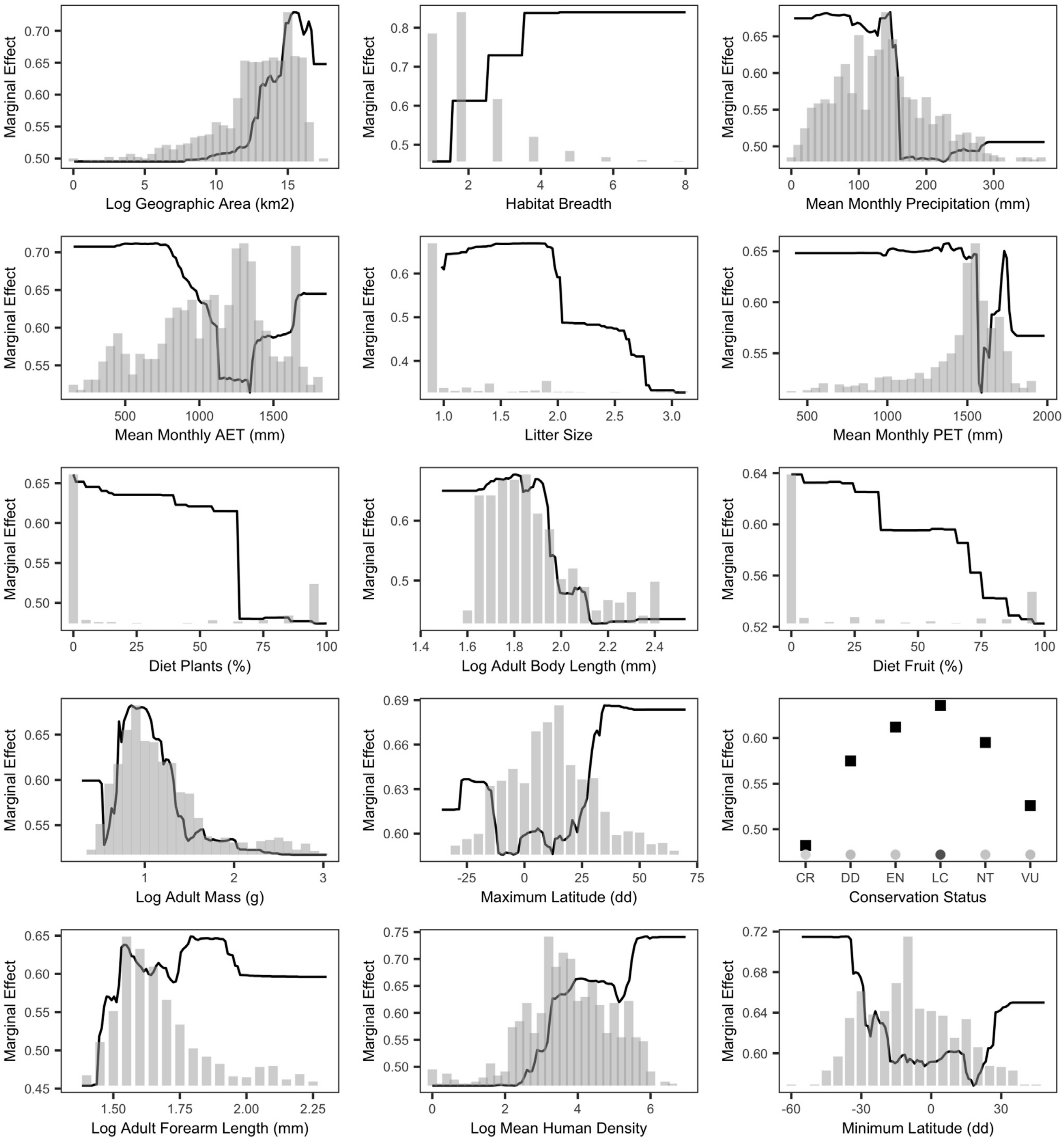

Figure 3. Trait profile of anthropogenic roosting bats

Partial dependence plots of the top BRT predictors ordered by relative importance. The black line displays the marginal effect of a given variable for the prediction of roosting status. Histograms and point color show the distribution of the continuous and categorical predictors, respectively, across the 1,045 bat species. The conservation status abbreviations are as follows: Critically Endangered (CR); Data Deficient (DD), Endangered (EN), Least Concern (LC), Near Threatened (NT), Vulnerable (VU).

Our analyses suggest that anthropogenic roosting can be predicted by species traits, with such bats having larger geographic ranges and broad habitat breadth, occurring in temperate regions, having small body size and low reproductive output, and consuming more invertebrates than plants. We also identified moderate phylogenetic effects, with particular clades having lower propensities to roost in

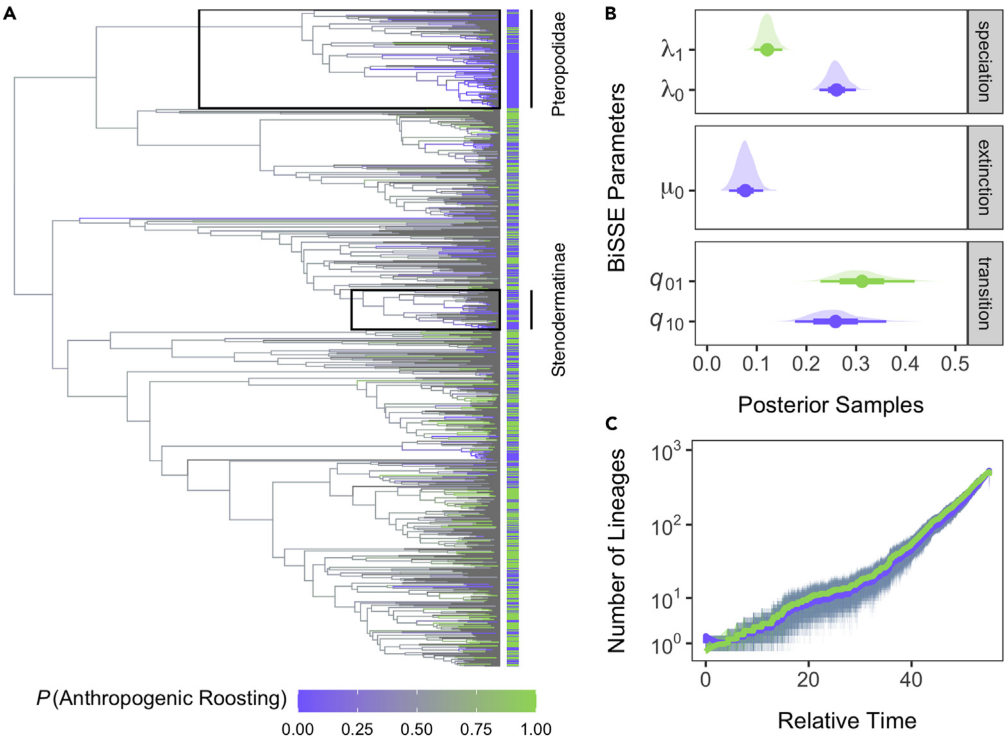

Figure 4. Evolution of the trait profile underlying anthropogenic roosting across bats

The extant bat phylogeny with tips colored by known roosting status (n = 1,045), with branches colored by posterior probabilities for anthropogenic roosting derived from stochastic character mapping of the transition matrix from the top BiSSE model (A). BiSSE parameters with posterior means, 66% and 95% credible intervals, and posterior densities are shown from MCMC sampling (B) alongside individually simulated and averaged lineages through time for natural and anthropogenic roosting states (C).

anthropogenic structures and that the trait profile that allows bats to utilize anthropogenic structures has undergone losses and gains throughout bat evolution.

Considering all traits included in our BRT model, geographic range was the most important predictor of anthropogenic roosting ability, with species characterized by large geographic ranges being more likely to roost in anthropogenic structures. This finding is intuitive, as some typical examples of anthropogenic roosting bats include very broadly distributed species such as *Esptesicus fuscus*, *Tadarida brasiliensis*, and *Pipistrellus pipistrellus*.[64,65] One possible explanation for this pattern could be that wide-ranging species also have smaller body sizes, which could enable them to use these unique roosts. However, evidence of a positive relationship between body size and geographic range size across bat species in the literature is lacking and has only been observed for vespertilionids.[73] We used phylogenetic least squares (PGLS) to test whether geographic range size could explain variation in forearm length (a proxy for body size) but found no significant relationship (β = 0.004, p = 0.13). Further comparative work is needed to understand the relationship between anthropogenic roosting and geographic range size, as the latter trait can be shaped by many other ecological and evolutionary factors.

Another explanation for the observed relationship between geographic range size and anthropogenic roosting could pertain to habitat generalism, as species with larger geographic ranges typically have greater environmental tolerance and niche breadth.[74] Supporting this explanation, we identified habitat breath, a common measure of tolerance to human disturbance in other taxa,[18,21,75–77] as the second most important trait in classifying anthropogenic roosting ability. Anthropogenic roosting ability was associated with broad habitat breath, which should allow these bats to capitalize on a wider range of environments, including roosting structures. Together, these results suggest bats utilizing anthropogenic roosts have broader environmental tolerance. Considering the implications of this finding, both geographic range size and habitat breadth play important roles in determining extinction, with species having smaller geographic ranges and narrower habitat breadths being more at risk.[74,78,79] As such, the ability to use anthropogenic roosts may help buffer bats from factors that threaten population decline.

Anthropogenic roosting bats were also rarer in the tropics compared to temperate areas. This finding is consistent with the larger proportions of these bats observed in the Nearctic and Palearctic in our descriptive analysis. As human occupancy is a prerequisite for bats to roost in anthropogenic structures, this pattern may be explained in part by the higher average density of human settlements in temperate regions compared to tropical regions.[80] Anthropogenic roosting bats may benefit from the increased availability of structures provided by the dense urban development required to accommodate such large populations. In support of this explanation, our models showed that anthropogenic roosting species more commonly occur in areas of greater human population density. However, human population density and associated

Table 1. Comparison among eight BiSSE models of trait-dependent diversification, including speciation (λ), extinction (μ), and transitions between binary states (q)

Model	ΔAIC	k	w_i
$\lambda_0 \neq \lambda_1, \mu_0 = \mu_1, q_{01} \neq q_{10}$	0.00	5	0.59
$\lambda_0 \neq \lambda_1, \mu_0 \neq \mu_1, q_{01} \neq q_{10}$	0.76	6	0.41
$\lambda_0 = \lambda_1, \mu_0 \neq \mu_1, q_{01} \neq q_{10}$	16.27	5	<0.01
$\lambda_0 = \lambda_1, \mu_0 = \mu_1, q_{01} = q_{10}$	17.82	3	<0.01
$\lambda_0 = \lambda_1, \mu_0 = \mu_1, q_{01} \neq q_{10}$	19.73	4	<0.01
$\lambda_0 \neq \lambda_1, \mu_0 \neq \mu_1, q_{10} = 0$	124.77	5	<0.01
$\lambda_0 = \lambda_1, \mu_0 \neq \mu_1, q_{10} = 0$	146.98	4	<0.01
$\lambda_0 \neq \lambda_1, \mu_0 = \mu_1, q_{10} = 0$	272.85	4	<0.01
$\lambda_0 = \lambda_1, \mu_0 = \mu_1, q_{10} = 0$	496.23	3	<0.01

Models are ranked by difference in Akaike information criterion from the top model (ΔAIC), the number of estimated parameters (k), and Akaike weights (w_i).

metrics (i.e., minimum human density, human density in the fifth percentile, and human density change) did not rank among the top 10 predictors of the anthropogenic roosting trait profile. This finding suggests that anthropogenic roosting is not solely determined by human density and that use of these structures is additionally determined by the geographic, life history, and dietary characteristics of individual species.

Our model suggested that anthropogenic roosting bats occur mostly in northern temperate regions with low precipitation. Additionally, anthropogenic roosting bats occur in areas with mostly low to moderate water loss, as suggested by partial dependence plots of AET and PET. However, these plots also showed a spike in anthropogenic roosting propensity at the higher extremes of AET and PET, potentially suggesting that bat species with this trait persist in areas within the temperate region that are drier and experience greater water loss. This result likely further emphasizes the importance of anthropogenic structures for the survival of bat species existing at these environmental extremes. Bats suffer high rates of evaporative water loss because of their membranous wings as well as the high energetic costs associated with sustained flight.[81] Roosts in anthropogenic structures may provide stable microclimatic conditions that minimize further evaporative water loss, especially in roosts with greater protection from sun exposure such as large bridges.[61] Additionally, roosting in anthropogenic structures may allow bats to stay in close proximity to water sources provided by humans in drier areas (e.g., ponds and pools).[82,83]

We also found anthropogenic roosting bats to have smaller litter sizes, body mass, and body length. The association between smaller litter size and anthropogenic roosting seemingly contradicts some prior studies of urban tolerance, where greater fecundity is instead associated with urban living.[16,21,76] Larger litter size is likely an advantageous trait that allows urban-tolerant species to cope with excess mortality unique to urban habitat (e.g., vehicle collisions, human–wildlife conflict, predation by cats).[16] However, anthropogenic roosting bats may be less impacted by certain external sources of mortality such as vehicle collisions and predation, whereas mortality may instead result from extirpation from human-made structures. Our finding of small body size in anthropogenic roosting bats also may reflect some unique facets of bat biology. Having a small body size facilitates fitting in crevices of anthropogenic structures and take up less space compared to species with larger body sizes,[84] which could buffer these bats from external sources of predation in urban habitats. Interestingly, we observed a peak effect for forearm size at small lengths, which may enhance maneuverability in cramped spaces.

Our analysis also showed that frugivorous bats are unlikely to be predisposed to use anthropogenic roosts. Rather, bat species that mostly consume invertebrates, typically insects, are more prone to roost in anthropogenic structures. Several reasons could explain this pattern. First, human-dominated environments provide resources that insectivorous bats can exploit to persist in anthropogenic structures. Built environments attract insects through the presence of standing water (e.g., ponds, sprinklers, birdbaths), plants (e.g., gardens, ornamental/landscaping plants, crops), and light sources.[85] Insectivorous bats also have wide behavioral or phenotypic plasticity that allow for survival in anthropogenic structures. For example, insectivorous bats adjust features of their echolocation[86] and alter foraging activity in anthropogenic environments.[87] Finally, anthropogenic structures may not be suitable roosts for frugivorous bats, which tend to have larger body sizes that could physically limit the use of such roosts. We again used PGLS for a post-hoc analysis to show that forearm length is positively correlated with fruit consumption ($\boldsymbol{\beta} = 0.18$, $p < 0.001$) and negatively with invertebrate consumption ($\boldsymbol{\beta} = -0.15$, $p < 0.001$). This is also supported by prior analyses, as multiple subclades of Pteropodidae (an entirely frugivorous and nectarivorous family) showed rapid increases in body sizes throughout their evolution.[88]

Whereas prior studies have assessed the traits underlying species propensities to use or tolerate urban habitats, few studies have assessed the evolution of these complex trait profiles. The sole prior phylogenetic assessment of urban tolerance in bats was restricted to Afrotropical species and focused broadly on urban occupancy rather than the use of anthropogenic structures.[89] We identified low-to-moderate phylogenetic signal in the anthropogenic roosting phenotype globally, indicating that the trait profile of anthropogenic roosting consists of particular clades that contain more bat species with high or low likelihood of having anthropogenic roosting ability. Phylogenetic factorization did not identify clades with a significantly high propensity to roost in anthropogenic structures, whereas the family Pteropodidae and subfamily Stenodermatinae were both identified as having significantly lower probabilities of harboring this phenotype. This is consistent with our BRT results, where the Pteropodidae also had low but non-zero importance.

Our BRT also found the family Vespertilionidae to have low-to-moderate influence in predicting anthropogenic roosting, although this clade was not identified by our phylogenetic analysis. Together, these taxonomic results suggest that vespertilionids possess many traits that predispose bats to roost in anthropogenic structures (e.g., small size and insectivory), but such traits are not unique to this family. Our BiSSE analysis also suggested the traits that predispose bats to capitalize on anthropogenic roosts may have impeded bat evolution, where anthropogenic roosting species showed lower rates of speciation but equivalent extinction rates in comparison to natural roosting species. This result is further supported by greater evolutionary success for natural roosting bats, as evidenced by more lineages over time in comparison to the anthropogenic roosting phenotype and slightly lower transition rates from anthropogenic roosting to natural roosting than the reverse process. These findings together agree with work that associates urbanization with the loss of phylogenetic diversity globally in birds[90] and emphasizes the need to preserve diversity in the face of increasing environmental change.

Taken together, our study demonstrates that anthropogenic roosting ability is predicted by both ecological and evolutionary characteristics of bat species. Supporting that, prioritizing the protection of roosting sites in anthropogenic structures and mitigation of conflicts between humans and wildlife may be beneficial for conservation in increasingly human-dominated spaces. Our analyses also show important knowledge gaps in bat ecology, evolution, and the impacts of anthropogenic roosting. Although our novel dataset provides a standardized baseline in bat behavior to observe changing patterns in anthropogenic roosting, the number of species for which roosting ecology is unknown (n = 234) highlights the lack of available data and emphasizes the need for further research to improve data coverage. For example, our evolutionary analysis showed an inconsistency in the transition rate between models using only known roosting ecology data versus also using pseudoabsence data. Having roosting ecology data for these unknown species could uncover undetected phylogenetic patterns and improve understanding of bat evolution. Owing to gaps in bat natural history, we also were unable to include other traits that could further differentiate anthropogenic roosting ability. For example, data on migratory behavior could contextualize anthropogenic roosting associated with large geographic range size, but data on this trait is only available in a standardized fashion primarily for bats in the family Vespertilionidae.[91] Further research is needed to improve the availability and standardization of data on migratory behavior, as well as on other relevant traits such as hibernation, to assess their role in shaping anthropogenic roosting ability.

In addition to further expanding bat trait data, an interesting future direction will be quantifying differences in reproductive outcomes between bat species that differ in their roosting ecology, as our BRTs revealed that anthropogenic roosting was associated with small litter sizes. Such analyses could also elucidate anthropogenic impacts on population dynamics and inform conservation efforts in species for which populations may not recover well under increasing human disturbance or conflict. Another logical next step is to understand co-roosting ecology of anthropogenic roosting bats in comparison to their natural roosting counterparts.[92] Geographic overlap due to human-made structures could allow species interactions that do not occur in natural environments and are possibly unique to anthropogenic structures. Lastly, a comprehensive dataset documenting those species that directly live alongside humans and their potential interactions could be a powerful tool for improving predictions of pathogen transmission among species when paired with host–pathogen association data. For example, living alongside humans has been associated with a greater probability of being a reservoir of zoonotic pathogens in rodents.[93] Similar work is needed for anthropogenic roosting in bats to improve surveillance and conflict mitigation relating to the risk of pathogen transmission.

Limitations of the study

The data used in this study reflect what is available in the current literature. In our dataset, some bat classifications were based on single accounts, and many were derived from summaries in historical records that do not describe the frequency in which bats were observed in a structure. Our binary classification could thus represent rare occasions of roosting in anthropogenic structures including, but not limited to, displacement resulting from extreme weather conditions or juvenile bats learning to select roosts. Additionally, not all sources of historical literature were in consensus about anthropogenic roosting. Although this did not occur often, we settled any discrepancies by searching any additional information available and the primary sources used by the reference, if provided. If looking further into the literature still proved inconclusive, the species was marked as unknown for primary analyses. As roost ecology data are sparse, including quantitative metrics relating to the size of the roost was not available for most bat species beyond the categorization of solitary or group roosting, but this information would be important for understanding the reliance on anthropogenic structures as roosts.

STAR★METHODS

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

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- METHOD DETAILS
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- ○ Phylogenetic analyses

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.110369.

ACKNOWLEDGMENTS

B.B. and D.J.B. were supported by funding to the Viral Emergence Research Initiative (Verena) Institute, including NSF BII 2021909 and NSF BII 2213854. We thank Daniel Bolnick, Robin Rowland, and two anonymous reviewers for helpful feedback on a previous version of this article.

AUTHOR CONTRIBUTIONS

Conceptualization, D.J.B. and B.B.; methodology, D.J.B. and B.B.; formal analysis, B.B.; investigation, B.B. and D.J.B.; data curation, B.B. and D.J.B.; writing–original draft, B.B. and D.J.B., writing –review and editing; B.B., D.J.B., L.M., and N.G.; supervision, D.J.B.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: October 18, 2023
Revised: April 20, 2024
Accepted: June 21, 2024
Published: June 25, 2024

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Bat roosting ecology data	This paper	https://github.com/babetke/synurbat
COMBINE	Soria et al.[63]	https://doi.org/10.1002/ecy.3344
PanTHERIA	Jones et al.[62]	https://doi.org/10.1890/08-1494.1
Conservation status and population trends	IUCN	https://www.iucnredlist.org/
Software and algorithms		
easyPubMed	Fantini[94]	https://CRAN.R-project.org/package=easyPubMed
rredlist	Gearty and Chamberlin[64]	https://CRAN.R-project.org/package=rredlist
gbm	Greenwell et al.[95]	https://cran.r-project.org/package=gbm
ROCR	Sing et al.[96]	https://ipa-tys.github.io/ROCR/
caper	Fritz and Pervis[97]	https://doi.org/10.1111/j.1523-1739.2010.01455.x
phylofactor	Washburn et al.[70]	https://doi.org/10.1002/ecm.1353
diversitree	FitzJohn[98]	https://doi.org/10.1111/j.2041-210X.2012.00234.x

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Briana Betke (babetke@utexas.edu).

Materials availability

This study did not generate any unique reagents.

Data and code availability

- Bat roosting ecology and trait data have been deposited at GitHub and are publicly available as of the date of publication. Intrinsic and extrinsic trait databases can be accessed from the cited sources. The DOIs and websites are listed in the key resources table.
- All original code can be found at https://github.com/babetke/synurbat and are publicly available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

METHOD DETAILS

Anthropogenic roosting data

We collected roosting ecology data for 1,279 extant bat species listed in the most recent mammal phylogeny,[69] representing most of the over 1,470 recognized species in the order Chiroptera.[68] Owing to taxonomic revision, we reclassified species in the genus *Miniopterus* from the Vespertilionidae to be the sole members of the family Miniopteridae.[99] Starting on August 25, 2021, data were compiled through a manual search of existing literature and historical records using sources such as Google Scholar, IUCN, Animal Diversity Web, and Walkers *Bats of the World*[100] to identify roosting status and human-made structure type (building, home, bridge, ect.) of each bat species.

Anthropogenic roosting status was recorded as a binary variable indicating if a given bat species has been recorded in any human-made structures or roosting exclusively in natural roosting structures. Classification for each species can be found in Table S3 and corresponding references to sources used to verify roosting structure are provided in the supplemental information. A code of 1 indicates the bat species roosts in structures such as mines, buildings, homes, bridges, tunnels, roofs, and attics. Bat species that roost exclusively in natural structures (palm leaves, caves, tree hollows, foliage, and so forth) were coded as 0. Species without roosting information or relevant citations (n = 234) were coded as pseudoabsences. We coded species as pseudoabsences in the absence of roosting information in the existing literature, having relatively few search returns (e.g., as occurs for poorly studied species), or not having relevant papers with roosting information within the first 10 pages of Google Scholar when searching with the following string: "Latin binomial'' AND "roost."[101] If a bat genus had consistent roosting ecology (i.e., all members used either anthropogenic or natural roosts), we updated any bats of that genus with missing values to the binary status of the group. However, if there were mixed values in a single genus specifically or the majority of species were considered NA, anthropogenic roosting remained NA until assigned as a pseudoabsence.

Bat sampling effort and ecological traits

To account for additional bias introduced into the dataset through unequal sampling of bat species in our downstream analyses, we conducted a PubMed search with the *easyPubMed* package in R to calculate a citation count for all 1,279 bat species names.[95,102–104] We next assembled a trait matrix of life history, dietary, morphological, geographic, and taxonomic traits to predict anthropogenic roosting. Trait data came primarily from COMBINE with additional geographic range variables from PanTHERIA.[62,63] Biogeographical realms were separated into binary covariates to observe the importance of presence in each realm individually. IUCN conservation status and population trends were extracted for all available bat species with the *rredlist* package.[64] In addition, binary covariates for all 18 bat families were generated to account for taxonomic relationships and to investigate whether a given family is disproportionately associated with anthropogenic roosting.[96,97,104] We calculated several descriptive statistics using these data, including data coverage and the proportion of species roosting in anthropogenic structures as stratified by bat family, IUCN status, and biogeographical realm.

Taxonomic reconciliation of trait datasets

We manually matched select bat species across trait datasets to be consistent with the most recent phylogeny used for the collection of roosting ecology data.[69] As the trait datasets were published in different years, many species were reverted to previous genus designations or updated to current names when necessary. For the PanTHERIA dataset, this included updating *Dermanura* from their former *Artibeus* classifications, switching *Hypsugo* species to *Pipistrellus*, and specific species of *Triaenops* to *Paratriaenops* (i.e., *Triaenops auritus* to *Paratriaenops auritus*, *Triaenops furculus* to *Paratriaenops furculus*). Species that were recently reclassified to another genus were also updated in the PanTHERIA binomial names to match our phylogenetic backbone (i.e., *Murina grisea* to *Hapoila grisea*, *Lissonycteris angolensis* to *Myonycteris angolensis*, *Eptesicus matroka* to *Neoromicia matroka, Hsunycteris thomasi* to *Lonchophylla thomasi*). Similar genus changes were made to COMBINE and IUCN binomial names to match with the phylogenetic backbone used in this analysis, apart from the switch to *Dermanura* to *Artibeus,* and species that needed to be changed to older names as these datasets reflect post 2019 taxonomic changes. This includes switching *Paremballonura* back to *Emballonura* (i.e., *Paremballonura atrata* to *Emballonura atrata*, *Paremballonura tiavato* to *Emballonura tiavato*), several *Macronycteris* species to *Hipposideros* (i.e., *M. commersoni*, *M. gigas*, *M. thomensis*, *M. vittatus*), *Lonchophylla* to *Hsunycteris* (i.e., *L. cadenai*, *L. pattoni*), *Gardnerycteris* to *Mimon* (i.e., *G. crenulatum*, *G. koepckeae*), *Baedon* to *Rhogeessa* (i.e., *B. alleni*, *B. gracillis*), *Austronomus* to *Tadarida* (i.e., *A. australis*, *A. kuboriensis*), *Vampyriscus* to *Vampyressa* (i.e., *V. bidens*, *V. brocki*, *V. nymphea*), and changes to select species including: *Scotonycteris ophiodon* to *Casinycteris ophiodon*, *Pteropus leucopterus* to *Desmalopex leucopterus*, *Rhyneptesicus nasutus* to *Eptesicus nasutus*, *Hypsugo affinis* to *Falsistrellus affinis*, *Lyroderma lyra* to *Megaderma lyra*, *Ozimops loriae* to *Mormopterus loriae*, *Mormopterus kalinowskii* to *Nyctinomops kalinowskii*, *Perimyotis subflavus* to *Pipistrellus subflavus*, *Boneia bidens* to *Rousettus bidens*, and *Chaerephon jobimena* to *Tadarida jobimena*. Additionally, species that were present in our dataset but were previously a subspecies, or closely related, to those in the trait datasets were synonymized. Across all trait datasets, the following species were considered to be synonyms: *Dermanura incomitatus* and *Dermanura watsoni*, *Harpiocephalus mordax* and *Harpiocephalus harpia*, *Hsunycteris thomasi* and *Lonchophylla thomasi*, *Lophostoma aequatorialis* to *Lophostoma occidentalis*, *Lophostoma yasuni* and *Lophostoma carrikeri*, *Miniopterus fuliginosus* and *Miniopterus schreibersii*, *Molossus barnesi* and *Molossus coibensis*, *Myotis flavus* and *Myotis formosus*, *Myotis midastactus* and *Myotis simus*, *Natalus saturatus* and *Natalus stramineus*, *Paracoelops megalotis* and *Hipposideros Pomona*, *Pipistrellus deserti* and *Pipistrellus kuhlii*, *Pteropus argentatus* and *Pteropus chrysoproctus*, *Pteropus yapensis* and *Pteropus pelewensis*, *Triaenops menamena* and *Triaenops rufus*, *Rhinolophus chaseni* and *Rhinolophus borneensis*, *Triaenops rufus* and *Triaenops persicus*, *Myotis aelleni* and *Myotis chiloensis,* and *Myotis hajastanicus* and *Myotis aurascens*. For the COMBINE and IUCN trait datasets, a few additional species were synonymized (*Natalus lanatus* and *Natalus mexicanus*, *Nyctophilus timoriensis* and *Nyctophilus corbeni*). Additionally, there were synonym reconciliations specific to the PanTHERIA dataset: *Carollia sowelli* and *Carollia brevicauda*, *Natalus mexicanus* and *Natalus stramineus, Myotis abei* and *Myotis petax, Myotis ricketti* and *Myotis pilosus, Pteropus insularis* and *Pteropus pelagicus, Pteropus insularis* and *Pteropus pelagicus*, and *Sturnira thomasi* and *Sturnira angeli*. Minor discrepancies in names were also corrected as needed throughout datasets (i.e., *Anoura carishina* to *Anoura canishina*, *Chiroderma vizzotoi* to *Chiroderma vizottoi*, *Dermanura azteca* to *Dermanura aztecus*, *Dermanura cinerea* to *Dermanura cinereus*, *Dermanura glauca* to *Dermanura glaucus*, *Dermanura gnoma* to *Dermanura gnomus*, *Dermanura rosenbergi* to *Dermanura rosenbergii*, *Dermanura tolteca* to *Dermanura toltecus*, *Diclidurus isabella* to *Diclidurus isabellus*, *Murina lorelieae* to *Murina loreliae*, *Neoromicia brunneus* to *Neoromicia brunnea*, *Neoromicia nanus* to *Neoromicia nana*, and *Neoromicia somalicus* to *Neoromicia somalica*).

QUANTIFICATION AND STATISTICAL ANALYSIS

Boosted regression trees

We used BRT models, a machine learning algorithm that determines variables of importance based on an ensemble of regression trees or classification trees, to identify the trait profiles of anthropogenic roosting bats. BRTs overcome many challenges associated with analyzing ecological data via traditional regression methods (e.g., non-independent data, non-randomly missing covariates, nonlinear patterns, complex interactions), making this approach ideal for analyzing bat trait data.[66] After removing predictors with no variance or missing values for over 30% of bat species, our BRTs included 61 predictor variables (Table S4). We log-transformed any continuous predictors with highly skewed distributions or that spanned multiple orders of magnitude (e.g., geographic range size, adult body mass). Models were then trained with the *gbm* R package, with anthropogenic roosting as a Bernoulli distributed response.[105] We did not perform out-of-sample predictions, as the roosting data is well represented across the bat taxonomy, and our intention was to identify the trait profile of anthropogenic roosting bats rather than prediction.[106] To mitigate the probability of overfitting, a grid search was used for hyperparameter tuning to determine the optimal values for the number of trees, learning rate (i.e., shrinkage), and interaction depth prior to fitting models (see optimizing BRT hyperparameters, later in discussion). We identified an optimal learning rate of 0.0005, interaction depth of 4, and a maximum number of trees of 20,000 (Figure S4). We derived several metrics of model performance with the *ROCR* R package (AUC, sensitivity, and specificity).[107] Additionally, all models were 10-fold cross validated. We determined the influence of each predictor on roost status by variable importance, the proportion of improvement in model fit that is attributed to each predictor. We also created partial dependence plots to visualize the marginal effects of individual predictor variables on roost status while controlling for all other predictors. We also assessed the influence of pseudoabsences on BRT performance.

Optimizing BRT hyperparameters

For the model of 1,045 bat species with known anthropogenic classification data and the pseudoabsence model where unknown species are assumed to be natural roosting (n = 1,279), a grid search was conducted to select optimal hyperparameters. We selected three interaction depths (2, 3, 4) and three learning rates (0.01, 0.001, 0.0005). In combination, we tested these interaction depts and learning rates with an assortment of initial trees (5000, 10000, 15000, 20000, 25000). Combinations of low number initial trees (i.e., 5000 and 1000) and small learning rates (0.0005) were removed, resulting in 39 parameterizations for each model. These parameters were run through BRTs with the *gbm* package.[105] To assess performance, metrics were derived with the *ROCR* package (AUC, sensitivity, and specificity)[107] and compared to select the parameters for the final models. Combinations with the highest performance values were considered. Visualizations of performance metrics are shown in Figure S4. For the pseudoabsence model, we identified an optimal learning rate of 0.001, interaction depth of 4, and a maximum number of trees of 25000. This option had the second highest AUC while optimizing sensitivity, at a very small cost to specificity.

Phylogenetic analyses

We used the above bat phylogeny for analyses of phylogenetic signal in anthropogenic roosting and the evolution of this trait across bats. In all analyses, we focused on known anthropogenic roosting status and assessed sensitivity of results after including pseudoabsences (n = 234).

We first used the *caper* package to calculate D in binary anthropogenic roosting, where a value of 1 indicates a phylogenetically random trait distribution and a value of 0 indicates phylogenetic clustering under a Brownian motion model of evolution.[94] Significant departure from either model was quantified with a randomization test (1,000 permutations). However, because traits may also arise under a punctuated equilibrium model of evolution, we also used a graph-partitioning algorithm, phylogenetic factorization, to flexibly identify clades with different propensity to roost in anthropogenic structures at various taxonomic depths.[70] Phylogenetic factorization partitions a phylogeny by iteratively identifying edges in a tree that maximize an objective function contrasting species separated by each edge; in this case, we used generalized linear models (binary anthropogenic roosting status) that also adjusted for citation counts.[108] We used the *phylofactor* package for this analysis and determined the number of phylogenetic factors to retain using Holm's sequentially rejective 5% cut-off for the family-wise error rate.[98]

To reconstruct the evolution of anthropogenic roosting across the bat phylogeny, we first used the *diversitree* package to fit candidate BiSSE models of trait-dependent diversification using maximum likelihood.[109] We used Akaike's information criterion (AIC)[110] and Akaike weights (w_i) to compare among a full BiSSE model (where speciation, extinction, and transition rates can vary between natural and anthropogenic roosting states; $\lambda_0 \neq \lambda_1$, $\mu_0 \neq \mu_1$, $q_{01} \neq q_{10}$) and eight constrained models, including an all-rates-different model with trait-independent speciation and/or extinction ($\lambda_0 = \lambda_1$ and/or $\mu_0 = \mu_1$, $q_{01} \neq q_{10}$), an irreversible model ($\lambda_0 \neq \lambda_1$, $\mu_0 \neq \mu_1$, $q_{10} = 0$) and variants with trait-independent speciation and/or extinction ($\lambda_0 = \lambda_1$ and/or $\mu_0 = \mu_1$, $q_{10} = 0$), and an equal rates model ($\lambda_0 = \lambda_1$, $\mu_0 = \mu_1$, $q_{01} = q_{10}$). We then used the most competitive BiSSE model (i.e., ΔAIC <2 and parsimony) and a Markov chain Monte Carlo (MCMC) sampling approach to estimate the posterior distribution of each parameter.[111] MCMC used an exponential prior, maximum likelihood estimates from BiSSE for starting values, and slice sampling, with the tuning parameter w set as the range of each BiSSE parameter via an initial chain of 100 steps. Final chains were run for 2,000 steps with the first 20% discarded as burn-in. We used the *posterior* and *ggdist* packages to summarize resulting posterior distributions. The posterior means of transition rates were lastly used to perform stochastic character mapping (n = 1,000 simulations) over the bat phylogeny with the *phytools* package.[112,113] We fixed the basal node to originate with natural roosting, given that the earliest bat fossils predate *Homo sapiens* by over 50 million years.[114] Stochastic character maps were used to reconstruct natural and anthropogenic roosting lineages through time and to show mean posterior probabilities of anthropogenic roosting across the bat phylogeny.[115]