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Highlights

The frequency of urban birds is higher than that of rural and peri-urban areas

Habitat structure and anthropogenic noise shape acoustic space of urban birds

Bird dominance frequency is increased by urbanization and low-frequency noise

Vegetation density and height reduce the upward trend of bird dominance frequency

Article

Anthropogenic noise and habitat structure shaping dominant frequency of bird sounds along urban gradients

Zezhou Hao,[1] Chengyun Zhang,[2] Le Li,[1] Bingtao Gao,[1] Ruichen Wu,[1] Nancai Pei,[1,*] and Yang Liu[3,4,*]

SUMMARY

The shifts of bird song frequencies in urbanized areas provide a unique system to understand avian acoustic responses to urbanization. Using passive acoustic monitoring and automatic bird sound recognition technology, we explored the frequency variations of six common urban bird species and their associations with habitat structures. Our results demonstrated that bird song frequencies in urban areas were significantly higher than those in peri-urban and rural areas. Anthropogenic noise and habitat structure were identified as crucial factors shaping the acoustic space for birds. We found that noise, urbanization, and open understory spaces are factors contributing to the increase in the dominant frequency of bird sounds. However, habitat variables such as vegetation density and tree height can potentially slow down this upward trend. These findings offer essential insights into the behavioral response of birds in a variety of urban forest habitats, with implications for urban ecosystem management and habitat restoration.

INTRODUCTION

Bird sounds play a crucial role in courtship rituals, territorial defense, alarm signaling, and other aspects vital for survival and reproduction.[1] The structure of bird sounds is shaped by species-specific evolutionary processes and adaptive pressures. They also serve as direct evidence revealing the impact of urbanization on biodiversity.[2] Anthropogenic noise and changes in vegetation structure are two important factors contributing to the loss of functional bird habitats during urbanization.[3] The increasing noise in urban environments due to the proliferation of human-made facilities (such as transportation and industries) may hinder bird adaptation to urban areas.[4] During the process of urbanization, urban forests and other green spaces have become new refuges for urban birds, with vegetation serving a crucial role in mitigating anthropogenic noise and creating quiet spaces.[5] Consequently, understanding the interactive effects of anthropogenic noise and habitat structure on bird sounds is essential for gaining insights into avian adaptability and ecological responses in urban environments.

The characteristics of anthropogenic noise include high amplitude and mostly low-frequency sounds (typically <4 kHz) that overlap with bird signals, reducing the effective space for communication.[6] Noise disrupts the transmission and reception of birdsongs, forcing them to employ adaptive strategies to sustain effective sound communication. In the face of anthropogenic noise, birds exhibit a range of behavioral adjustments, including changes in singing frequency and pitch and reduced song complexity and diversity,[7,8] as well as alterations in song amplitude and the duration.[9–12] Among the strategies for regulating bird vocalizations, frequency regulation has been the focus of previous studies. Increasing the minimum or dominant frequency is one of the strategies employed by many oscine birds to cope with noise interference.[13–15] High-energy noise occupying low-frequency spaces prompts birds to shift their singing frequencies to a higher range to improve audibility and propagation efficiency.[16] Complex spatial structures, such as forest habitats should favor low-frequency signals, as high-frequency signals are more susceptible to reverberation and echo effects.[17] Moreover, there are also species-specific responses and adaptations to urban environments.[18] However, in certain species, noise seems to be the primary driving factor underlying frequency shift, as vocalization frequencies exhibit an increase alongside escalating noise levels across diverse habitats.[19] Nevertheless, studies on single species solely demonstrate a rise in vocalization frequency when exposed to amplified noise levels within less urbanized regions.[20] Research involving multiple species is essential to fully comprehend how anthropogenic noise affects biodiversity, as it unveils trends and effects that may be missed in studies focusing on a single species. Moreover, multispecies research helps to clarify the mechanisms by which bird vocalizations react to noise in urban environment.[21]

The habitat structure of urban green spaces is a crucial factor influencing bird singing behavior, jointly shaping the acoustic niche of birds in urban environments. The interior vegetation structure and spatial structure of forests influence attenuation and reflection of sound.[22] This has an impact on the propagation of both noise and birdsongs. Vegetation absorbs, scatters, and reflects noise waves, reducing the intensity and
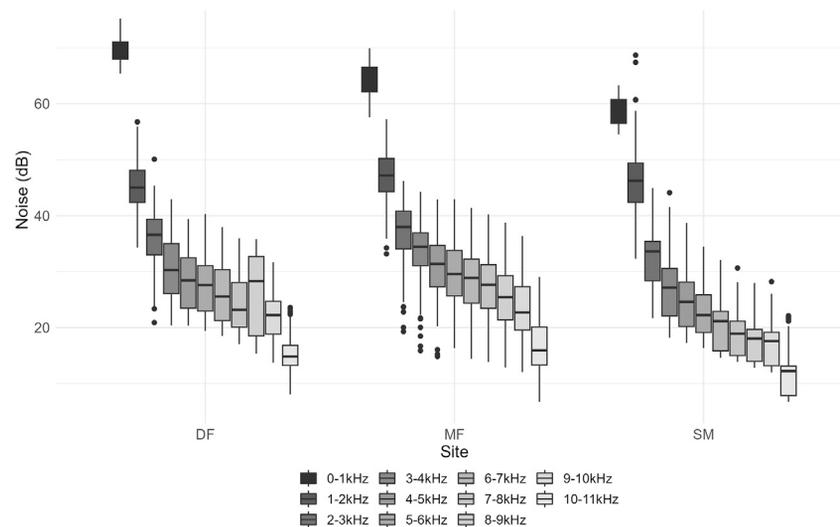
Figure 1. Boxplots showed the value of the noise level in different frequency bands of all three urban gradients in this study

Note: The colors in the boxplots represent frequency ranges from dark gray to light gray, corresponding to frequency intervals such as 0–1 kHz, 1–2 kHz, 2–3 kHz, 3–4 kHz, 4–5 kHz, 5–6 kHz, 6–7 kHz, 7–8 kHz, 8–9 kHz, 9–10 kHz, 10–11 kHz. Data are represented as mean $\pm$ SEM.

propagation distance of noise, thus mitigating noise disturbance to birds to some extent.[23,24] Research has confirmed the noise-reducing effect of plant communities in urban areas. Structural features such as the width, canopy structure, and configuration of plant communities all influence their noise-reducing capability.[25,26] Measurements of traffic noise intensity at different greenbelt widths showed that larger green spaces had greater noise reduction capacity.[27] Furthermore, vegetation structure directly or indirectly affects the propagation conditions of birdsongs.[28] Canopy structure is a key factor influencing birdsongs,[29] and variables like canopy height variation,[30] leaf height diversity,[31] and vegetation cover[32] all show correlations with birdsongs. Habitat vegetation structure constructs the acoustic space for birds, providing them with relatively quiet surroundings for vocalization transmission and reception. This enables them to communicate effectively, maintain social connections, and adapt to the complex noise background in urban environments.

This study explores the impact of anthropogenic noise and habitat structure on the dominant frequency of birdsong, which is defined as the frequency corresponding to the maximum amplitude of bird vocalizations.[33,34] Previous studies have shown that increasing the minimum frequency of vocalizations is a common strategy employed by birds to cope with low-frequency urban noise.[20] Some studies have also revealed that raising the dominant frequency is an adaptive strategy employed by certain bird species to mitigate noise interference.[35] Because urban biodiversity conservation is challenged by changes in habitat structure brought about by urbanization and the growing disturbance caused by anthropogenic noise,[36] examining bird song adaptation to urbanization can unravel processes that maintain urban biodiversity. Therefore, this research focuses on two principal questions, which are as follows. Do the dominant frequencies of bird calls vary across various urbanized areas? What are the specific habitat variables that influence the dominant frequencies when there are disparities, and what mechanisms exert their influence?

In this study, we constructed an automatic bird vocalization recognition model based on convolutional neural networks (CNNs) to analyze the dominant frequencies of sounds for six common songbird speciesin urban areas of southern China. By deciphering the variation mechanism of vocalization information for generalist bird species in the context of urban noise and vegetation structure, we aim to reveal how birds adjust their singing behavior in response to noise interference and the effects of urbanization on ecological community diversity. We hypothesize that the dominant frequency of bird sounds varies across different urbanized areas, primarily influenced by a combination of anthropogenic factors (noise and urbanization) and vegetation characteristics (crown base height and vegetation density). This study will gain a deeper understanding of the sound adaptation mechanisms of birds during the process of urbanization and explore the interaction between birdsongs adaptation and forest structure, as well as their importance for bird social communication, ecosystem stability, and urban ecological environment.

RESULTS

The energy distribution characteristics of ambient anthropogenic noise

According to the energy distribution of anthropogenic noise in various frequency ranges, the anthropogenic noise surrounding the study area is primarily concentrated in the 0–1 kHz range (Figure 1). The environmental noise levels in the 0–1 kHz range were calculated at different urbanization gradient sites. The Dafushan Forest Park (DF) sites close to the city showed the highest average environmental noise level (mean $\pm$ standard deviation: 69.7 ± 2.23 dB). The Mafengshan Forest Park (MF) sites in the urban periphery had the next highest average environmental noise level (64.4 ± 2.95 dB), while the Shimen National Forest Park (SM) sites in the urban outskirts exhibited the lowest average environmental noise level (58.6 ± 2.54 dB) ($F_{2,244} = 313.49$, $p < 0.05$).
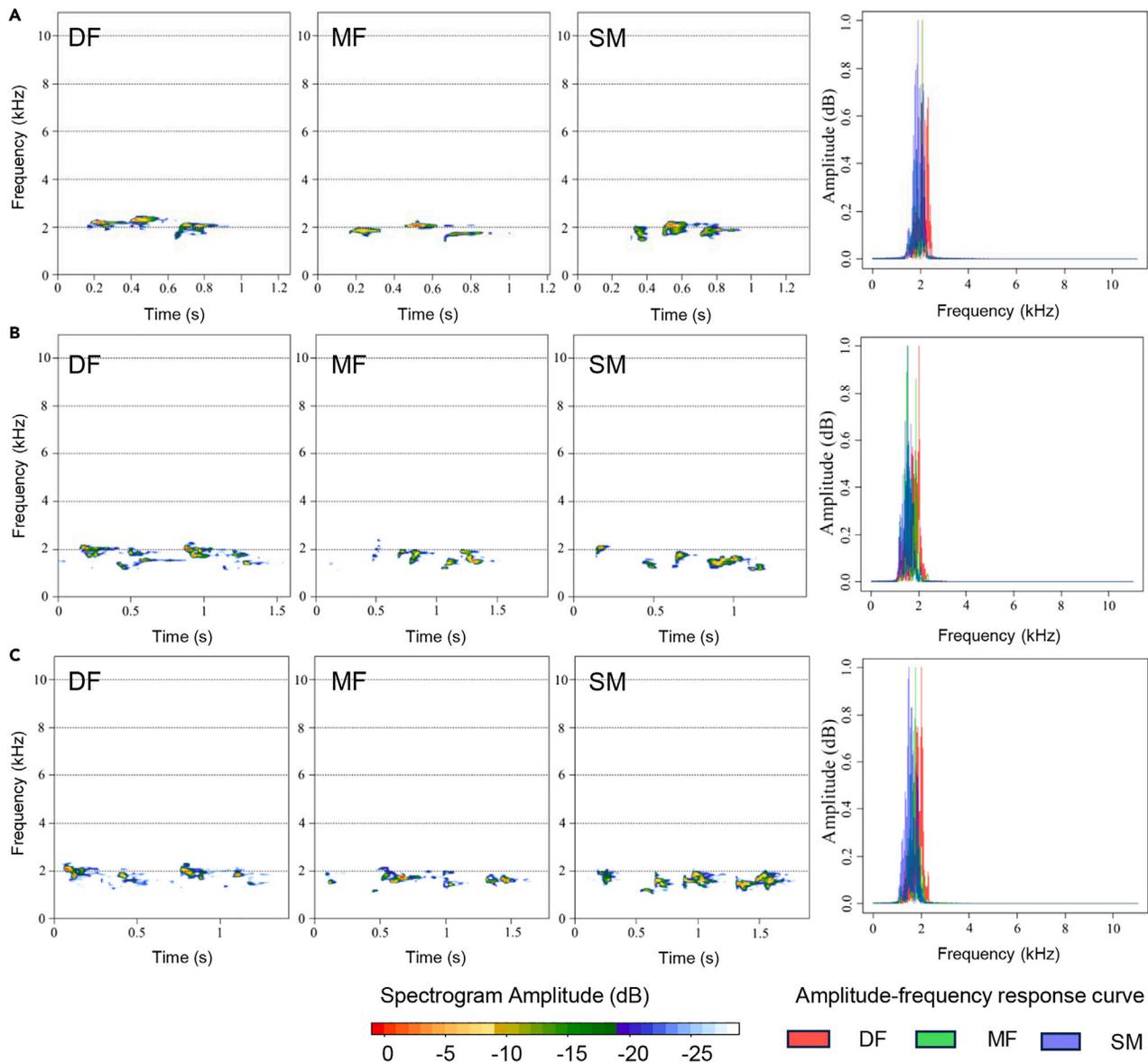
Figure 2. Bird sounds spectrograms and power spectra of dominant frequencies under three urban gradients
(A–C) Example of (A) chestnut bulbul, (B) red-whiskered bulbul, and (C) light-vented bulbul.

Dominant frequency differences between sites and species

A two-way ANOVA was performed to compare the differences in birdsong at both the sites and species levels. For the site factor, the ANOVA showed a significant effect ($F_{2, 1062}$ = 117.19, $p < 0.05$), indicating significant differences in bird vocalizations among different sites. Further *post hoc* comparisons revealed that in the urban environment close to the city (DF), the dominant frequency of bird vocalizations was significantly higher than in the urban periphery (MF) and urban outskirts (SM) sites ($p < 0.01$ - Figures 2 and 3). For the species factor, the ANOVA showed a highly significant effect ($F5, 1062$ = 2220.57, $p < 0.05$), indicating significant differences among different bird species. Further *post hoc* comparisons revealed that, except for red-whiskered bulbul and light-vented bulbul, which showed no significant differences between sites, the dominant frequency differences among other species were found to be statistically significant. There was a statistically significant interaction between site and species level on dominant frequency ($F10, 1062$ = 9.00, $p < 0.05$). Additionally, multiple comparisons were used to test the influence of the urbanization gradient on the frequency distribution of bird vocalizations (Table 1). Specifically, in the urban environment close to the city (DF), the dominant frequency of bird vocalizations was significantly higher compared to bird vocalizations in areas further away from the city (MF and SM) ($p < 0.05$). However, for the chestnut bulbul (*Hemixos castanonotus*), red-whiskered bulbul (*Pycnonotus jocosus*), light-vented bulbul (*Pycnonotus sinensis*), and scarlet minivet (*Pericrocotus speciosus*), the differences in dominant frequency among sites further from the city were relatively small ($p > 0.05$). Although most comparisons reached statistical significance, it appears
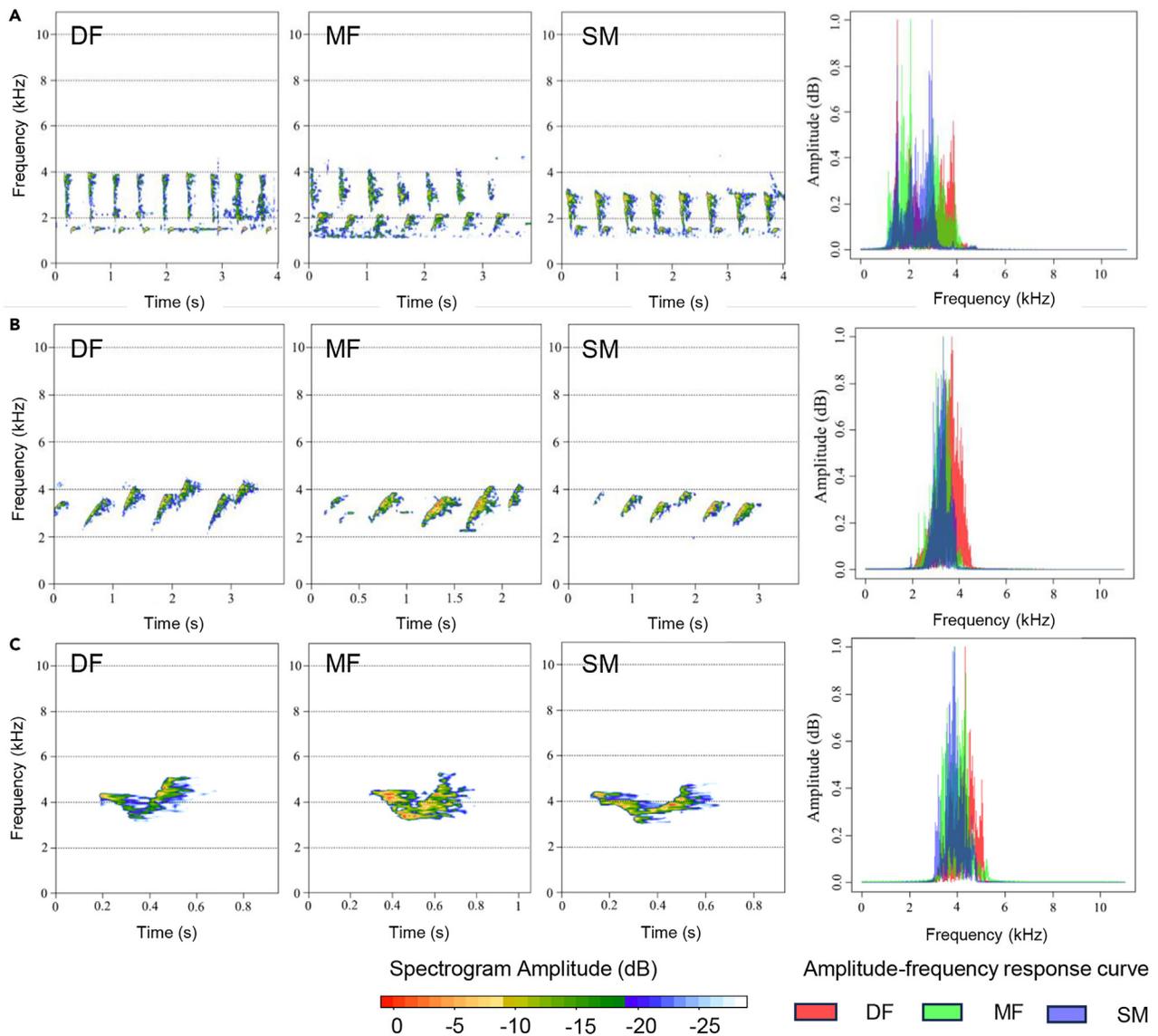
Figure 3. Bird sounds spectrograms and power spectra of dominant frequencies under three urban gradients
(A–C) Example of (A) common tailorbird, (B) scarlet minivet, and (C) yellow-browed warbler.

that in urban areas birds tend to sing at higher frequencies, which aligns with a potential influence of ambient noise on bird songs. For the common tailorbird (*Orthotomus sutorius*) and yellow-browed warbler (*Phylloscopus inornatus*), significant differences in dominant frequency were observed among different sites (p < 0.05). In summary, these results indicate that different bird species exhibit differential sensitivity to noise, and this variation is influenced by the degree of urbanization.

Dominant frequency responses to noise and habitat structure

The model sets for species with higher inherent dominant frequencies, such as the common tailorbird, yellow-browed warbler, and scarlet minivet, showed more complex combinations of explanatory variables (Table S1) than those for species with lower inherent frequencies, like the chestnut bulbul, red-whiskered bulbul, and light-vented bulbul. Furthermore, the goodness-of-fit tests indicated that models for species with higher inherent dominant frequencies had better fits (common tailorbird: $R^2 = 0.28$, scarlet minivet: $R^2 = 0.29$, and yellow-browed warbler: $R^2 = 0.32$), compared to somewhat weaker predictive values for species with lower inherent dominant frequencies (chestnut bulbul: $R^2 = 0.18$, red-whiskered bulbul: $R^2 = 0.11$, and light-vented bulbul: $R^2 = 0.19$).

Linear mixed model (LMM) analysis of the effects of anthropogenic noise and habitat characteristics on the dominant frequency of bird vocalizations is summarized in Figure 4. The results revealed significant correlations between dominant frequencies and various

Table 1. Statistical results of multiple pairwise comparisons between the species

Species	Sites	Dominant frequency (Hz)	Group 1	Group 2	df	F	p value
Chestnut bulbul (*Hemixos castanonotus*)	DF	3260 ± 278	DF	MF	1062	3.38	<0.01
	MF	3047 ± 243	DF	SM	1062	5.18	<0.01
	SM	2954 ± 288	MF	SM	1062	1.80	0.22
Red-whiskered bulbul (*Pycnonotus jocosus*)	DF	2732 ± 233	DF	MF	1062	2.73	0.02
	MF	2570 ± 224	DF	SM	1062	4.27	<0.01
	SM	2553 ± 247	MF	SM	1062	1.54	0.37
Light-vented bulbul (*Pycnonotus sinensis*)	DF	2640 ± 231	DF	MF	1062	2.74	0.02
	MF	2483 ± 129	DF	SM	1062	4.07	<0.01
	SM	2434 ± 152	MF	SM	1062	1.32	0.56
Common tailorbird (*Orthotomus sutorius*)	DF	4548 ± 600	DF	MF	1062	8.11	<0.01
	MF	4198 ± 779	DF	SM	1062	12.57	<0.01
	SM	3636 ± 203	MF	SM	1062	4.46	<0.01
Scarlet minivet (*Pericrocotus speciosus*)	DF	5149 ± 196	DF	MF	1062	3.88	<0.01
	MF	4861 ± 118	DF	SM	1062	4.38	<0.01
	SM	4865 ± 203	MF	SM	1062	0.50	1.00
Yellow-browed warbler (*Phylloscopus inornatus*)	DF	6221 ± 362	DF	MF	1062	8.68	<0.01
	MF	5302 ± 602	DF	SM	1062	4.32	<0.01
	SM	5773 ± 480	MF	SM	1062	−4.36	<0.01

environmental variables, especially anthropogenic noise, urbanization (*city*), crown base height, and vegetation density. The results of the LMM indicated a predominantly positive influence of urbanization levels and anthropogenic noise on the dominant frequency of bird sounds, suggesting an increase in the dominant frequency for most bird species concurrent with the rise in anthropogenic noise and urbanized area. In terms of habitat vegetation factors, an increase in crown base height similarly led to an elevation in the dominant frequency for some bird species, whereas an increase in vegetation density and tree height had a negative impact on the dominant frequency of bird sounds. These outcomes demonstrate varied responses of different bird species to environmental variables. Specifically, anthropogenic noise exhibited a significant positive effect on five bird species, excluding the light-vented bulbul (p = 0.38). The rise in urbanization level significantly increased the dominant frequency of sounds for the light-vented bulbul, scarlet minivet, and yellow-browed warbler, while the impact was not significant for the other three species. Regarding vegetation-related variables, an increase in crown base height positively correlated with the dominant frequency of sounds in the red-whiskered bulbul, light-vented bulbul, scarlet minivet, and yellow-browed warbler (p values all less than 0.05) but had no significant impact on the chestnut bulbul (p = 0.38) and common tailorbird (p = 0.26). An increase in vegetation density had a significant negative effect on birds with higher dominant frequencies, but not on those with lower frequencies. An increase in tree height was significantly negatively correlated with the dominant frequency of sounds in the chestnut bulbul (p < 0.01), but not in other bird species.

DISCUSSION

By analyzing the effects of noise and vegetation structure on the dominant frequency of bird songs, this study aims to elucidate the distinct impacts of various environmental factors on bird sound frequencies and further deepen our understanding of the mechanisms that contribute to urban biodiversity conservation. Firstly, our research findings show significant variations in the dominant frequency of bird calls across different urbanized areas. The ANOVA analysis results indicate that, in sites with higher urbanization levels (DF), bird dominant frequencies were significantly higher compared to urban periphery (MF) and urban outskirts (SM) sites. Based on the results of the LMM model, noise and urbanization are the primary factors contributing to the increase in bird dominant frequencies, consistent with previous research that highlights the importance of noise environments and urbanization levels on birdsongs.[18,34,37–39] However, it is crucial to note that our results indicate variation in noise sensitivity among different bird species.[40] Specifically, chestnut bulbul, red-whiskered bulbul, light-vented bulbul, and scarlet minivet showed relatively small differences in dominant frequency among sites further from the city, whereas common tailorbird and yellow-browed warbler exhibited significant discrepancies in their dominant across different sites. These differences may stem from the ecological characteristics and adaptability of different species, as some birds can adapt to sound propagation under varying noise levels and vegetation structure conditions, while others may be more sensitive to environmental changes, contributing to the decline of urban biodiversity.[41] Additionally, based on the results of the LMM analysis, this study also found that vegetation density and tree height have a negative impact on the dominant frequency of bird, while understory height shows a positive influence. Although our findings indicate that birds tend
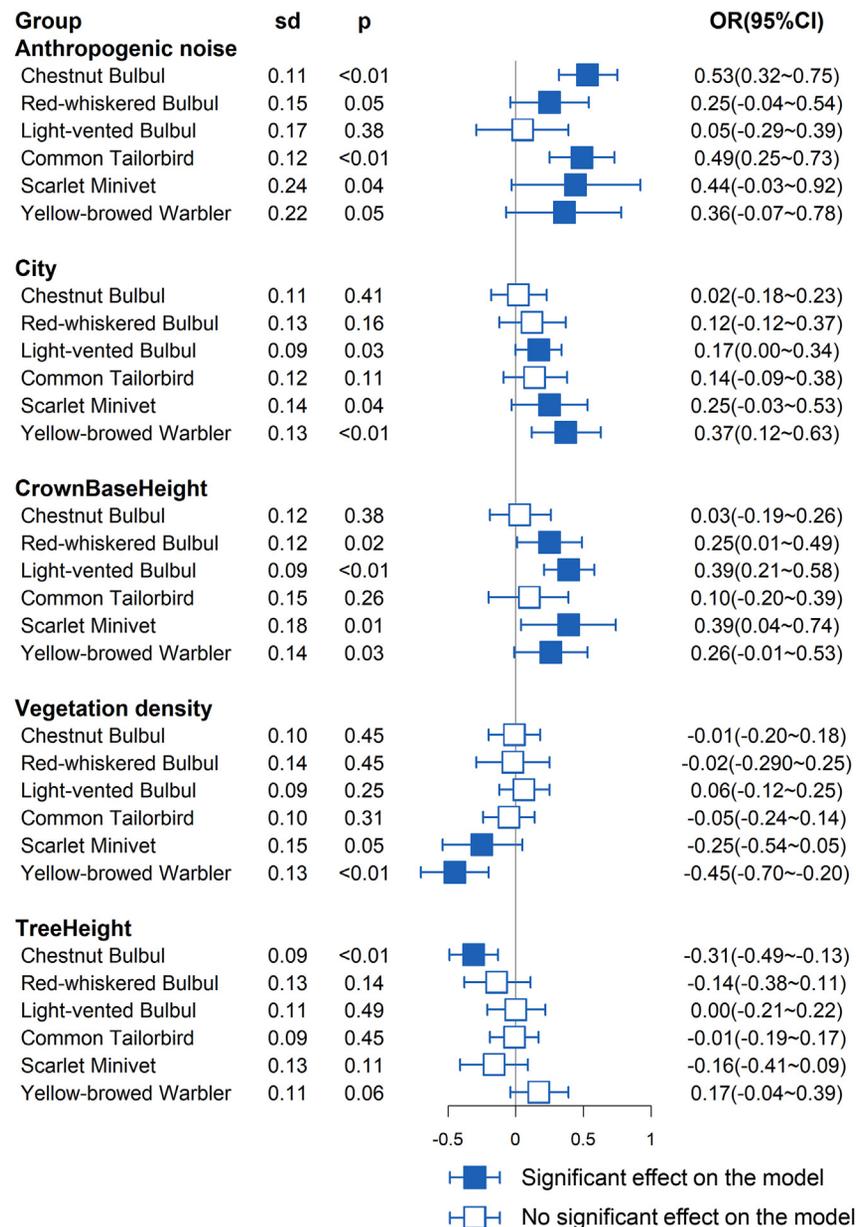
Figure 4. Effect sizes for explanatory variables are derived from the complete averaged coefficients of the model
The plot displays estimates using mean values (depicted by blue boxes) and their corresponding 95% confidence intervals (shown as horizontal lines). Completely blue boxes denote factors that exert a significant impact on the average model, whereas blank boxes indicate insignificance of impact.

to sing at higher dominant frequencies in more urbanized areas, the presence of a more complex vertical vegetation structure in habitats can potentially slow down this upward trend. The presence of dense vegetation promotes sound isolation, highlighting the important function that vegetation plays in the acoustic environment of birds.[42] Abundant vegetation structure not only provides suitable habitats and foraging areas but may also offer birds an improved acoustic environment, facilitating the propagation of their sounds and interspecies communication. Nevertheless, further investigation is required to determine whether birds in denser vegetation do not need to raise their frequencies in response to anthropogenic noise, or if the influence of vegetation structure causes birds to make lower-frequency sounds, which is in line with the acoustic adaptation hypothesis.

The impact of urbanization on bird communities is manifested not only in noise pollution but also in habitat fragmentation and reduced habitat functionality caused by urban development, directly affecting the foraging behavior of urban birds. Among the six common urban bird species studied, chestnut bulbul, red-whiskered bulbul, and light-vented bulbul are omnivorous birds with lower vocalization

Table 2. Bird activity, feeding, and residence characteristics

Order	Family	Scientific name	Common name	Activities level	Feeding group	Residence type
Passeriformes	Cisticolidae	*Orthotomus sutorius*	common tailorbird	ground	insectivore	resident
Passeriformes	Campephagidae	*Pericrocotus speciosus*	scarlet minivet	canopy	insectivore	resident
Passeriformes	Phylloscopidae	*Phylloscopus inornatus*	yellow-browed warbler	canopy	insectivore	winter visitor
Passeriformes	Pycnonotidae	*Pycnonotus jocosus*	red-whiskered bulbul	canopy	omnivore	resident
Passeriformes	Pycnonotidae	*Hemixos castanonotus*	chestnut bulbul	canopy	omnivore	resident
Passeriformes	Pycnonotidae	*Pycnonotus sinensis*	light-vented bulbul	medium canopy	omnivore	resident

frequencies, while scarlet minivet, yellow-browed warbler, and common tailorbird are insectivorous birds with higher vocalization frequencies (Table 2).[43] This provides some clues for analyzing the reasons for the differences in dominant frequency changes and environmental responses among different dietary groups. In our study, we observed a significant decrease in dominant frequency for insectivorous birds in urban environments. Insectivorous birds are typically particularly sensitive to human disturbances such as habitat loss and fragmentation.[44,45] Some studies suggest that the vulnerability of these birds to various direct threats arises from their evolutionary feeding specialization and limited dispersal ability.[46] Understory insectivores are an important focus of bird diversity conservation and research, as they are highly responsive to environmental changes caused by human interference and can serve as sentinels for shifts in forest ecosystems.[47] The key findings of our study indicate that, compared to omnivorous birds, insectivorous birds exhibit greater frequency changes in response to urban noise disturbances. Unlike a previous study which relied on evaluation metrics such as species richness and abundance,[48] this study suggests that monitoring changes in the vocalizations of insectivorous birds may be a potential indicator of their response to environmental changes. Future research should be conducted on more representative lineages of insectivorous birds to both verify if frequency adjustment is a general strategy among this dietary guild and assess whether the adjusted vocal frequency is beneficial for their adaptation to habitat environments under human disturbance. Such research will contribute to a more comprehensive understanding of bird ecological adaptability and behavioral responses, providing more specific guidance and recommendations for the conservation and management of urban ecosystems.

This study indicates that differences in bird vocalization frequencies may influence their adaptability to environmental changes. Birds with lower-frequency sounds, which propagate better in complex settings, can communicate effectively in noisy environments but are vulnerable to low-frequency noise interference.[49] In contrast, birds with higher-frequency sounds are less impacted by noise but more affected by absorption in dense vegetation.[24] Bird size correlates with vocalization frequency: larger species emit lower frequencies, while smaller species have higher frequencies.[50] In this study, larger birds like the chestnut bulbul and red-whiskered bulbul exhibited an average vocal frequency increase by 230 Hz, while smaller birds like the yellow-browed warbler and common tailorbird showed increases up to 548 Hz, in urban environments. Notably, the common tailorbird's frequency decreased by 912 Hz from less to more urbanized areas, a more significant change compared to the red-whiskered bulbul's smallest variation of 179 Hz. This suggests that birds with higher inherent frequencies adapt their vocalizations more in response to urban noise.[51,52] When shifting vocal frequencies, birds balance between minimizing noise interference and adapting to vegetation. Lower frequencies are useful in complex areas but are noise prone, while higher frequencies suit dense vegetation but run with the risk of absorbing energy. This difference reflects the behavioral responses and adaptability mechanisms of birds in different environments, providing a deeper understanding of their survival and reproductive strategies in complex ecosystems.

Our research results support the hypothesis that birds adapt to low-frequency noise interference by adjusting their sound frequencies, among other strategies. Furthermore, we have validated the impact of habitat factors such as spatial configuration and vegetation structure on the frequency selection of bird sounds, aiding in a better understanding of the complexity and adaptability of avian acoustic ecology. The consideration of vegetation complexity in urban bird habitat conservation and restoration efforts should be prioritized, based on the findings of this study. This will contribute to providing birds with suitable vocalization spaces and mitigating the adverse impact of urbanization on avian biodiversity. This study demonstrates a significant elevation in the dominant frequency of bird calls in urban environments, correlating with higher crown base height. These findings indicate that vegetation openness in understory spaces intensifies noise disturbance, which in turn disrupts avian vocal communication.[53] Therefore, in designing the external buffer zones of habitats, it is critical to consider mitigating traffic, industrial, and other anthropogenic noise, for instance, by enhancing the spatial complexity of urban green space vegetation or by using acoustic isolation structures to produce necessary noise buffers and provide a quiet acoustic environment. Simultaneously, in designing the core areas of habitats, attention should be paid to creating open and semi-open spaces through methods like creating canopy gaps,[54] to improve the efficiency of bird call signal transmission. Protecting urban birds and restoring urban biodiversity will be aided by rethinking urban bird habitats from an acoustic perspective and offering a variety of acoustic settings.

Previous studies on animal acoustic behavior have primarily relied on linear scales, such as hertz or kilohertz, to measure frequency-related parameters. However, in this study, a log-transformation approach has been employed for assessing the dominant frequency. This method aligns more closely with how animals perceive sound frequencies and modulations in vocalization. Linear methods may potentially lead to an overestimation of variations in high-frequency samples in comparison to low-frequency ones, particularly when making interspecies comparisons.[55] Therefore, characterizing these distinctions using log-transformed frequencies, rather than linear scales, is more suitable. Employing

log transformation in sound frequency analysis enhances statistical robustness and deepens our understanding of bird vocalizations, making it a recommended approach in studies of animal communication and evolutionary behaviors.[56]

Limitations of the study

There are some limitations to be aware of. Firstly, our research focused on specific geographic regions and a limited number of bird species. The results may not be applicable to other areas or bird communities with different ecological characteristics. Future studies could cover a wider range of locations and bird species to enhance the generalizability of the findings. Secondly, the bird sound data in our study were obtained through passive acoustic monitoring. The distance between the recording devices and singing spot of birds could not be controlled, which prevented us from investigating the sound intensity of bird sounds. In future, we hope to improve the data collection methods or sound intensity algorithms to address this limitation. Finally, the composition of environmental sounds is complex, and high-frequency insect noise (such as cicadas) may also be one of the factors influencing bird vocalizations,[57] which deserves further attention in future research. While our study has made important progress in exploring the factors influencing bird sound in urban environments, further research is needed to overcome the aforementioned limitations and gain a deeper understanding of the impact of urbanization on bird vocal behavior.

STAR★METHODS

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

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109056.

AUTHOR CONTRIBUTIONS

Conceptualization, Z.H., C.Z., and Y.L.; funding acquisition, Z.H. and N.P.; data collection, Z.H., L.L., B.G., and R.W.; analysis, Z.H., L.L., B.G., and R.W.; visualization, Z.H.; writing – original draft, Z.H. and Y.L.; writing – review and editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw data and analysis scripts	Open Science Framework	osf.io/976wn
Software and algorithms		
R 4.2.1	R Project	https://www.r-project.org/
Python 3.10.9	Python Software Foundation	https://www.python.org
Avisoft SASLab Pro	Avisoft Bioacoustic	https://www.avisoft.com/
scikit-maad	scikit-maad development team	https://scikit-maad.github.io/

RESOURCE AVAILABILITY

Lead contact

Requests for further information or materials should be directed to and will be fulfilled by the lead contact, Yang Liu (liuy353@mail.sysu.edu.cn).

Materials availability

This study did not generate any new unique reagents.

Data and code availability

- The datasets and analyses code from the current study have been deposited in a public repository. https://osf.io/976wn/.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this work paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

The bird song data used in the study were all obtained through passive acoustic monitoring in the wild, therefore this study does not use experimental models.

METHOD DETAILS

Field recordings

The study was conducted in Guangzhou, which serves as the capital of Guangdong Province. It is one of the four core cities in the Guangdong-Hong Kong-Macao Greater Bay Area in southern China. The region is characterized by subtropical evergreen broad-leaved forests, with hills and mountains covered by secondary forests and plantations. Over the past several decades, rapid urban growth has occurred in select areas within the region. To examine the impact of urbanization on bird sounds, we selected forest parks located in three urbanization gradients as study areas, namely Shimen Forest Park (suburban), Maofengshan Forest Park (peri-urban) and Dafushan Forest Park (urban). And Shimen National Forest Park (SM) was more than 5 km away from highways and 20 km away from urban area; Mafengshan Forest Park (MF) was more than 2 km away from highways and 5 km away from urban area, and Dafushan Forest Park (DF) was less than 1 km from highways and urban area (Figure S1). In each gradient, we conducted passive acoustic monitoring in three urban forests, totaling nine monitoring points. This study design enabled us to analyze the bird sounds within different urbanization contexts and assess the impact on various ecological factors and dynamics. To validate hypotheses, we proposed three selection criteria based on all species observed during the study period: 1) The selected species' sounds must be recorded at all nine monitoring points. 2) Each bird species should have a minimum of twenty individuals recorded. 3) The repertoire of vocalizations should remain consistent across different monitoring points. Based on these criteria, only the following six species were included in the analysis (Table 2): Common Tailorbird, Scarlet Minivet, Light-vented Bulbul, Red-whiskered Bulbul, Chestnut Bulbul, and Yellow-browed Warbler. In total, 1080 individuals from these six species were recorded at the nine monitoring points.

We placed a total of nine Song Meter SM4 in different urban forests along an urbanization gradient (Figure S1). Each gradient had three devices. The recording setup involved capturing ambient sounds for 1 min every 10 min over a one-year period from October 19, 2021, to October 9, 2022, which resulted in 1,296 daily samples for each device. To ensure comprehensive recordings of bird sounds and anthropogenic noise, we used a stereo setup with 16-bit audio and a 32 kHz sampling rate. The recording equipment was mounted on a healthy tree with a DBH of ≥10 cm to avoid ground reverberation. To minimize the impact of insect sounds, such as cicadas, as well as natural geophonic

sounds like rain and wind, on bird sounds, we specifically chose audio files recorded during the dry season (from October to May of the following year). The recordings were captured during periods of stable weather conditions and were specifically chosen for the analysis of bird sounds in this study.

Sound analysis

Anthropogenic noise measurement

The sound pressure level (dB SPL) was utilized to compare the ambient noise level. 1) Sound pressure level measurement: the spl module in scikit-maad, which is a collection of functions used to quantitatively measure the sound pressure energy of acoustic waves in Python. The recording samples used for estimating the noise level were manually selected to avoid interference from other non-noise elements. In the end, the durations of the noise files from DF, MF, and SM were 104 min, 96 min, and 47 min, respectively. Regarding the specific settings for the acoustic recording unit (SM4) parameters, the microphone sensitivity was set to -35 dBV, the preamp and postamp gains were set to 26 + 16 dB, and the voltage range of the analog-to-digital converter was set to 2. Furthermore, the sound pressure level was calculated for eleven frequency ranges: 0–1 kHz, 1–2 kHz, 2–3 kHz, 3–4 kHz, 4–5 kHz, 5–6 kHz, 6–7 kHz, 7–8 kHz, 8–9 kHz, 9–10 kHz, and 10–11 kHz. These calculations were performed to analyze the distribution of energy in anthropogenic noise.

Bird sounds detection and quantification

A one-step progressive representation transfer learning method for bird sound detection was proposed. This method integrates self-supervised representation and supervised classification learning into a two-branch network and uses a time-dependent loss weight transfer strategy to transfer bird sound, and self-supervised representation learning to bird sound classification learning. This model emphasizes self-supervised representation learning during the early stages of training to maximize the similarities among bird sounds across different data augmentation versions. By utilizing the loss weight transfer strategy, the self-supervised bird sound representation learning transitions to supervised bird sound classification learning, thus enabling the model to acquire specific bird sound classification capabilities in the later stages of training. The method achieved a recognition accuracy of 98.2% on a bird vocalization dataset namely 'Birdsdata'. In contrast, this method outperformed self-supervised classification learning (SSCL) by 1.3% and supervised classification learning (SCL) by 2.9%.[58] In contrast to traditional bird behavior investigation methods, our approach (Figure S2), which combines passive acoustic monitoring and deep learning, minimizes the negative impact of observer activities on bird behavior during the sound collection process. Furthermore, it allows us to gather a more extensive range of bird vocalization information across various time and spatial scales, which is crucial for revealing the intrinsic connections between bird vocalizations and environmental changes.

Based on the aforementioned bird vocalization recognition model, we retained bird vocalization data with recognition confidence levels higher than 0.8. As a result, we successfully detected vocalizations from 44 different bird species, with a total duration of 2,665 min. Adhering to the three principles for selecting bird vocalizations, we ultimately identified vocalizations from 6 Passeriformes bird species as the subjects of our study. The Avisoft SASLab Pro Version 5.3 (Avisoft Bioacoustic, Berlin, Germany) was used to extract the dominant frequency information of bird vocalizations. The spectrogram settings were as follows: FFT length 1024 with 100% frame size and Hamming Window. We employed the automatic parameter measurement function to measure the dominant frequency parameters. The purpose of utilizing this function was to ensure consistency and minimize bias in measurements.[18,59] In the configuration of the automatic parameter measurements, a specific threshold (-10 dB) and hold time (25 ms) were applied to the spectrogram to identify the individual elements in the element separation function. For the analysis, we examined at least one vocalization for each individual included in this study. All vocalizations were measured individually and then averaged for each individual. Before taking the measurements, a cut-off frequency function was applied to the recordings of avian vocalizations. The determination of the cut-off frequency for each bird sound file was achieved through visual inspection of spectrograms, considering the spectral characteristics of vocalizations across different species. This process facilitated the removal of extraneous frequency ranges, thereby preserving the pertinent vocal components for subsequent analysis. Measurements of dominant frequency of bird sounds were log10-transformed before statistics analysis.

Habitat structure parameters

Vegetation structure parameters

The terrestrial laser scanner (TLS) has been utilized to characterize the structural diversity of canopies and provide precise estimations of forest structure indices.[60–62] In this study, vegetation structure parameters were measured by a RIEGL VZ-400i terrestrial laser scanner (RIEGL Laser Measurement Systems GmbH, Austria), which was mounted on a tripod. The VZ-400i operates at a wavelength of 1550 nm and has a laser pulse repetition rate set to 1200 kHz. It captures four returns per outgoing pulse and can record data up to a range of 250 m. To ensure comprehensive coverage, we utilized one central scanning position for each plot along with an additional four scanning positions (Step 1 of Figure S3). Each recording plot yielded high-resolution point cloud data spanning an area of up to 1,600 m^2. Prior to analysis, the point cloud data obtained from each scan RiSCAN Pro software's automatic registration module (developed by RIEGL Horn, Austria). Subsequently by Green Valley Company in China) was employed for further pre-processing steps including subsampling (with minimum points spacing set at 0.001), outlier removal (using neighbor points criteria: number = 10; multiples of standard deviations = 5), and ground point classification.

For accurate segmentation of forest point clouds into individual trees (Step 2 of Figure S3), we manually completed this task utilizing the TLS seed point editor function within the TLS forest module available in LiDAR 360. And we employed quantitative structure models (QSM) to

accurately measure the individual tree structures, enabling a nondestructive estimation of above-ground biomass that closely aligns with reference values obtained through destructive sampling.[63] The segmentation of individual trees within the nine recording plots was performed using Lidar 360, followed by the calculation of single-number tree attributes from the quantitative structure models using TreeQSM software in MATLAB.[64] Previous findings suggest that individual tree parameters, such as tree height and crown base height, may be key factors influencing bird diversity[65,66] and noise propagation.[67,68] Therefore, the aforementioned method primarily focuses on extracting individual tree height data, including tree height and crown base height. Subsequently, the height data of all individual trees within each plot are averaged for facilitating comparisons between sample sites.

Vegetation density is a potential factor influencing the propagation characteristics of both bird diversity[69,70] and urban noise.[26] Therefore, employing a voxel approach, we constructed a three-dimensional voxel information data frame (xyz) incorporating leaf area density (LAD) values to characterize the vertical diversity and density of forest structure at different horizontal heights with a resolution of 0.5 m (Step 3 of Figure S3). This voxel-based representation allowed for an intricate depiction of horizontal components within forest layers. Based on LAD values, Vegetation density at each sample site is determined by calculating the cumulative Leaf Area Density (LAD) across various heights. Furthermore, point cloud data were pixelized and vegetation structure parameters were computed utilizing the leafR package[71] in R language for analysis.

Urban structure parameters

The relative area of built-up (*city*) area was assessed within a 200-meter radius around the recording points. The previous research results suggest that within a 200-meter radius in this study area, bird sound exhibit the most pronounced response to changes in land cover.[72] Land-use information was acquired utilizing the Google Earth Engine platform and Sentinel-2A L1C level data spanning from January 2021 to April 2022. Following cloud removal from the satellite images, the land-cover labeling process was conducted through visual interpretation. Specifically, 128 reference points were employed for 'city' to manually assign land-cover types to the corresponding samples. Subsequently, the labeled samples were divided into training and validation subsets using a 70:30 split ratio, an essential step to prevent overfitting and ensure generalization. The land classification model was developed using the 'smileRandomForest' classifier from the Google Earth Engine's 'ee.Classifier' library, configured with 5 decision trees. Training of the classifier incorporated the designated class property ('landcover') and features extracted from the imagery within the training partition. Accuracy assessment was conducted, yielding an Overall Accuracy of 0.86 and KAPPA coefficient of 0.82. The trained classifier was used to classify the selected image. The resulting categorical image denoted land cover classes. To compute class areas, pixel areas were summed within each class using a grouped reducer, considering a specified geometry at 10-meter intervals.

QUANTIFICATION AND STATISTICAL ANALYSIS

One-way ANOVA was used to assess the differences in anthropogenic noise levels among three urbanization gradients (urban area, peri-urban area, and suburban area). The normality assumption was examined using the Shapiro-Wilk test ($p > 0.05$). The assumption of homogeneity of variances was assessed using the Levene's test, with a significance level of 0.05. To account for the occurrence of heteroscedasticity, the Welch one-way ANOVA test was employed, followed by pairwise comparisons using the Games-Howell test. Boxplots were created to visualize the distributional differences of noise levels across different frequency ranges. A two-way ANOVA was performed to compare the prominent frequencies of bird sounds across various levels of urbanization gradients. Normality, homogeneity of variances, and homogeneity of covariances ($p > 0.05$) were confirmed prior to the analysis. The dominant frequency was treated as the dependent variable, while sites and species were considered as independent variables in the two-way ANOVA. The interaction effect and main effect of each variable were tested. The statistically significant simple main effect was followed by conducting multiple pairwise comparisons between the species groups by site. To interpret all possible pairwise comparisons, we employed Bonferroni correction and considered statistical significance of the simple main effect analyses at a Bonferroni-adjusted alpha level of 0.025 (the current significance level of $p < 0.05$ divided by the calculated number of simple main effects, which is 2). The statistical analyses were performed using the R packages "tidyverse",[73] "ggpubr",[74] and "rstatix",[75] with a significance level (α) set at 0.05.

To allow hypothesis testing, we analyzed the variant effects of habitat variables on the dominant frequency of bird species using Linear Mixed Models (LMMs). A normality test on the dependent variable, the dominant frequency of different birds, was conducted to ensure that the residuals of the model adhered to a normal distribution, validating the assumptions underlying LMMs. In the LMMs, habitat variables hypothesized to influence the birds' dominant frequency were treated as fixed effects. The dominant frequency of different birds was analyzed as separate response variables, while recording points, potentially introducing variability in frequency measurements, were considered as random effects. To avoid multicollinearity in model selection, a Pearson correlation matrix was utilized. If a pair of covariates exhibited significant correlation (rho $\geqq |0.7|$), only the variable more relevant according to the hypothesis was retained. Consequently, seven variables were chosen as explanatory variables for subsequent analysis: *City, Noise, Density, TreeHeight, CrownBaseHeight*. All explanatory variables were standardized for model parameter estimate comparisons. The effects of these habitat variables on the dominant frequency of different bird species were assessed individually through a model selection procedure. Models with various combinations of habitat characteristics were ranked based on the Akaike Information Criterion corrected for small sample sizes (AICc). Model averaging was employed for models with a ΔAICc value less than 2.[76] Explanatory variables that significantly influenced the dominant frequency in the best-supported models were identified. The goodness-of-fit for the highest-ranked model was estimated using the fixed effect R^2 (marginal R^2), to understand the variance in dominant frequency explained by the fixed effects. Statistical analyses were performed using the "lme4",[77] "MuMIn",[78] and "aiccmodavg"[79] packages in R.