Cities alter the latitudinal diversity gradient of birds in North America

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Abstract

The latitudinal diversity gradient (LDG) is a widely recognized biogeographic pattern, yet its persistence under increasing human impacts remains unclear. Leveraging 17 million eBird records, we investigated how urbanization alters LDGs in North America. We quantified LDGs across 662 cities and their surroundings, and found that LDGs vary by season and native status: non-native species exhibited weak or no LDG, whereas native birds showed the strongest LDG during winter. Notably, native birds showed a significantly flatter winter LDG in cities than in surrounding areas. Although human population density generally reduced bird diversity, it exerted positive effects under cold conditions in high latitudes. These findings indicate that urbanization can reshape classic biodiversity patterns, with cities potentially acting as winter refuges for native birds at higher latitudes.

Keywords

Latitudinal diversity gradient; Bird diversity; Urbanization; Human activities; Native status.

Introduction

Increasing human impacts are reshaping biodiversity patterns globally, with urbanization being one of the most significant drivers of the change (*1*). It is well known that cities can attract species of various traits at a local scale (*2*–*4*), though the impacts of urban environments on large-scale ecological patterns, such as the latitudinal diversity gradient, remain poorly known (*5*–*8*). Given the rapid increase of urbanization and human footprint across the globe, it is crucial to have a better understanding of how urbanization influences these patterns (*1*, *7*, *9*, *10*).

The latitudinal diversity gradient is one of the world's earliest recognized and striking biogeographic patterns (*11*, *12*). It describes the decrease of biodiversity from the equator to the poles (*13*). The latitudinal diversity gradient is found widely across taxa (*14*) and forms the basis of many fundamental theories in ecology and evolution about how diversity is maintained (*15*–*17*). While this pattern is mainly observed under natural settings, the question remains, however, whether and how this pattern will be maintained under increasing anthropogenic modification of the earth's surface. Humans can directly modify natural environments that drive natural biodiversity patterns, and human-generated conditions can also serve as additional dimensions of environments that alter biodiversity distributions (*18*). Anthropogenic factors are increasingly recognized for their role in breaking biogeographic boundaries (*19*) and shaping biodiversity patterns (*20*). While the negative impacts of anthropogenic factors on biodiversity are broadly known (such as species extinction (*21*) and range contraction (*22*)), urban areas could also provide refuges and food sources for species in harsher environments (*8*, *23*). How these effects vary across space and time, how such effects differ for native and non-native species, and how these effects together affect the natural latitudinal diversity gradient remain to be addressed.

This study uses birds as an example to explore the potential impact of urbanization on the latitudinal diversity gradient. As mobile and sensitive organisms, birds are often considered important bioindicators of ecosystem health (*24*). Since birds are important to many ecosystem services, such as pollination, seed dispersal, and pest control (*25*, *26*), any shifts in bird diversity could have both direct and indirect effects on broader ecological dynamics (*27*). In addition, compared to other animal groups, birds are relatively easy to observe and identify and have a well-established community of enthusiasts (*28*, *29*). As a result, citizen science platforms like eBird offer extensive and high-density bird diversity data (*30*), far surpassing data available for other taxa (*31*). These make birds an ideal model group for studying macroecological patterns under global changes (*32*).

We consider two alternative hypotheses for how urbanization could affect the latitudinal diversity gradient. First, urbanization might decrease bird diversity compared with that in natural settings in a generally consistent manner across latitude, resulting in different intercepts but similar slopes. Alternatively, we hypothesize that the impact of human activities on bird diversity is not consistent across latitude; humans could potentially provide support for bird survival under cold situations (e.g., via food subsidy and refuge habitat), such that the latitudinal gradient of bird diversity is shallower in urban compared to natural settings. To test this hypothesis, we processed hundreds of millions of bird checklist data from the world's largest birding citizen science platform, eBird (http://www.ebird.org), in North America between 2015 and 2019 (Fig. 1). We investigated the latitudinal patterns of bird diversity across hundreds of cities and compared that with city surroundings. We note that city surroundings are used as reference conditions to approximate more natural environments, but they could still include suburban areas that experience low to moderate human impacts compared with urban cores; however, since human activities have considerably modified 50 to 70% of Earth's land surface (*33*–*35*), truly "pristine" ecosystems are inherently rare (*36*). We also distinguish the diversity in breeding and wintering seasons, as well as for species of native and non-native status. This study discovered significant influences of humans in reshaping biodiversity patterns.

Results

The latitudinal gradients of bird diversity

We found varied latitudinal patterns for bird diversity depending on native/non-native status and observation season (Fig. 2A-D & S2A-D). Native bird diversity exhibited a strong negative relationship in the wintering season (decreasing diversity with latitude, $p < 0.001$ in both cities and city surrounding areas, Fig. 2B) and a moderately strong positive relationship in the breeding season ($p = 0.003$ for cities and 0.005 for city surroundings Fig. 2A).Non-native species generally showed no significant relationship with latitude regardless of season or-city versus natural setting ($p = 0.99$ in breeding season and $p=0.09$ in wintering city surroundings, Figs. 2C, D), except for a significant but weak negative ($p = 0.02$) latitudinal trend in the wintering season in city surroundings (Figs. 2D). The latitudinal patterns based on the literature approach (see Methods) are largely consistent with results based on the strict sampling approach. The area of a city or its surrounding always had a significant positive effect on bird diversity regardless of season or native status ($p < 0.001$). After controlling for the effect of area, the effects of latitude on native diversity remain significant, while the effects on non-native diversity were either less pronounced or non-significant (Fig. S3).

Differing latitudinal trends between cities and city surroundings in wintering native bird diversity

Interestingly, we found that in winter, latitudinal trends of native bird diversity in cities and city surroundings were statistically different ($p < 0.001$), with the trend in cities flatter than that in city surroundings; thus, the two latitudinal trend lines show a distinct "crossover" (Figs. 2B & S2B). The difference in latitudinal trends was further confirmed by a significant negative interaction between latitude and location type (city/surrounding) for native diversity in the wintering season ($p < 0.001$, Fig. S3). This interaction term was not significant for native diversity in the breeding season, nor for non-native diversity in any season (Fig. S3). Further, we found a significant relationship between the native diversity difference (diversity of a city minus diversity of its surrounding) and latitude in the wintering season (Figs. 2F, S2F & S4); as latitude increases, the diversity difference also significantly increases (Figs. 2F & S2F). Species diversity in the surrounding areas is generally higher than in the city at lower latitudes; however, at higher latitudes and cooler climates, diversity in the city gradually approaches or slightly exceeds that of the surrounding areas (Fig. 2F). Results based on the literature approach are largely consistent with results based on the strict sampling approach.

Direct and indirect effects of human population density, vegetation, and temperature on bird diversity

Human population density serves as a strong proxy for urbanization (i.e., cities have higher human population density than their surroundings, $p < 0.001$, Figs. S5 & S6). Human population density shows a negative direct effect on native bird diversity in winter [estimated coefficient (marked as "β" in the following) = -0.03, $p < 0.001$, Fig. 3C], but it has no significant effect during the breeding season ($p = 0.14$, Fig. 3A) or on non-native bird diversity ($p = 0.70$ in wintering season while $p = 0.10$ in breeding season, Fig. 3B, D).

Temperature is strongly negatively correlated with latitude in both seasons ($p < 0.001$; Figs. S5 & S6). Temperature has a significant positive direct effect on both native and non-native bird diversity in winter ($p < 0.001$ for native birds while $p = 0.03$ for non-native birds) but negative direct effect in summer ($p < 0.001$). Among these effects of temperature, the positive effect on native bird diversity in winter has the largest absolute effect size ($\beta = 0.79$, $p < 0.001$, Fig. 3C).

Normalized Difference Vegetation Index (NDVI), a proxy of vegetation conditions and productivity, generally shows a positive effect on native and non-native bird diversity in breeding and wintering seasons ($\beta = 0.09$-0.10, $p < 0.001$, Fig. 3A, C and D), with an exception of non-native birds in the breeding season ($\beta = -0.14$, $p < 0.001$, Fig. 3B).

Human population density can also indirectly influence bird diversity via the pathway of increasing temperature ($\beta = 0.01$, $p = 0.004$ in breeding season while $p<0.001$ in wintering season, Fig. 3) and reducing NDVI ($\beta = -0.30$ in breeding season and -0.05 in winter, $p < 0.05$, Fig. 3). Temperature can also indirectly influence bird diversity via the pathway of altering vegetation ($\beta = -0.38$ in breeding season and $\beta = 0.85$ in winter, $p < 0.05$, Fig. 3).

Overall, considering both direct and indirect pathways (Fig. S7), higher latitude (and its associated temperature gradient) leads to reduced bird diversity in the cold season but increased diversity in the warm season, with the pattern strongest for native species in winter, matching the sharper winter latitudinal gradient (Fig. 2B). Human population density consistently depresses native bird diversity in both seasons, whereas non-native diversity shows a weak negative association in the cold season but a strong positive association in the warm season. This pattern also indicates that the within-city vs. outside-city difference in native bird diversity is overall more frequently below zero (Fig. 2E, F). Results based on the literature approach are largely consistent with results based on the strict sampling approach.

Positive association between human population density and native bird diversity in wintering season

In particular, we included the interaction term between temperature and human population density into the SEMs to examine whether the interplay between latitude-structured temperature gradients and urbanization shapes patterns of bird diversity. Notably, this interaction term was only significant for native bird diversity in the wintering season ($p < 0.001$, Fig. 3). According to the visualized human-temperature interaction effects, in winter, as temperature decreases, the negative effect of higher human population density on native bird diversity weakens and gradually shifts toward a positive effect (Figs. 4 & S9). This pattern was not evident for non-native birds in winter (Fig. 3). Also, in the breeding season, the effects of human population density on native/non-native diversity were negative regardless of temperature (Fig. 3).

The human-temperature interaction term also had a significant and relatively strong negative effect on NDVI in winter (Fig. 3). As temperature decreases, the effect of human factors on vegetation conditions (e.g., greenness) also tends to shift from negative to positive (Fig. 10). Because NDVI in winter was positively associated with bird diversity (Fig. 3), potential human-driven increases in greenness in colder regions may also indirectly help increase bird diversity.

Results above reinforce the pattern: the latitudinal gradients of native bird diversity in cities vs. their surroundings were different in winter (Fig. 2A), and the city–city surrounding diversity difference uniquely exhibits a significant latitudinal gradient (Fig. 2B). This further supports our hypothesis that, while intensive human impacts tend to reduce bird diversity overall, in harsh cold conditions they can also create settings that help birds cope with winter stress; this shift is most evident for native species.

Discussion

This study provides an overall picture and compelling evidence that urbanization can significantly alter classic latitudinal biodiversity patterns, however, this effect depends on the season and the origin of the species. Our results indicate that, while the latitudinal gradient of native bird diversity is significantly flatter in cities compared to surrounding areas, such deviation is most obvious during the wintering season. The different pattern of latitudinal diversity gradient inside and outside the city core suggests that cities may act as “shelters” for native birds at higher latitudes. The buffering effects of city environments with stronger and more focused human activities could potentially relieve the harsh conditions of cold season, thus increasing bird diversity and resulting in a weakened latitudinal gradient of native bird diversity in cities.

In contrast, this pattern is weaker and less consistent for non-native species across seasons. On the other side, temperature is likely not a limiting factor in the breeding season (*37*, *38*), and the diversity of non-native species could be determined by other factors such as disturbance and land-use change (*39*, *40*).

Nevertheless, high human population density, especially in cities, typically had a negative effect on native bird diversity (*41*, *42*). We found that the diversity of birds, especially native species, is generally lower in cities than in surrounding areas, particularly in the warmer regions in low latitudes (Fig. 2). While a city often acts as a “human filter” that removes sensitive and specialized species (*43*), extreme cold conditions can be an even stronger filter in natural environments, especially for endotherms like birds (*44*). Active organisms may face resource shortages and run short of food under extreme cold; staying warm would cost more energy (*44*, *45*). This energy loss can cause death or lower reproduction in natural environments (*46*), and overwintering energetics constrain distributions of species (*44*, *47*). In these contexts, the thermal advantages and stable food supplies of cities may outweigh the costs of habitat degradation for many native birds, allowing them to overwinter in regions that would experience extreme cold conditions. Higher human population density in cities can increase particular food resources such as garbage and the chance of direct feeding (*48*, *49*). This reduces birds' reliance on natural foods that are often blocked by snow and ice in cold conditions, decreasing the predation pressure and making foraging easier (*50*). In contrast, denser buildings resulting from higher human population can create warm microclimates in cold seasons (*51*, *52*) (*53*, *54*). These microclimates provide safe shelter from wind and snow, as well as additional refugia that are much safer than city surroundings (*55*). Together, these changes extend the time available for activity and improve access to resources, raising birds' energy efficiency in winter. However, during warmer seasons or at lower latitudes, the support provided by human activities is no longer a necessity, as food availability and survival conditions are no longer constrained by extreme cold.

There are distinct latitudinal diversity patterns for native and non-native birds. Non-native bird diversity consistently lacked a significant relationship with human population density across seasons (Fig. 3); moreover, unlike native species, the impact of human population density on non-native diversity did not exhibit significant variation or even trend reversal across warm and cold conditions. This highlights the different ecological drivers for native and non-native birds. Non-native species have a greater ability to exploit human-altered environments and habitats that most native species rarely use (*56*, *57*). Thus, it could be inferred that non-native birds have already been filtered for high tolerance to human disturbance and are decoupled from natural climatic constraints to some extent (*58*).

Productivity is known to have a positive relationship with bird diversity (*23*, *59*, *60*), though we found an interesting modification of this relationship in urban settings and different temperature regimes. First, we found an overall positive correlation between NDVI (representing vegetation conditions and productivity) and temperature at the annual scale (Fig. S7), but considerable seasonal variations, with a negative correlation during the breeding season and a positive correlation during the wintering season (Fig. 3). Such relationships and variations are consistent with the literature that warm conditions support vegetation greening (*61*), while excessive heat in summer can trigger water stress and reduce photosynthesis, leading to lower vegetation greenness and carbon gain (*62*). Second, urbanization poses a significant intervention on the relationship between vegetation and bird diversity. Urbanization and human activities have led to widespread conversion of vegetated cover to impervious surfaces at large scales (*63*), and here we found a negative relationship between vegetation condition measured by NDVI and human population density (Fig. 3). However, similar to bird diversity, we found a significant effect of human-temperature interaction on NDVI in winter (Fig. S10), suggesting the effect of human activities on vegetation shifts from negative to positive under extreme cold. Humans could bring up an artificial greenness by intentionally selecting evergreen species and providing management subsidies (e.g., winter protection measures) (*64*, *65*) that may buffer against the seasonal "browning" in natural settings. Since vegetation serves as a crucial source of food and shelter for birds (*59*), human activities can exert a positive indirect effect on bird diversity by maintaining or introducing functional vegetation such as artificial green belts during winter. Notably, during the climatically favorable breeding season, non-native bird diversity exhibited a negative relationship with NDVI, in contrast to the pattern observed in native species. It is possible that high-quality green spaces are more likely to be occupied by native species, and successful invasive non-native species tend to occupy artificial habitats that native species cannot utilize during this period (*66*, *67*).

In summary, we find a clear difference in the latitudinal gradients of native bird diversity between cities and their surroundings during winter. High human population density mostly has a negative effect on bird diversity, though such negative effects weaken at high latitude and partly reverse toward a positive effect under cold conditions, thus resulting in a flatter latitudinal pattern of native bird diversity. Our findings have important implications for ecological and biogeographic studies: anthropogenic factors should be included as additional dimensions of ecological niches, not just to account for the multifaceted role of direct human impact, but also to consider their interactions with classic abiotic factors (*18*). While cities only occupy ~3% of terrestrial land area (*68*), human activities have considerably modified 50 to 70% of Earth’s land surface (*34*, *69*, *70*). Given the ongoing and projected rapid urban expansion (*71*, *72*), our study calls for leveraging the positive effects of cities in support of biodiversity conservation (e.g., promoting bird-friendly green landscaping designs) (*73*), where cities may serve as “stepping stones” or critical wintering outposts (*74*) or facilitate range shift under global changes (*75*).

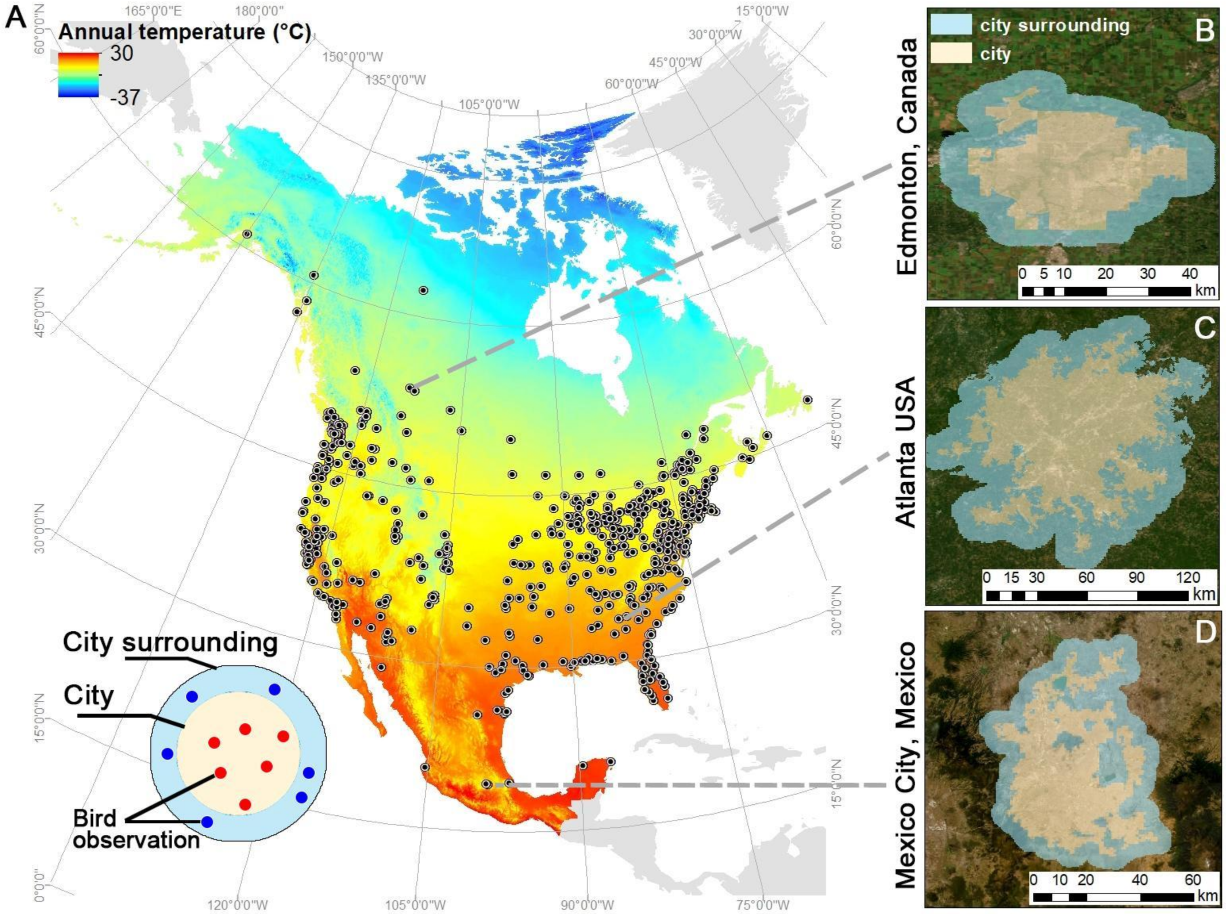

Figure 1. Spatial distributions of the 519 North American cities and their surrounding areas involved in the study. A city-surrounding is defined to have the same area as a city. We included the paired city and its surrounding in this study if adequate eBird observations are available and they meet the strict sampling approach (see Methods). This study also considered an alternative data filtering method (literature approach) with 662 cities included (Fig. S1). Three examples of cities and their surroundings are shown in panels b-d. Bird diversity in cities and their surroundings is calculated from the eBird observations via a rarefaction approach.

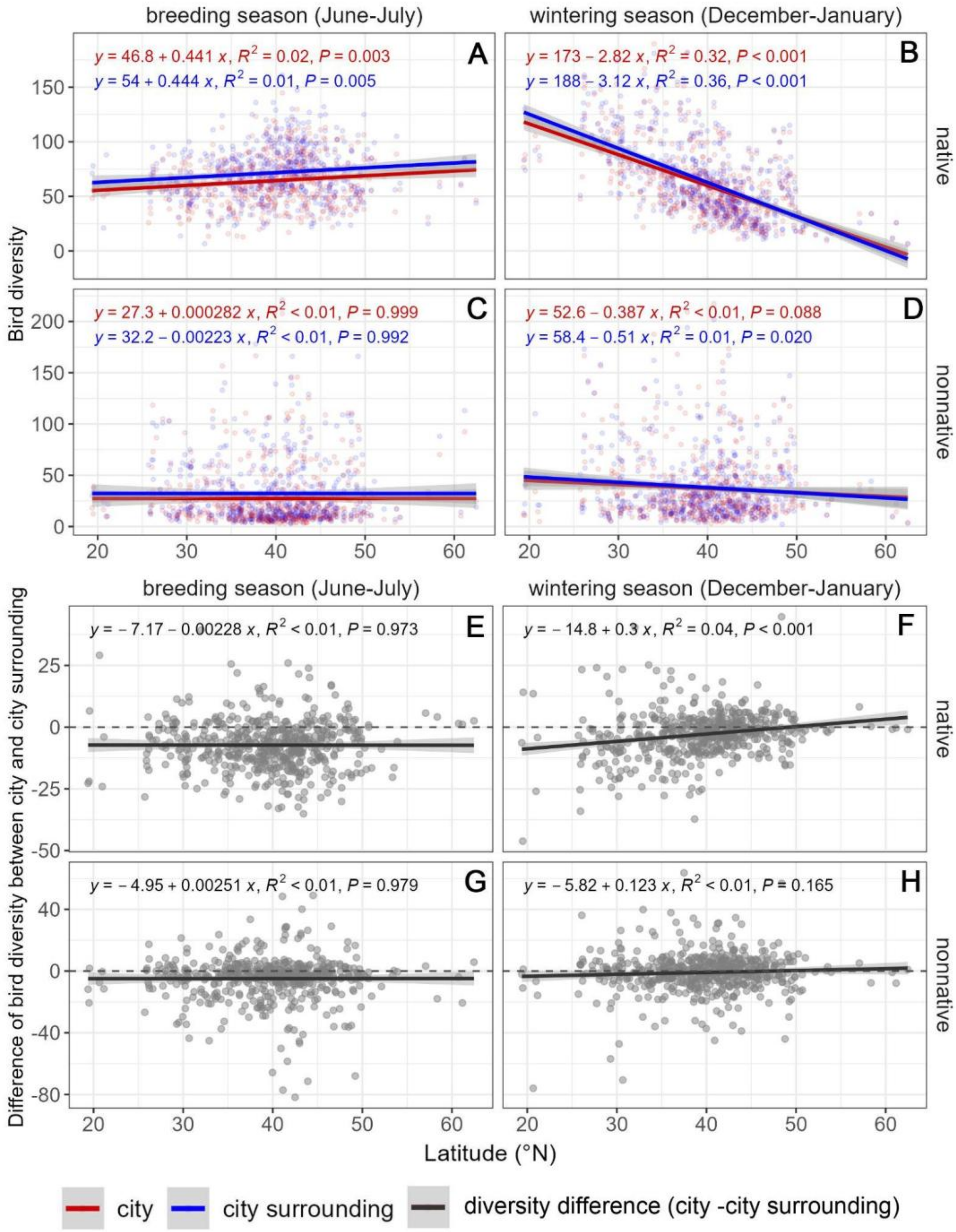

Figure 2. Latitudinal patterns of bird species diversity in North American cities and surrounding areas across different seasons and native statuses. (A-D) Scatter plot of bird diversity in cities (red) or city surroundings (blue) and their linear relationships with latitude. **(E-H)** Scatter plot of diversity difference (diversity of a city - diversity of its surrounding) and their linear relationships with latitude. Results of different seasons (breeding, wintering) are shown in columns, and results of native/non-native statuses are shown in rows, respectively. Results based on the strict sampling approach are shown here; results based on the literature approach are shown in Fig. S2.

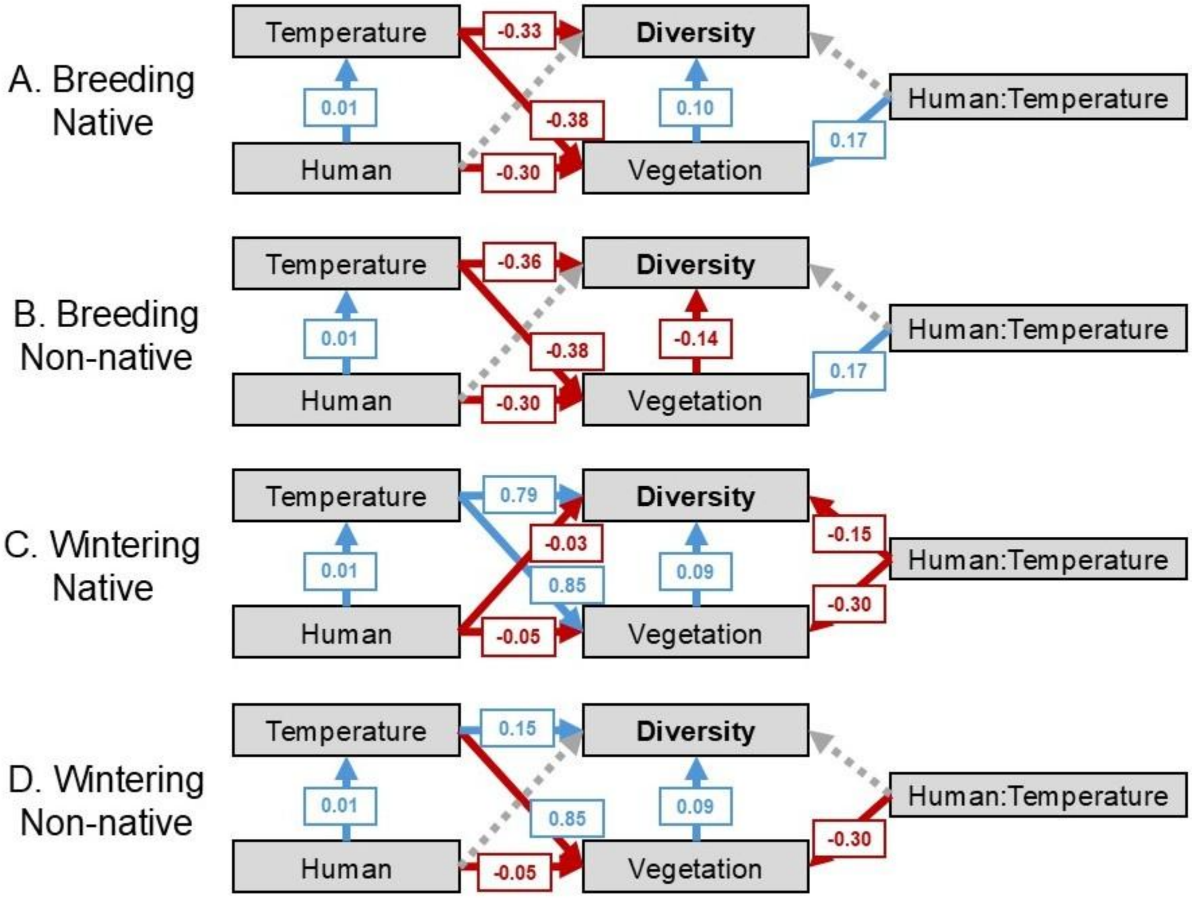

Figure 3. Structural Equation Models (SEMs) for bird diversity across different seasons and native/non-native status. The model illustrates the direct and indirect pathways of the core variables: temperature, human population density (marked as Human), vegetation conditions measured by Normalized Difference Vegetation Index (marked as Vegetation), and the interaction between temperature and human population density (Human:Temperature) on bird diversity. Red and blue solid arrows represent significant positive and negative pathways ($p < 0.05$), respectively, with path coefficients indicating standardized effect sizes on the arrows. Non-significant pathways are represented by dashed arrows. The results of the complete SEM pathways (including latitude, area, and city location) are displayed in Fig. S5. Results based on the strict sampling approach are shown here; SEMs based on the literature approach are shown in Fig. S6.

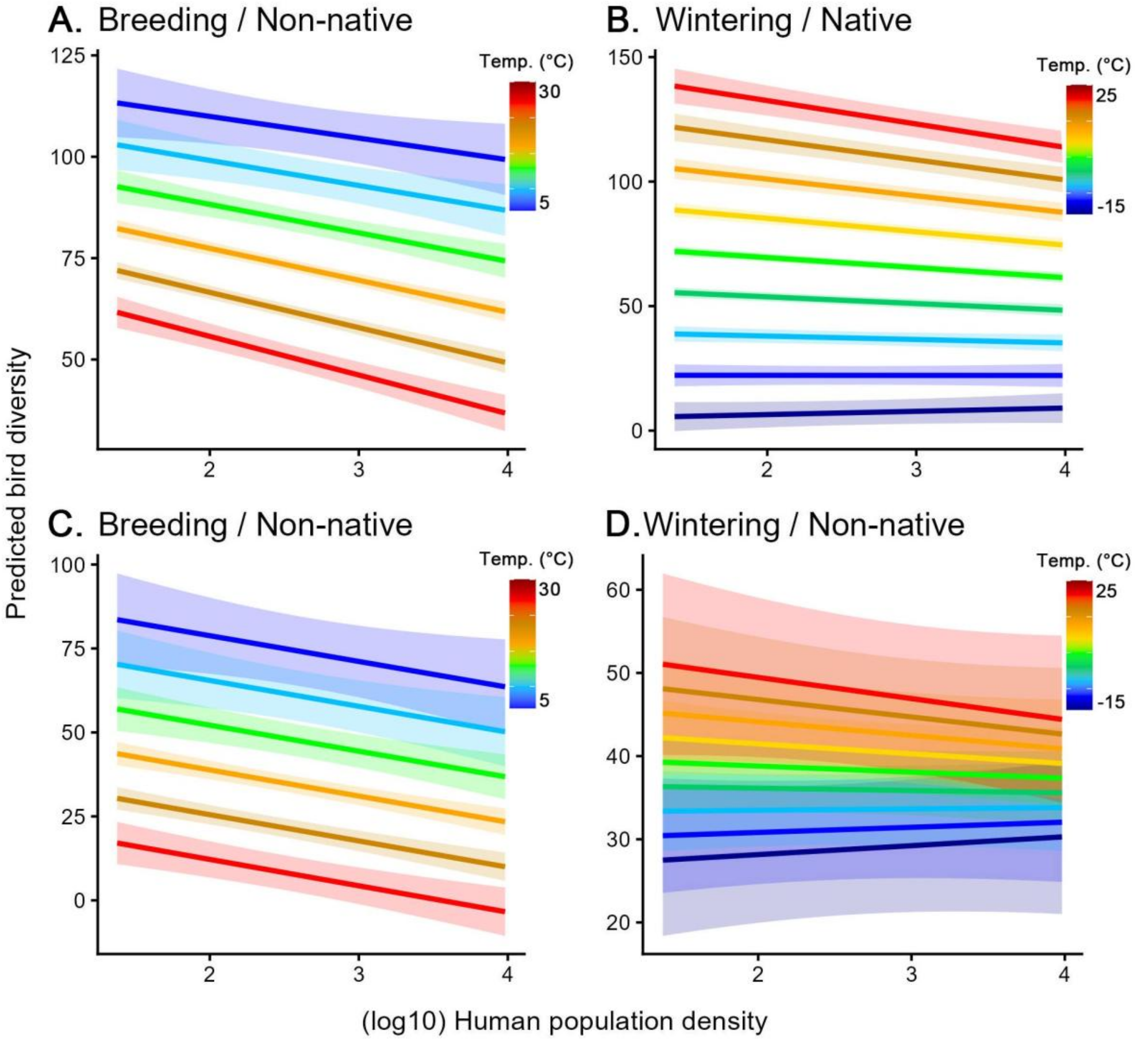

Figure 4. Marginal response of bird diversity to the interaction between human population density and temperature across different observation seasons and native/non-native statuses. The figure shows the linear responses of bird diversity to human population density (Human) at different temperature levels (coded in the gradients of colors), assuming all other variables are held constant at their median. The lines indicate the fitted regression lines based on these predicted results. The shaded areas represent the 95% confidence intervals of the lines fitted. Only results based on a strict sampling approach are shown here; results based on the literature approach are shown in Fig. S9.

Methods

In this study, we calculated bird diversity in hundreds of cities and their surrounding areas across North America based on eBird, one of the world's largest citizen-science-driven biodiversity databases. We distinguished bird diversity by native and non-native and by breeding and wintering seasons to quantify the latitudinal gradient, respectively. We also investigated the environmental drivers (temperature, human population density, vegetation conditions, and their interactions) of the diversity gradient using structural equation models (SEMs) and evaluated their differences between native and non-native and between breeding and wintering seasons. All of the analyses were performed using the R language (v 4.4.0).

Collecting bird observations from eBird

We downloaded bird observation data from eBird (accessed on Sep. 21, 2021). Specifically, we used the eBird Basic Dataset (EBD) (*76*) and kept the data collected during 2015-2019, when a large number of records were consistently collected over that period and the collection efforts were not impacted by the COVID-19 pandemic (*77*, *78*). We limited our study area to North America (Mexico, United States, and Canada), where collecting efforts from eBird were largest in quantity, as well as good spatial consistency and fewer spatial gaps (*79*). The cities across North America also fall along a latitudinal gradient from 16 to 71°N that makes the study area an ideal system to explore bird latitudinal diversity. We retained ~228 million records collected between 2015 and 2019 in North America. Those records were further refined to ~5-17 million in the following analysis.

We performed a series of steps to clean and standardize the eBird data following the methodology used in existing literature. We removed the unvetted data that have been flagged as potentially erroneous based on date, location, or count by the eBird review process (*80*). We restricted the data to "complete checklist" when the observer reported all species detected by sight and by ear to the best of their ability (*80*–*82*). A complete checklist helps better understand detection probabilities and, with a large enough sample, can serve as a substitute for absence data (*81*). The checklists were further restricted to those collected with the "stationary," "traveling," or "area" protocols; a stationary survey requires an observer to remain stationary in an area (≤ 30 m diameter); a traveling survey involves observations made over a known period of time while traveling a known distance (> 30 m); and an area survey involves thoroughly searching an area with a known size. The three protocols represent common survey methods in the eBird dataset (*81*) characterized by recorded sampling effort and large spatial coverage. The regionally unique protocols (e.g., California Brown Pelican Survey) or incidental observations that do not include or distance/area components were excluded. To minimize the variation of sampling effort and make the observation data more comparable (*83*, *84*), we restricted the start times to daylight hours to be between 05:00 and 20:00 (*84*). We further developed two strategies for filtering the data to decrease the variation of sampling effort, and thus a more robust diversity evaluation. The first strategy used filtering criteria that have been used in the literature to ensure more robust evaluations (literature approach); more specifically, we restricted the total search time to be >6 minutes (*85*) and < 3 hours (*84*), and restricted traveling survey to be <5miles (or 8.1 km) (*84*, *86*) and area survey to be < 56 km^2 (*82*). Building upon this strategy, we developed a more strict strategy (strict sampling approach);we restricted the total search time to be between 30 and 60 minutes; to reduce the uncertainty caused by fatigue from long-term monitoring, and the distance and range of the traveling survey and area survey are halved compared to the former, which are < 2.5 mile (or 4.1 km) and < 28 km^2, respectively. We removed duplicated checklists when checklists were shared between multiple observers based on observation group ID (*85*). The resultant data set consisted of ~227 million checklists for the literature approach and ~46 million for the strict sampling approach.

Native and seasonal status

Human-mediated introduction of species has been happening at a global scale, and that constitutes a signal in affecting species richness (*87*). This is especially pronounced for areas under high intensity of human impacts, such as cities studied here (*8*, *88*). Therefore, we distinguished the eBird data as native and non-native observations (see paragraph below) because geographic distribution and diversity of native and non-native species could be driven by different environmental factors (*89*). In addition, since many birds are migratory and the richness can be season-dependent (*90*), we distinguished the observations into breeding season (June-July) and wintering season (December-January), based on the date of the observation event. The temporal window of the breeding and wintering season mimics the timing of two long-standing bird survey initiatives, which is mid-December to early January for the Christmas Bird Count (*8*) and (mostly) June for the Breeding Bird Survey (*91*).

We further integrated the two schemes (native/non-native and breeding/wintering) that led to four different categories. An observation during the breeding season (June-July) will be further classified as “breeding-native” or “breeding-non-native,” depending on if the location of the observation falls in the IUCN range map (“origin” field was coded as native or historical range and “season” field was coded as resident or breeding season) (*92*). Similarly, an observation during the wintering season (December-January) will be classified as “wintering-native” or “wintering-non-native,” depending on if the location of the observation falls in the IUCN range map (“origin” field was coded as native or historical range and “season” field was coded as resident or wintering season). We recognized that IUCN range polygons are sometimes coarse and may miss fine-scale range edges (*93*). Therefore, observations falling slightly outside the edge will be labeled as “non-native” under our method, which could potentially overestimate the non-native category. The potential misclassifications should mainly occur near range edges; broad-scale patterns based on range maps would not be strongly affected by the details (*94*, *95*). An alternative approach, such as expanding the range map with a spatial buffer, may be able to partly mitigate the issue, though the size of the spatial buffer can be subjective, and the varied uncertainties embedded in each range map can be further amplified with a uniform buffer. Further, the presences outside the IUCN range could represent recent range expansions (thus non-native in the strict sense), which can be correlated with human impacts (*96*). Therefore, we didn’t do further modification of the IUCN range maps and considered this the most parsimonious strategy to investigate the signals behind native and non-native diversity.

We recognize the presence of different definitions of non-native status (*97*). For example, a species native or endemic to Africa will be considered as non-native in North America. However, there are also cases that are less clear-cut. A species native to an area of the U.S. could be observed outside their (historically known) home range in the U.S., though this can be caused by natural expansion or human introductions; this leads to a blurry context: are those observations native (as they are still found in the native country or continent) or non-native (as they are outside the known home range)? Thus, the definition of "non-native" could be scale dependent. Another complication is the long-distance migration (of birds and bats) that increases the difficulty in defining native range; further, individuals of a migratory species may not migrate for various reasons and may reside in the same or a new location that provides suitable conditions (*98*, *99*). Nevertheless, we did not directly distinguish species as native or non-native to North America; instead, we defined native/non-native at the level of observations: if an observation meets the “expectation” of IUCN range ranges (i.e., falls inside the expected range boundary given a season), it is considered as native; otherwise, it is considered as non-native. We expect this classification scheme to better capture the potential environmental drivers of bird diversity.

Since eBird and IUCN use different taxonomic reference systems (*100*), we have resolved the naming inconsistency between them using Avibase (*101*), a large taxonomic database that organizes authoritative avian taxonomic concepts from 151 taxonomic checklists (including the ones used by IUCN and eBird). The majority of the cases were 1-1 matches, meaning a scientific name from IUCN is uniquely matched with a scientific name in eBird. When a scientific name from IUCN was matched with multiple scientific names in eBird, the eBird observations would be considered as one species. When a scientific name from eBird was matched with multiple scientific names in IUCN, the IUCN range maps of the multiple species would be considered as one species. The unified scientific names were used to calculate bird diversity in the next step.

Cities and city surroundings

We used urban areas in North America and their surroundings as study units to calculate bird diversity. The boundaries of 4,789 urban areas in Mexico, the United States, and Canada were downloaded, respectively, from Natural Earth (*102*), U.S. Census Bureau (*103*), Statistics Canada (*104*). Such areas consist of high population density and urban land use, resulting in a representation of the "urban footprint” (*105*). We also created spatial buffers around cities to represent urban surroundings (hereafter city surroundings) equal in area to their respective cities. Because of the complexity of urban footprint shapes, there was no single buffer distance that universally resulted in a surrounding area of equal area; thus, for each city, we created a series of 400 spatial buffers ranging from 0.01 to 2 times the width of a focal city, where the width was calculated as the square root of the city area. We then chose the buffer that resulted in an area closest to the city area. If a city surrounding overlaps with another city nearby, the overlapped area would be excluded when calculating the area of a city surrounding; this step is to avoid including highly urbanized areas in a city surrounding.

Standardized bird diversity

We calculated bird diversity for cities and city surroundings based on the eBird observations that fall within their respective polygons. Sampling bias is broadly recognized in citizen science data (*106*), and higher sampling intensity can be positively related to the species diversity. Therefore, we adopted Hill numbers (or the effective number of species, q = 0), an intuitive and statistically rigorous alternative to other diversity indices (*107*, *108*), to measure bird diversity in cities or city surroundings. This method builds upon the relationship between cumulative observation effort and total diversity, i.e., the more observations lead to higher diversity, and diversity will reach saturation when all species are observed given high observation efforts. We did not use the count information from eBird data because of the potential uncertainty and inconsistency. Since two sites could have different species pools and different sampling efforts, a direct comparison of the observed richness can be inappropriate. A better comparison could be based on the same sampling effort. This relies on an estimated sampling effort and species richness curve; this is also termed rarefaction when the site with higher sampling effort is rarefied to the lower sampling effort of the other site, or extrapolation when the site with lower sampling effort is extrapolated to the higher sampling effort (*108*). This approach was further improved by considering the degree of sample completeness (*109*). Here we used the iNext package (version 2.0.20) to calculate Hill numbers (*107*) and used the rarefaction approach to compare bird diversity between each pair of a city and its surrounding at the lower completeness (or coverage). For each pair of a city and its surroundings, such calculation was performed for the 4 different combinations of native and seasonal status defined above. To avoid scenarios of inadequate data, we excluded a pair of a city and its surrounding, if the number of eBird checklists in that city or its surrounding was below a threshold for any combination of native and seasonal status. The threshold was 20 for the literature approach, and the resultant data consisted of ~17 million eBird checklists across 662 pairs of cities and their surroundings. When using the strict sampling approach, we set the threshold for the number of eBird checklists to 10 to prevent the data from being too sparse, and the resultant data set finally consisted of ~5 million eBird checklists across 519 pairs of cities and their surroundings. In the main text, we mostly present the following results based on the strict sampling approach, while the results based on the literature approach are similar and are provided in the supplementary materials.

Latitudinal pattern of bird diversity

To provide an overview of latitudinal gradients in bird diversity, we first performed linear regressions against latitude for both cities and city surroundings, with comparisons made between native and non-native species across different seasons (Fig. 2). We then calibrated linear mixed models to investigate the effects of city environment on the latitudinal gradient of bird diversity. Here we used cities to represent areas under greater human impact, and used city surroundings as reference conditions to approximate more natural environments. We note that city surroundings could still include suburban areas that experience low to moderate human impacts compared with urban cores; however, since human activities have considerably modified 50 to 70% of Earth's land surface (*33*–*35*), truly natural areas can be rare (*36*). We investigated if cities and city surroundings have different latitudinal gradients of bird diversity. In the linear mixed model, we used bird diversity as the dependent variable; latitude, the category of city/city surrounding, and area as fixed effects; and the identity of the pair of cities and their surroundings as the random effect. We also included an interaction between latitude and city/city surroundings to capture the potential nonstationary effect of cities on bird diversity. The linear mixed model was fit for the four different datasets (native/non-native status and wintering/breeding season) using the "lmerTest" (*110*) R packages. The latitude of the centroid of a city polygon was used to represent the latitude of a pair of a city and its surrounding. In addition, we calculated the difference of the standardized bird diversity between each pair of city and surrounding, and performed a linear fit with latitude and city area as independent variables to evaluate if the effect of city on diversity varies across latitude.

Explaining the factors affecting bird diversity

We investigated the effects of temperature, human population density, and the Normalized Difference Vegetation Index (NDVI) in cities and their surroundings on bird diversity. Latitude determines the temperature gradient, which is known as one of the major drivers of the latitudinal diversity gradient (*16*). Compared with temperature, productivity is recognized as a stronger and less variable driver for species diversity (*111*), especially for birds (*60*). Thus, we used Normalized Difference Vegetation Index (NDVI), a proxy of vegetation conditions, including structural characteristics such as leaf area index and fractional vegetation (*112*), as an indicator of net primary productivity (*60*).Human population density directly reflects the level of urbanization (*113*) and is a surrogate measure of human impacts on nature and biodiversity (*105*, *114*, *115*).

We compiled temperature, human population, and NDVI datasets at 1 km resolution from CHELSA v2.1 (*116*), WorldPop global mosaics R2025A v1 (*117*) and MOD13A3 V6.1 (*117*, *118*). CHELSA and MOD13A3 are monthly datasets. We first calculated the multi-year average for each month from 2015 to 2019, then calculated the average for the breeding (June-July) and winter (December-January) seasons. Next, we used the polygons of cities or surrounding areas to calculate the mean value of each city or its surrounding. WorldPop is an annual dataset. We first calculated the average for 2015-2019, then used the polygons of cities or surrounding areas to calculate the sum of the covered grids, divided by the polygon area to obtain the mean population density. In subsequent model analyses, we log10-transformed human population density, considering that population density spans orders of magnitude and is highly right-skewed because of a small number of extremely high-density megacities (*119*). We also included area as a predictor together with environmental variables.

We constructed a series of linear mixed models and Structural Equation Models (SEMs) to capture the direct or indirect effects of environmental factors on bird diversity. We hypothesized that temperature and human impacts are directly related to latitude gradients of diversity (*120*). The distinction between city and city surroundings can directly affect human population density (*121*, *122*) and vegetation conditions (*123*), which subsequently affect bird diversity. Furthermore, we introduced the effects of the interaction between human population density and temperature into the model to test whether the effects of human population density on bird diversity (and vegetation) varies as temperature changes. The fixed effects of each path in the SEM are represented by equations 1-4. We also included the identity of a pair of cities and their surroundings as a random effect in equations 1-4 to account for other unaccounted environmental or anthropogenic variations. We performed SEMs for the four different combinations of native and seasonal status defined above. The analyses were based on the “lmerTest” (*110*) and “piecewiseSEM” (*124*) R packages.

In the key path directly linked to bird diversity (eqn.1), temperature, log10-transformed human population density, the interaction between the two, and vegetation conditions (measured by NDVI) were considered. We also included the area of cities or surroundings to control for the species-area relationship (*5*, *10*). The second path (eqn. 2) reflects that vegetation conditions (measured by NDVI) are potentially shaped by both human activities and temperature and their interactions. This path can potentially capture the indirect effects of temperature and human population density on bird diversity via impacting vegetation conditions. The third path represents the association between temperature and latitude and also represents the potential impact of urbanization (represented by human population density) on regional temperature (*125*). The fourth equation aims to account for the higher human population density in cities than in city surroundings.

Diversity ~ Human + Temperature + Vegetation + Human: Temperature + Area   [eqn. 1]
Vegetation ~ Human + Temperature + Human: Temperature   [eqn. 2]
Temperature ~ Human + Latitude [eqn. 3]
HumanPop ~ City/surrounding   [eqn. 4]

We further visualized the effects of the interaction between human population density and temperature using the “visreg” R package (v2.8.0) (*126*). We plotted the predicted values of bird diversity or NDVI along a gradient of human population density, conditioned on different temperatures.

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Supplementary Information

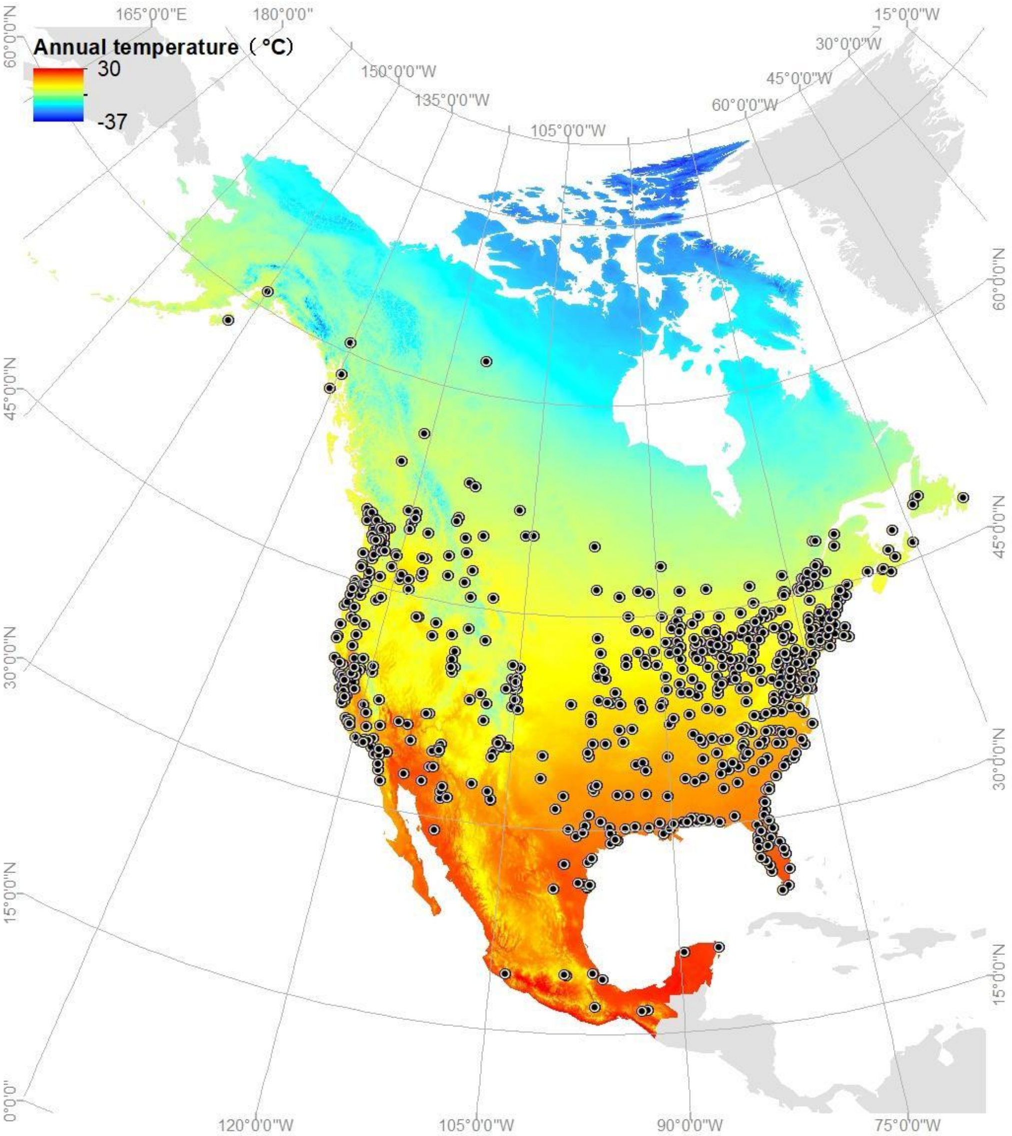

Fig. S1. An overview of 662 North American cities and their surrounding areas involved in the study. A city-surrounding area has the same area as a city. A pair of a city and its surroundings will be included in this study if adequate eBird observations are available and they meet the literature approach (see Methods). Bird diversity in cities and their surroundings is calculated from the eBird observations via a rarefaction approach.

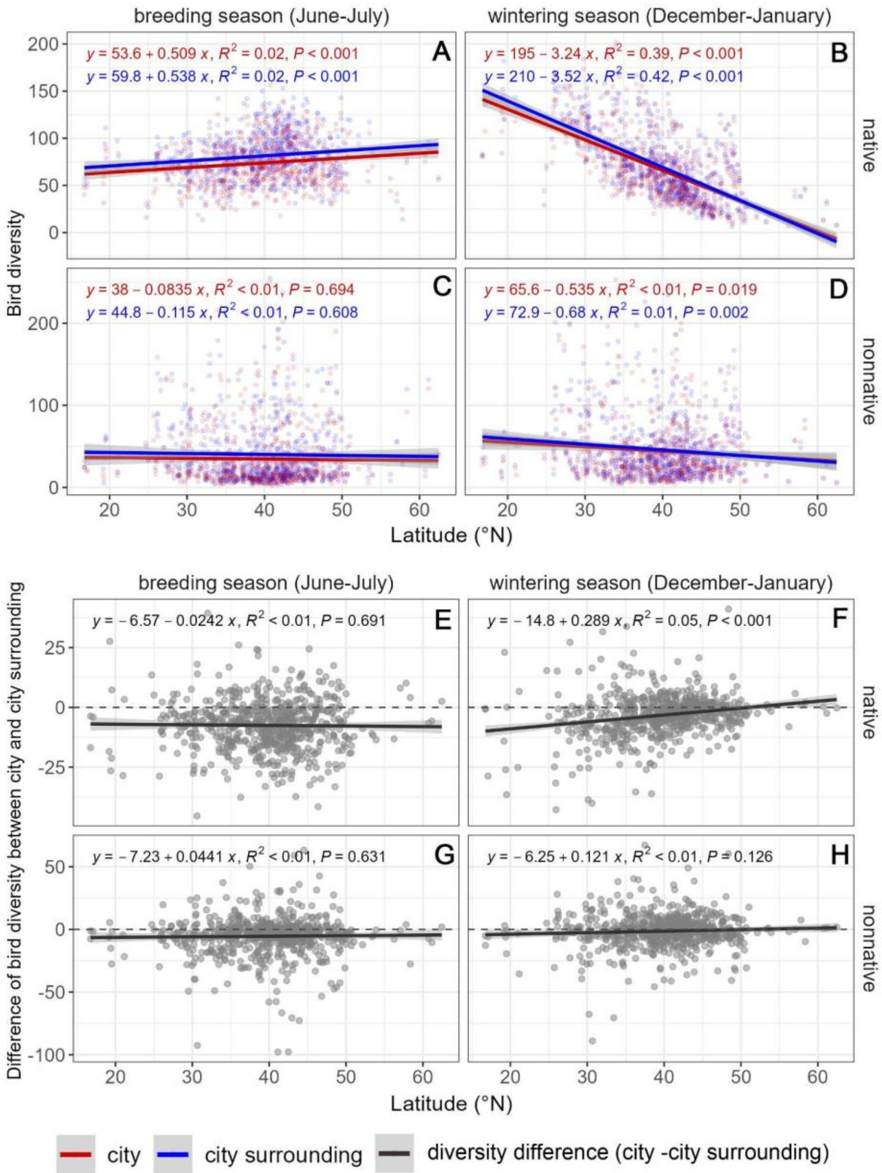

Fig. S2 Latitudinal patterns of bird species diversity in North American cities and surrounding areas based on literature sampling approach. (A-D) Scatter plot of bird diversity in cities (red) or city surroundings (blue) and the linear fitness with latitude. **(E-H)** Scatter plot of difference in bird diversity between the city and its surrounding areas (city minus surrounding) and the linear fitness with latitude. For both group A and B, the two columns represent different seasons (breeding, wintering), and the two rows represent different native status (native, nonnative).

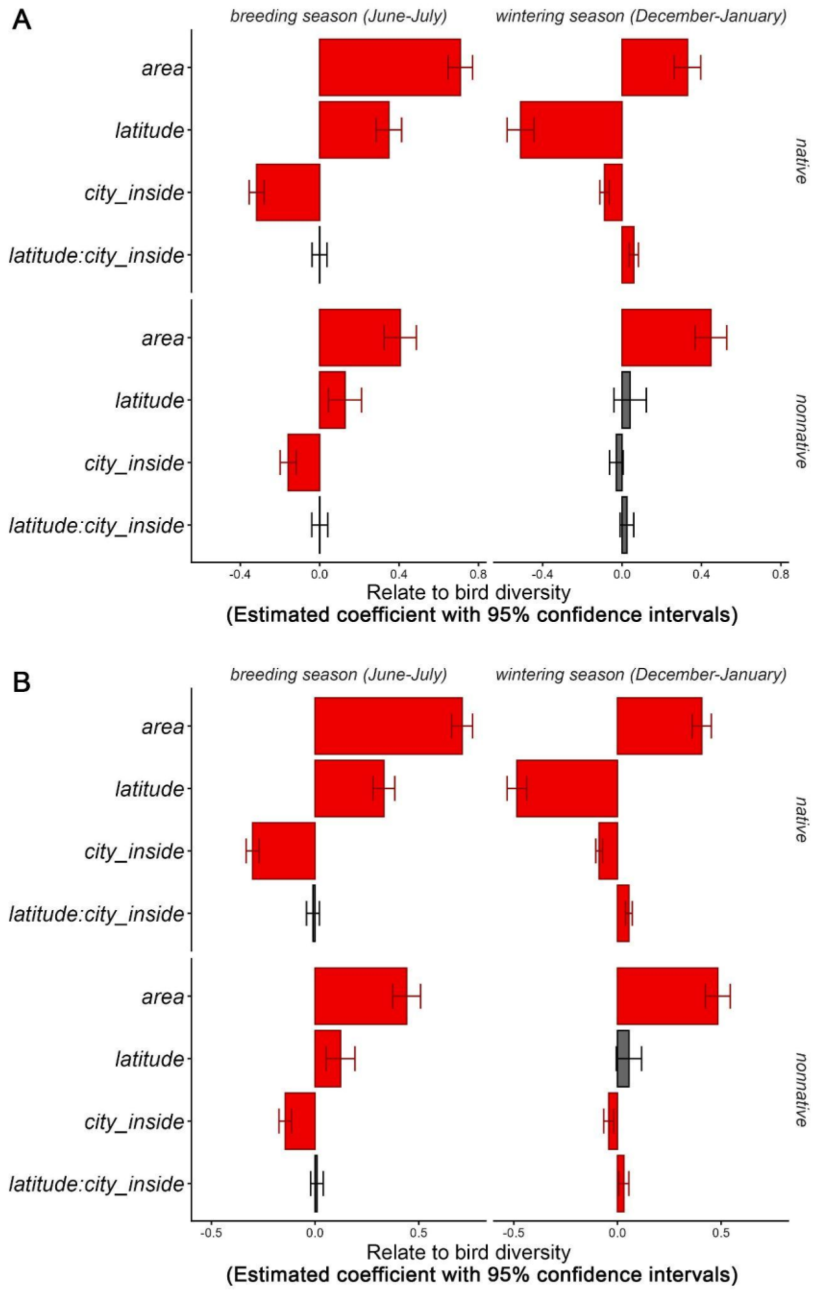

Fig. S3 Summary of the linear mixed models based on strict (A) and literature (B) sampling approaches. The bar chart indicates the standardized regression coefficients of the fixed effects, and the error bars represent the 95% confidence intervals of each coefficient. The dependent variable is the bird diversity (i.e. bird species richness). The fixed effects include area, latitude, the category of city/city surrounding (city_inside), and the interaction between latitude and city/city surrounding (latitude:city_inside). The name of the city (and its surrounding) is used as a random effect. Red color indicates significant effect ($p < 0.05$), while gray indicates non-significant effect ($p > 0.05$).

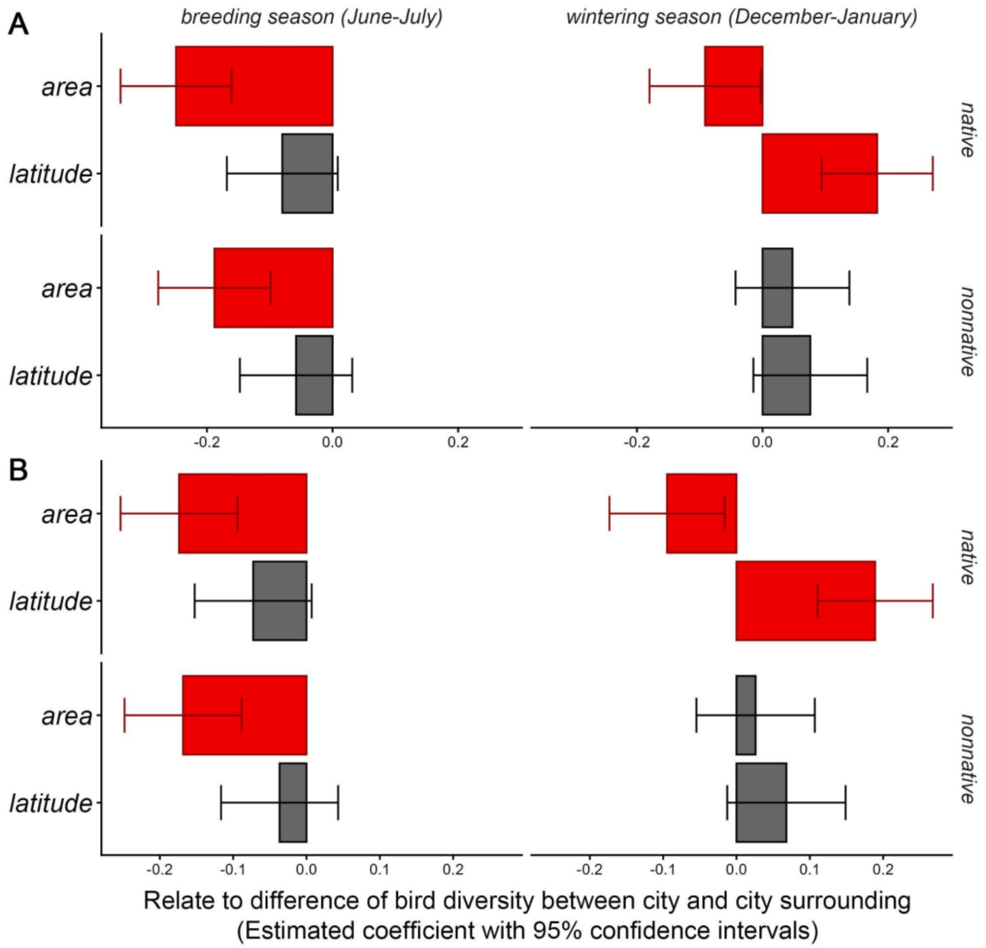

Fig. S4 Summary of the linear models based on strict (A) and literature (B) sampling approaches. The bar chart indicates the standardized regression coefficients of the dependent variables, and the error bars represent the 95% confidence intervals of each coefficient. For each model, the dependent variable is the difference of bird diversity (bird species richness) between the city and its surrounding areas (city minus surrounding). The independent variables include the area and latitude. Red color indicates significant effect (p < 0.05), while gray color indicates non-significant effect (p > 0.05).

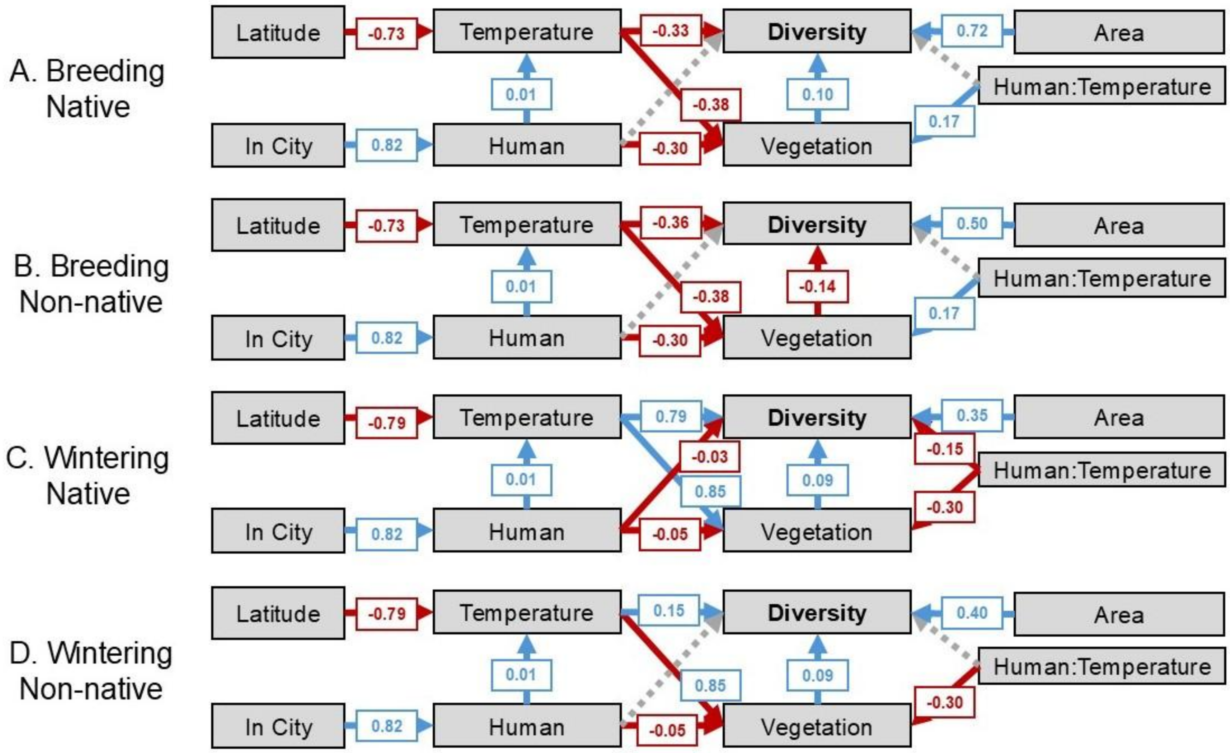

Fig. S5 Explanation of the Structural Equation Models (SEMs) for bird diversity across seasons and different native status based on the strict sampling approach. The model illustrates the direct and indirect pathways of the core predictors: temperature, log10-transformed population density (Human), NDVI (Vegetation), as well as the interaction between temperature and human activity (Human:Temperature) on bird diversity. Geographical predictors such as latitude, area, and urban location are also included. Red and blue solid arrows represent significant negative and positive pathways ($p < 0.05$), respectively, with the corresponding path coefficients indicating standardized effect sizes on the arrows. Non-significant pathways are represented by gray dashed arrows.

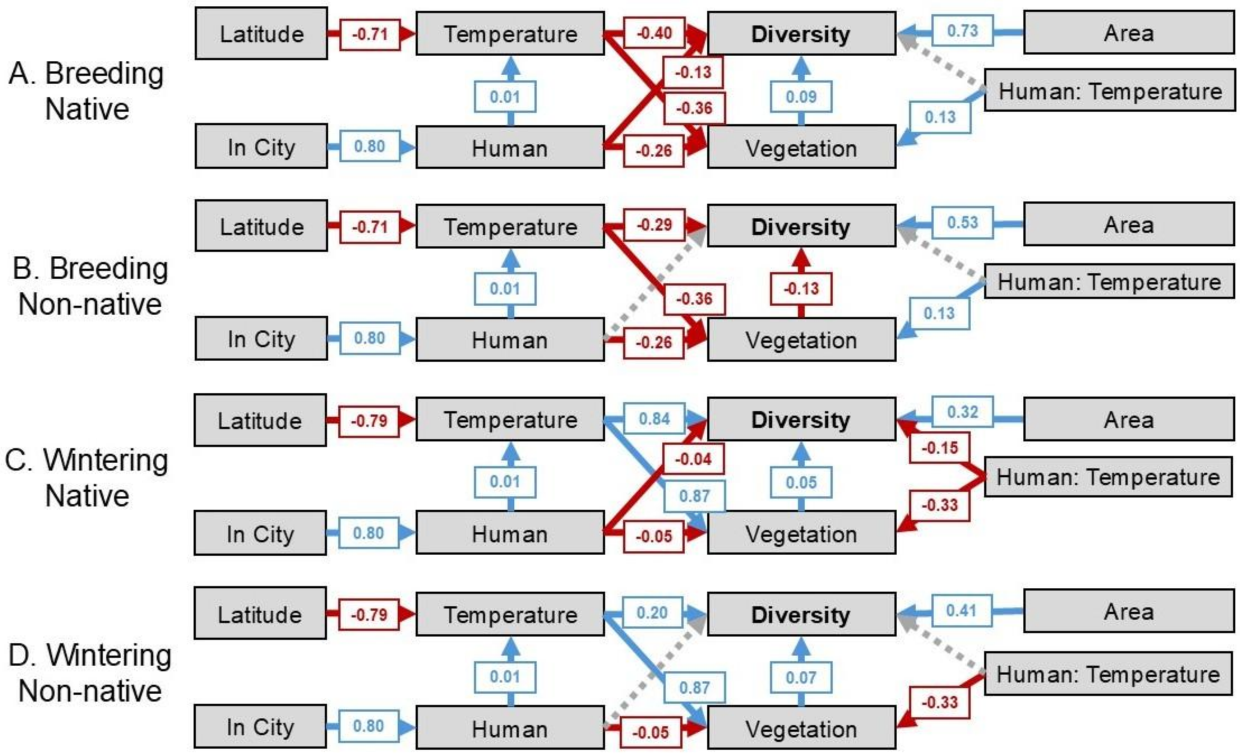

Fig. S6 Explanation of the Structural Equation Models (SEMs) for bird diversity across seasons and different native status based on the literature sampling approach. The model illustrates the direct and indirect pathways of the core predictors: temperature, log10-transformed population density (Human), NDVI (Vegetation), as well as the interaction between temperature and human activity (Human:Temperature) on bird diversity. Geographical predictors such as latitude, area, and urban location are also included. Red and blue solid arrows represent significant negative and positive pathways ($p < 0.05$), respectively, with the corresponding path coefficients indicating standardized effect sizes on the arrows. Non-significant pathways are represented by gray dashed arrows.

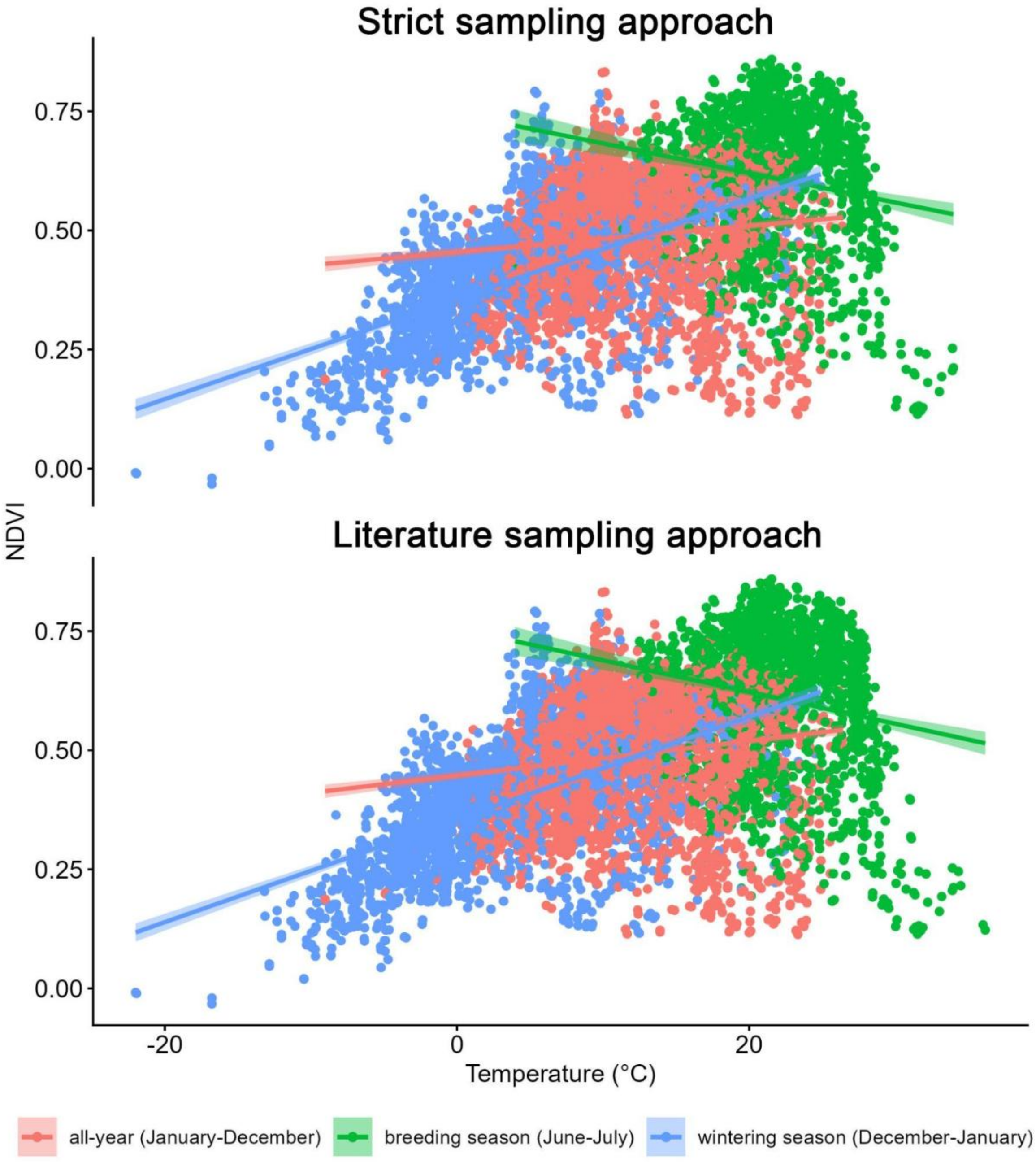

Fig. S7 The linear relationships between vegetation (NDVI) and temperature across different seasons based on the strict and literature sampling selections. All linear relationships are statistically significant ($p < 0.05$).

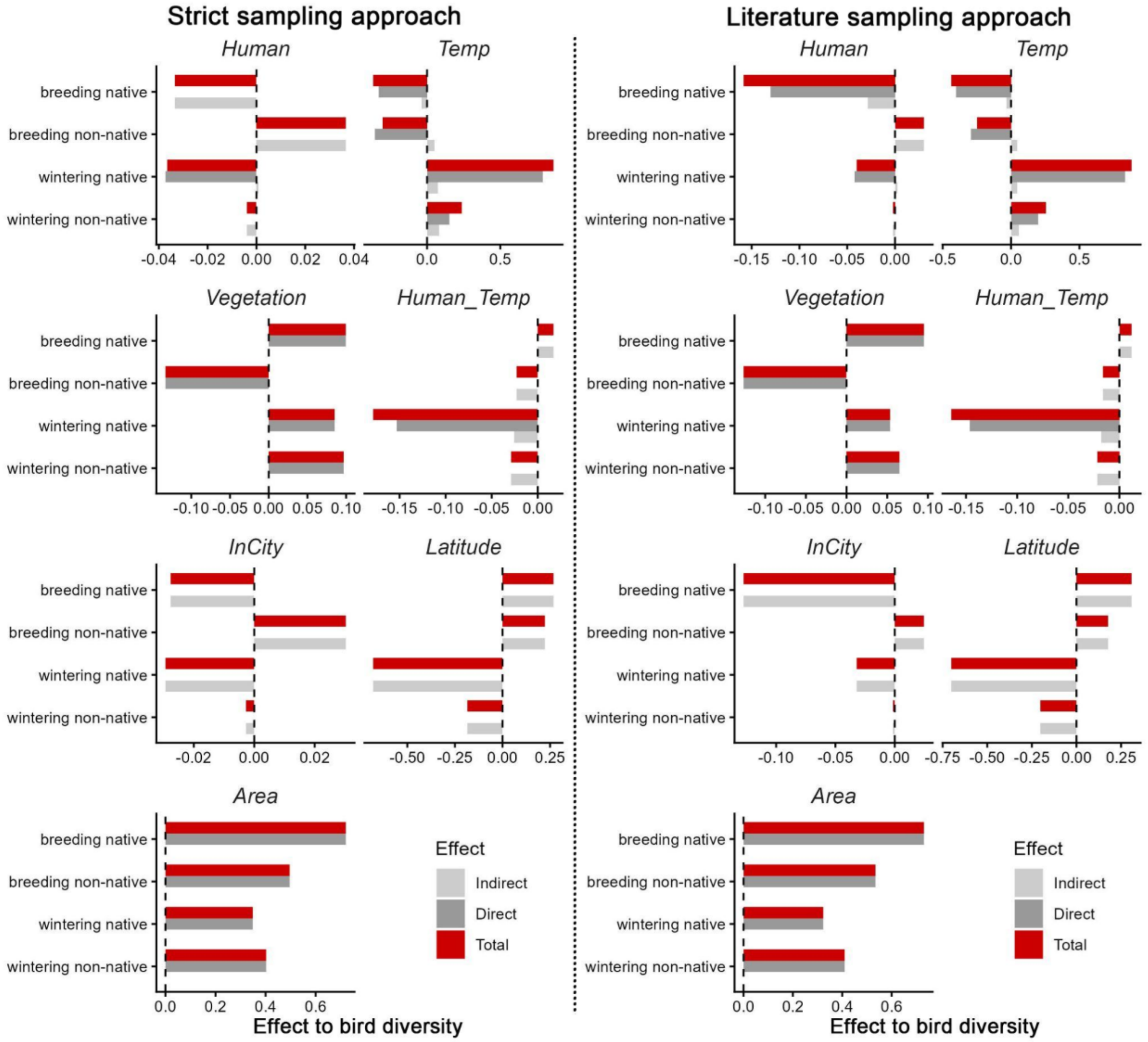

Fig. S8 The direct, indirect, and total (direct + indirect) effects of each predictor on bird diversity quantified by the Structural Equation Models (SEMs). Direct effects are defined as standardized path coefficients from each predictor to bird diversity, whereas indirect effects are calculated as the sum of products of standardized path coefficients along all mediated pathways linking each predictor to bird diversity.

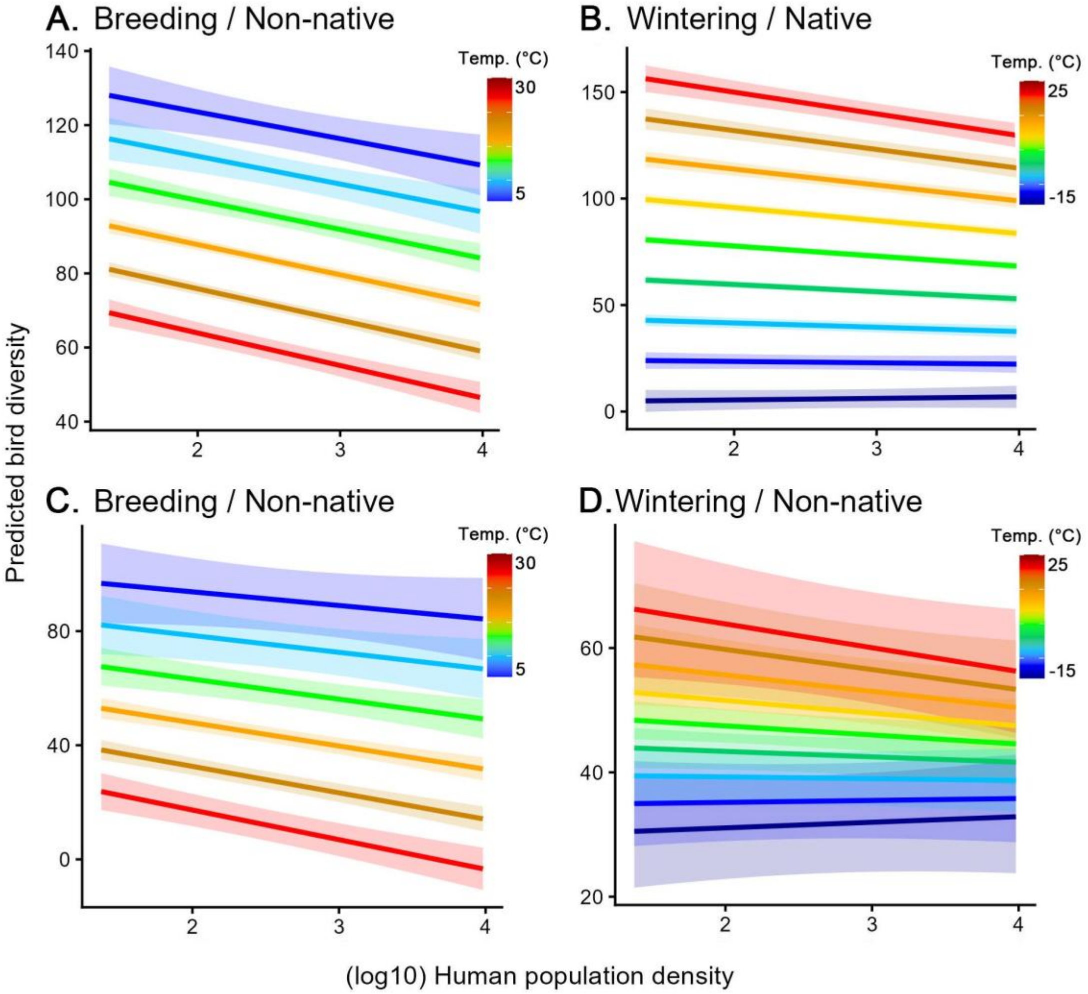

Fig. S9 Marginal response of bird diversity to the interaction between human population density and temperature across different observation seasons and native/non-native statuses based on the literature sampling approach. The figure shows the linear responses of bird diversity to log10-transformed human population density (Human) at different temperature levels (coded in the gradients of colors), assuming all other variables are held constant at their means (median for other variables except Human and temperature).The lines indicate the fitted regression lines based on these predicted results. The shaded areas represent the 95% confidence intervals of the lines fitted.

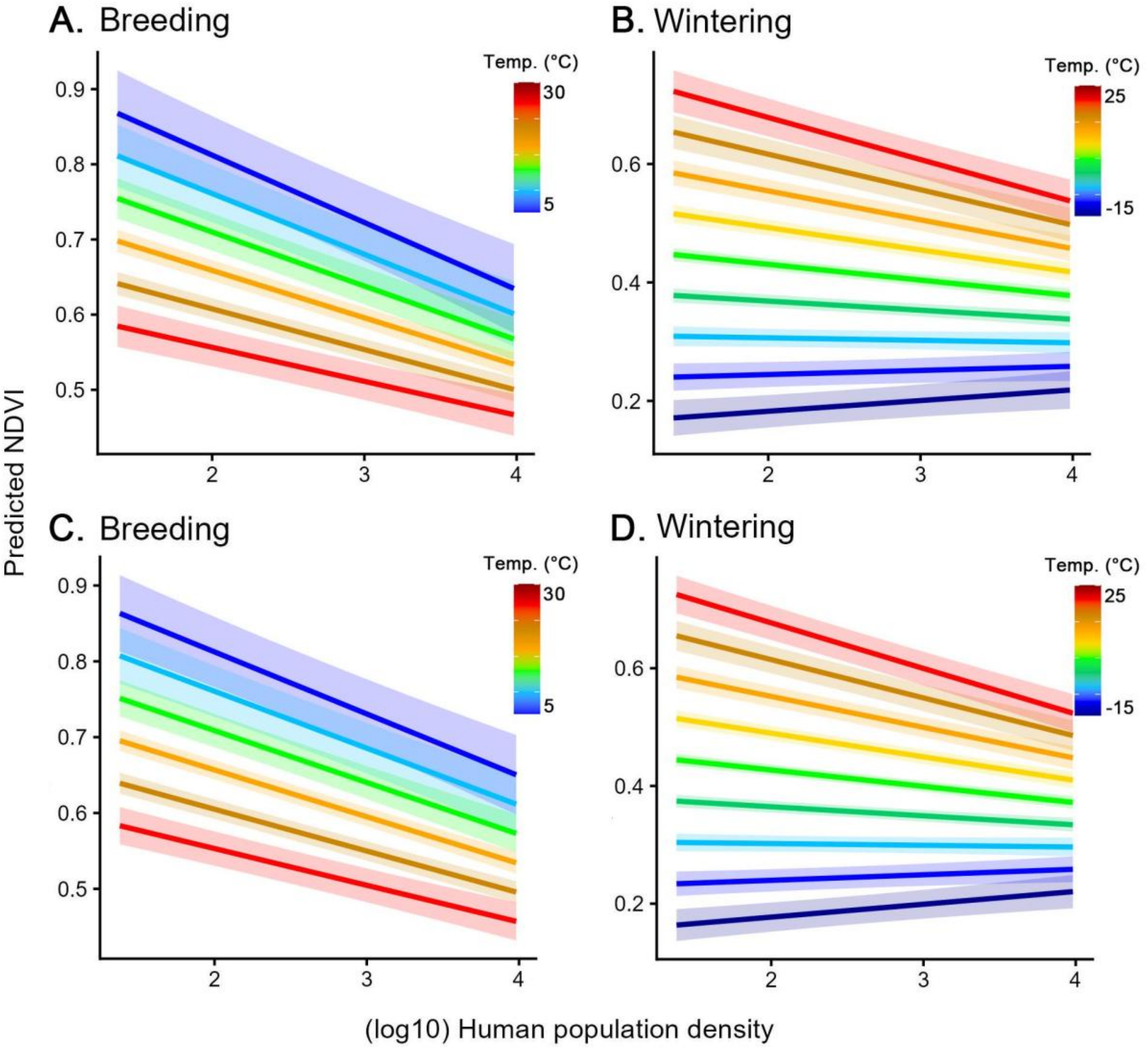

Fig. S10 Marginal responses of vegetation to the interaction between humans (log10-transformed population density) and temperature across seasons based on strict (A, B) and literature (C, D) sampling selection, respectively. The figure shows the linear response of NDVI to humans at different temperature levels (coded in the gradients of colors) while holding all other variables constant at their medians. The shaded area represents the 95% confidence interval of each fitted line.