# URBANIZATION DAMPENS THE LATITUDINAL DIVERSITY GRADIENT IN BIRDS

Master of Science

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#### ABSTRACT

Urbanized areas are rapidly expanding, causing the rise of a brand new biome that is globally distributed. The large-scale habitat transformation caused by urbanization often leads to local declines in species diversity. However, little is known about how urbanization affects biodiversity patterns on global scales. The most-studied biodiversity pattern is the latitudinal diversity gradient, where species richness declines from the equator to polar regions. Urbanization has the potential to alter this pattern by filtering out specialist species that are not tolerant of high disturbance, however, few studies have examined this, and none at a global scale. Using the citizen science database eBird and the European Commission Global Human Settlement data, we examined how urbanization affects the latitudinal diversity gradient in birds by comparing the relationship between species richness and latitude in urban, suburban, and rural areas globally and between seasons. We recovered a strong latitudinal diversity gradient in natural areas, and found that the latitudinal gradient is weakened in urban and suburban areas. This dampening effect is strongest in summer, erasing the latitudinal gradient entirely. Furthermore, we found evidence that this dampening is largely driven by the disproportionate loss of specialist species with narrow habitat and diet niches from urban areas at lower latitudes, where there is a higher proportion of specialists that are not suited to urban environments. These results demonstrate how urbanization has disrupted a well-established and ubiquitous biodiversity pattern at a global scale.

#### RÉSUMÉ

Les zones urbanisées s'étendent rapidement, provoquant l'apparition d'un tout nouveau biome réparti à l'échelle mondiale. La transformation de l'habitat à grande échelle causée par l'urbanisation entraîne souvent un déclin local de la diversité des espèces. Cependant, on sait peu de choses sur la façon dont l'urbanisation affecte les schémas de biodiversité à l'échelle mondiale. Le modèle de biodiversité le plus étudié est le gradient de diversité latitudinal, où la richesse des espèces diminue de l'équateur aux régions polaires. L'urbanisation peut potentiellement modifier ce schéma en filtrant les espèces spécialistes qui ne tolèrent pas les fortes perturbations, mais peu d'études ont examiné cette question, et aucune à l'échelle mondiale. En utilisant la base de données de science citoyenne eBird et les données de la Commission européenne sur l'établissement humain mondial, nous avons examiné comment l'urbanisation affecte le gradient de diversité latitudinal chez les oiseaux en comparant la relation entre la richesse des espèces et la latitude dans les zones urbaines, suburbaines et rurales à l'échelle mondiale et entre les saisons. Nous avons retrouvé un fort gradient latitudinal de diversité dans les zones naturelles et constaté que le gradient latitudinal était affaibli dans les zones urbaines et suburbaines. Cet effet d'atténuation est le plus fort en été, effaçant complètement le gradient latitudinal. En outre, nous avons trouvé des preuves que cet affaiblissement est largement dû à la perte disproportionnée d'espèces spécialistes ayant des niches étroites d'habitat et de régime alimentaire dans les zones urbaines à des latitudes plus basses, où il y a une plus grande proportion de spécialistes qui ne sont pas adaptés aux environnements urbains. Ces résultats démontrent que l'urbanisation a perturbé un modèle de biodiversité bien établi et omniprésent à l'échelle mondiale.

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This thesis was undertaken at McGill University on land that has long served as a site of meeting and exchange among Indigenous peoples, including the Kanien'keha:ka, Haudenosaunee and Anishinabeg nations.

**Format** - This thesis was written in manuscript format whereby chapter 1 forms a single manuscript. Chapter 1 will be submitted as a stand-alone research paper in a scientific journal.

**Chapter 1** - Dr. Anna Hargreaves conceptualized the idea to look at the effect of urbanization on the latitudinal diversity gradient using eBird. Jory Griffith refined and extended the research question to look at seasonal differences in the latitudinal diversity gradient across urbanization levels. Dr. Anna Hargreaves, Dr. Jenn Sunday, and Jory Griffith developed the idea to look at niche breadth of urban and non-urban species. Jory Griffith gathered the data, performed the analyses, and wrote the manuscript with help and input from Dr. Anna Hargreaves and Dr. Jennifer Sunday.

#### LITERATURE REVIEW

The latitudinal diversity gradient is a well-known biogeographic pattern that is fundamental to the way we understand the distribution of biodiversity on earth (Hillebrand, 2004; Kinlock et al., 2018). This pattern of decreasing diversity from the equator to the poles was first described by Alexander Von Humboldt over two centuries ago and has fascinated ecologists ever since (Kinlock et al., 2018; Mannion, 2020). Numerous studies have tried to understand the evolutionary history and mechanisms that underlie the latitudinal diversity gradient, and dozens of hypotheses have been proposed, tested, and debated with no clear consensus (Allen & Gillooly, 2006; Condamine et al., 2012; Jablonski et al., 2006; Mittelbach et al., 2007). However, the latitudinal diversity gradient is not static, and can be influenced by factors such as seasonality, climate change, and land use change (Fisher et al., 2008; Perez et al., 2022; Sorte et al., 2010). Examining how these factors affect this quintessential biogeographic pattern can improve our understanding of how humans are altering biodiversity patterns at a global scale.

Human impacts such as urbanization have global effects on biodiversity, and therefore have the potential to impact the latitudinal diversity gradient (Li et al., 2022). Although cities cover only a small fraction of the Earth's land area (Schneider et al., 2010), they contain over half of the world's population and are growing rapidly; urban expansion is projected to cause the loss of an additional 11-33 million hectares of natural habitat by 2100 (Jiang & O'Neill, 2017; Li et al., 2022; United Nations 2018). There has been a rise of studies on urban ecology (McDonnell, 2011; Wu, 2014) to understand and minimize the effect of urbanization on the natural environment and increase human health and wellbeing in cities (Taylor & Hochuli, 2015). These studies tell us a great deal about how urbanization affects patterns of diversity within and among cities, but we lack knowledge on how this scales up to affect biodiversity patterns globally (Aronson et al., 2014; McDonald et al., 2020).

Urbanization often causes a decline in species richness, but this effect can vary depending on geography, city structure, taxonomic group, and level of urbanization. Typically, vertebrate species richness decreases along a rural to urban gradient because many species cannot withstand an environment that is drastically different from their native habitat (Aronson et al., 2014; Batáry et al., 2018; Garaffa et al., 2009; McKinney, 2008). Globally, there is around a 50% decline in terrestrial species richness in urban areas compared to natural areas (Newbold et al., 2015). However, there is a great deal of variation in how cities affect biodiversity, depending on geographic location, composition of local diversity and city attributes such as amount of green space and its connectivity across the urban matrix (Haight et al., 2023; Huang et al., 2023; Leveau, 2021; Nielsen et al., 2014). The effect of urbanization on richness also varies by taxonomic group; for example plant species richness can increase in urban areas because of the introduction of nonnative species planted in gardens and parks (Faeth et al., 2011; McKinney, 2008; Walker et al., 2009). Additionally, species richness and abundance can sometimes increase at intermediate levels of urbanization because of species introductions and increased habitat heterogeneity (Batáry et al., 2018; McKinney, 2008). These highly variable effects make it difficult to predict how urbanization will impact biodiversity patterns on a global scale.

Urbanization also affects the community composition of biological communities (Concepción et al., 2017; Swan et al., 2012). One framework used to understand community assembly in cities is that of an environmental filter, in which the urban community is made up of species from the regional species pool with characteristics that allow them to establish and persist in urban habitats (Aronson et al., 2014). Indeed, several studies have found that urban

areas act as a non-random environmental filter, and urban communities are composed of species with certain traits that allow them to thrive in high disturbance environments (B. S. Evans et al., 2018; Hensley et al., 2019; C. P. Silva et al., 2016). One trait that seems to be consistently beneficial in urban environments is niche generalism; species with wider thermal, diet, and habitat breadths are more urban-tolerant, likely because highly specialized species are unlikely to find their niche in urban environments (Bonier et al., 2007; Callaghan et al., 2019, 2020; K. L. Evans et al., 2011; Palacio, 2020). This environmental filtering can cause a decline in functional diversity in cities and functional homogenization across cities (Devictor et al., 2007; B. S. Evans et al., 2018; Luck & Smallbone, 2011; Marcacci et al., 2021).

There is evidence that urban environments are not only becoming functionally homogenized, but also taxonomically homogenized (Aronson et al., 2014; Lokatis & Jeschke, 2022). The urban biotic homogenization hypothesis posits that species within urban areas will be more compositionally similar than natural areas that are the same distance apart (McKinney, 2006). This is based on the idea that urbanization is creating replicated environments worldwide that select for the same species, and mass movement of humans is facilitating dispersal pathways that allow for these urban-adapted species to spread (Aronson et al., 2014; Lokatis & Jeschke, 2022; McKinney, 2006). The biotic homogenization hypothesis has been frequently tested using measures of beta diversity or comparing the distance decay of community similarity in urban and non-urban areas (Lokatis & Jeschke, 2022). However, results of such studies have been mixed, with some finding evidence of increased taxonomic homogenization (Clergeau et al., 2006; Luck & Smallbone, 2011; Marcacci et al., 2021; Murthy et al., 2016), and some finding no evidence for increased compositional similarity between cities (Aronson et al., 2014; Blood et al., 2016; Harrison et al., 2018; Hensley et al., 2019; Jokimäki & Kaisanlahti-Jokimäki, 2003). The

detection of biotic homogenization may depend on the scale of analysis and the use of abundance versus presence/absence indices (Jokimäki & Kaisanlahti-Jokimäki, 2003; Leveau et al., 2017; Luck & Smallbone, 2011; Yang et al., 2015). However, biotic composition still varies considerably between cities, and the taxonomic makeup of cities is still mostly a reflection of the regional diversity (Aronson et al., 2014; Leong & Trautwein, 2019).

Much of the work on urban ecology has focused on birds, likely because of the wealth of biodiversity and occurrence data worldwide (Marzluff, 2001, 2017). Many studies have looked at the characteristics that make some birds urban adapted, including diet guilds, nesting preferences, and life history strategies (Chace & Walsh, 2006; B. S. Evans et al., 2018; K. L. Evans et al., 2011; Kark et al., 2007; Neate-Clegg et al., 2023). Some of these studies have found consistent traits that make species urban adapted, such as nesting in trees and shrubs (B. S. Evans et al., 2018; K. L. Evans et al., 2011; Kark et al., 2007; Lakatos et al., 2022). The effect of other traits on urban tolerance, such diet guild and migratory strategy, have been inconclusive (B. S. Evans et al., 2018; K. L. Evans et al., 2011; Kark et al., 2007; Lakatos et al., 2022). Niche breadth consistently emerges as beneficial to urban tolerance (K. L. Evans et al., 2011; Neate-Clegg et al., 2023; Sol et al., 2017). However, the associations of certain species traits with urban tolerance have been shown to vary systematically with latitude and human population density (Neate-Clegg et al., 2023). For example, diet breadth becomes more important to urban tolerance at high latitudes, while habitat breadth becomes less important (Neate-Clegg et al., 2023). This suggests that the strength of environmental filters in urban environments vary geographically.

Furthermore, there is evidence that the strength of the environmental filter imposed by urbanization also varies by season (Hensley et al., 2019). In North America, bird species are more urban-tolerant in the winter (Callaghan et al., 2021), likely because species are taking advantage of the increased availability of resources (Anderies et al., 2007) or increased temperature in urban areas (Alonso-Crespo & Hernández-Agüero, 2023). This seasonal variation in urban tolerance suggests that bird species richness patterns within cities may vary throughout the year because species are able to live in urban environments during winter but not summer. Moreover, global species richness patterns in birds are already highly seasonal, as birds undergo a massive redistribution of biodiversity every year because of migration, changing the pattern of the latitudinal gradient between seasons (Somveille et al., 2013). Therefore, it is important to take into account seasonal differences in the effect of urbanization on diversity patterns, which has not previously been done.

The question remains as to how these effects of urbanization on bird richness and community composition scale up to affect global biogeographic patterns such as the latitudinal diversity gradient. Previous studies have examined this at smaller scales and produced contrasting results. Along 14 degrees of latitude in Argentina, urbanization decreased diversity and eliminated the latitudinal diversity gradient (Filloy et al., 2015). However, in North America from 30-55° N, urbanization had no effect on richness or the pattern of the latitudinal diversity gradient (Murthy et al., 2016). The incongruencies between these results could be due to differences in the scale of analysis (50 m radius vs. 12 km radius), geographic differences (northern vs. southern hemisphere), differences in season (summer vs. winter), or a lack of sufficient latitudinal coverage to detect the pattern. The only study to date that has looked at whether urbanization affects the latitudinal diversity gradient globally found that the gradient was dampened but did not disappear in urban areas in ants (Perez et al., 2022). This study was based on a literature review of ant biodiversity data collected in using various methods in 35 cities globally, but a larger-scale analysis will give greater insights into biodiversity patterns.

Based on what we know about how urbanization affects community composition at local scales, we can make predictions for how urbanization will affect the latitudinal diversity gradient. We know urbanization often causes a decrease in species richness compared to surrounding areas (Aronson et al., 2014; Batáry et al., 2018; Garaffa et al., 2009; McKinney, 2008), but there is variation in how urbanization affects richness both within and between cities (Beninde et al., 2015; Huang et al., 2023; Leveau, 2021; Nielsen et al., 2014). Therefore, the effects of urbanization on richness could be so variable within and among cities that there is an increase in noise in urban areas but no systematic effect of urbanization on the pattern. Alternatively, if urbanization has an equal negative effect on richness across latitudes, it could cause the same proportional loss of species richness across latitudes, which would cause a slight dampening of the latitudinal diversity gradient.

Alternatively, there could be a greater proportional loss of species richness in urban areas compared to natural areas at low latitudes because of biogeographic patterns in the distribution of species traits. Urban areas generally favor species that are more generalized in their niches, as they are more likely able to tolerate the wide range of conditions and variety of resources in urban environments, while specialist species are unlikely to find their specific diet or habitat niche in cities (Bonier et al., 2007; Callaghan et al., 2019, 2020; K. L. Evans et al., 2011; Palacio, 2020). Furthermore, niche generalization is thought to increase with latitude, as predicted by MacArthur's latitude-niche breadth hypothesis (MacArthur 1972) and supported by a number of studies (Granot & Belmaker, 2020; Salisbury et al., 2012; Saupe et al., 2019; Sunday et al., 2010). Therefore, if there are more specialists at lower latitudes, and specialist species are filtered out of urban environments at higher rates, there may be a greater proportional loss of species in urban environments at lower latitudes compared to higher latitudes. In

agreement with this, there is evidence that the proportion of the regional species pool found in urban areas increases with latitude (Ferenc et al., 2014) and this is related to an increase in geographic range size at higher latitudes (Ferenc et al., 2019), which generally correlates with niche breadth (Slatyer et al., 2013). However, to our knowledge, no studies have directly looked at whether patterns in niche breadth affect geographic patterns in the effect of urbanization on species richness.

Together, previous research illustrates that there may be a latitudinal pattern in the extent to which urbanization affects species richness, and that urbanization may dampen the latitudinal diversity gradient by filtering out more specialist species at lower latitudes. However, no studies to date have examined the effect of urbanization on the latitudinal diversity gradient in birds globally. Additionally, no studies have examined seasonal variation in the effect of urbanization on the latitudinal gradient. Furthermore, no studies have looked at the causes of this pattern, and how it relates to the habitat breadth of species and the strength of the environmental filter of urbanization. This study addressed these knowledge gaps to create a more comprehensive understanding of how urbanization affects global biogeographic patterns.

# **THESIS CHAPTER:** URBANIZATION DAMPENS THE LATITUDINAL DIVERSITY GRADIENT IN BIRDS

Jory Griffith, Jennifer Sunday, and Anna Hargreaves

#### INTRODUCTION

Humans are profoundly altering the environment through urbanization. Urban areas are rapidly expanding and are projected to cause 11-33 million hectares of natural habitat loss by 2100 (Li et al., 2022). Although there is a great deal of variation in structure, age, density, socioeconomics, and geographical context, cities around the world share a similar fundamental structure, where natural habitats are replaced by buildings and pavement, transforming landscapes and creating areas of high disturbance (Grimm et al., 2008; Johnson & Munshi-South, 2017). In this way, urbanization can be seen as a novel biome that is globally distributed, rapidly expanding, and having substantial negative effects on biodiversity (McKinney, 2008; Pincetl, 2015; Walker et al., 2009). Because urbanization is a global phenomenon, it provides an opportunity to test how large-scale habitat alteration affects biodiversity patterns on a global scale (McDonald et al., 2020).

Perhaps the most well-known global biodiversity pattern is the latitudinal diversity gradient, where species richness is highest at the equator and decreases towards the poles. The latitudinal diversity gradient is found across many taxa, habitats, and biogeographical realms (Hillebrand, 2004; Kinlock et al., 2018). This gradient could be altered in urban and suburban areas because urbanization affects local patterns of species richness. Numerous studies have found that biodiversity decreases along an urbanization gradient, where species richness is highest in natural areas, intermediate in suburban areas, and lowest in highly urbanized areas, especially for vertebrate and invertebrate species (plant species richness can increase in the urban

center due to the introduction of invasive species; Aronson et al., 2014; Batáry et al., 2018; Garaffa et al., 2009; McKinney, 2008). However, the effects of urbanization on richness are highly variable between cities, depending on geographical location, pre-existing ecological features, city structure, amount of green space, and level of urbanization (McKinney, 2008). There is even evidence that urbanization can increase richness at some spatial scales due to increased habitat heterogeneity and the introduction of non-native species (Marzluff, 2001; McKinney, 2008). This variation in the effect of urbanization on richness makes it difficult to predict how these patterns scale up globally (Aronson et al., 2014; McKinney, 2008).

The effect of urbanization on richness may vary with latitude because of geographical patterns in species' traits. Cities can act like an environmental filter, filtering out species that cannot withstand the high disturbance environment (Aronson et al., 2016; B. S. Evans et al., 2018). Species inhabiting urban areas tend to possess broader thermal, habitat, and dietary preferences, likely because these generalist traits allow them to thrive amidst the novel conditions and resources found in cities, unlike specialist species which struggle to find suitable niches (Bonier et al., 2007; Callaghan et al., 2019, 2020; Ducatez et al., 2018). Additionally, generalization is thought to increase with latitude, as posited by MacArthur's latitude-niche breadth hypothesis (MacArthur 1972) and supported by a number of studies (Granot & Belmaker, 2020; Salisbury et al., 2012; Saupe et al., 2019; Sunday et al., 2010), but also refuted by others (Cirtwill et al., 2015; Vázquez & Stevens, 2004). If niche breadth generally increases with latitude, cities situated at lower latitudes may experience a greater decline in regional species richness compared to those at higher latitudes. Indeed, cities at higher latitudes retain a greater proportion of the regional (natural) avian species pool compared to low-latitude cities

(Ferenc et al., 2014). Additionally, in ants, there is greater species loss in urban areas in the tropics, leading to a dampening of the latitudinal diversity gradient (Perez et al., 2022).

We sought to examine how urbanization and the environmental filtering of specialist species alters the latitudinal diversity gradient using birds, as they have been the subject of much of the work in urban ecology due to the wealth of diversity data worldwide (Marzluff, 2001, 2017). There are mixed results on the effect of urbanization on the latitudinal diversity gradient in birds, with some evidence that urbanization eliminates the gradient along 14 degrees of latitude in Argentina and some evidence that urbanization has no effect on richness or the strength of the gradient along 25 degrees of latitude in North America (Filloy et al., 2015; Murthy et al., 2016). The discrepancy between these studies could be due to geographic (northern vs. southern hemisphere) or seasonal (spring vs. winter) differences in the effect of urbanization on richness patterns. Therefore, a more comprehensive global study would help us understand how the rapid expansion of urban areas is altering this fundamental biogeographic pattern in birds at a global scale. Furthermore, because some bird species are migratory, it is important to examine how these patterns vary seasonally.

Bird migration is a massive seasonal redistribution of biodiversity that must be considered when mapping avian biogeographic patterns. At low absolute latitudes, there is higher avian species richness in winter compared to summer because birds are overwintering there, while the opposite is observed at high absolute latitudes as birds migrate north to breed (Somveille et al., 2013). Additionally, there is evidence that birds may be more urban-tolerant in winter than in summer at higher absolute latitudes because urbanization buffers the effects of winter harshness through increased availability of resources (Callaghan et al., 2021) or increased temperatures (Alonso-Crespo & Hernández-Agüero, 2023; Sumasgutner et al., 2023). Cities can

provide important overwintering areas for bird species (Jokimäki & Kaisanlahti-Jokimäki, 2012) and urbanization can decrease the likelihood that individuals migrate to lower latitudes in winter (Bonnet-Lebrun et al., 2020). Therefore, urbanization could have less of a negative impact on richness at higher latitudes where temperature and resource availability fluctuate throughout the year. However, it remains to be seen whether there are seasonal differences in how urbanization affects biodiversity patterns.

Here, we examine whether urbanization dampens the latitudinal gradient by comparing latitudinal richness patterns of birds between natural, suburban, and urban areas and between summer and winter. Our questions were: 1) Is the pattern of latitudinal diversity gradient altered in urban and suburban areas compared to natural areas? 2) Does niche breadth increase with latitude and does this cause a disproportionately greater loss of specialist species in urban areas at lower latitudes? 3) Does the effect of urbanization on the latitudinal diversity gradient vary between seasons?

We formulated three competing hypotheses for the effect of urbanization on the latitudinal diversity gradient in birds (question 1). First, urbanization may cause the latitudinal gradient to become noisier if the effect of urbanization on richness is so variable within and between cities and latitudes that there is no discernable change in the pattern (Fig. 1H1). Second, if the environmental filter of urbanization is equally strong across latitudes, urbanization could cause an equal proportional loss of local richness across latitudes, thereby slightly dampening the latitudinal diversity gradient (Fig. 1H2). Third, if species at lower latitudes are more specialized, and if specialized species are less tolerant of urban environments, the environmental filter of urbanization could be stronger at lower latitudes, and a greater proportion of species would be filtered out of urban environments. Under this hypothesis, the proportional loss of richness in

urban areas would be highest at the equator and decrease toward the poles, leading to a stronger dampening of the latitudinal diversity gradient (Fig. 1H3). Because suburban areas represent an intermediate level of disturbance between natural and urban areas, and richness often declines along a rural-urban gradient (Aronson et al., 2014; Batáry et al., 2018; B. S. Evans et al., 2018; Garaffa et al., 2009; McKinney, 2008), we predict that the latitudinal gradient in suburban areas will have intermediate richness values and a slope between natural and urban areas. If we observe a greater proportional loss of richness in urban areas at low latitudes, and this is driven by a loss of specialist species (question 2), we would expect species that are filtered out of urban environments to have narrower diet and habitat breadths than species that are present in urban environments, and that this difference would be largest in the tropics where there are more specialist species.

We also formulated two competing hypotheses for the seasonal effects of urbanization on the latitudinal diversity gradient (question 3). Because of seasonal migration, we expect the latitudinal gradient to be steeper in winter than summer for all urbanization levels. If urbanization has the same effect on the latitudinal gradient between seasons, the proportional difference in species richness between urbanization levels at a given latitude will be the same between seasons (Fig. 1H4). Alternatively, if cities become more attractive to birds in winter as buffers from winter harshness (Jokimäki & Kaisanlahti-Jokimäki, 2012), we expect that the difference in richness between urban and natural areas will decrease or potentially disappear at higher latitudes in winter (Fig. 1H5). In the summer, we expect richness to remain higher in natural areas than urban and suburban areas across latitudes (Fig. 1H5).

Here, we test these hypotheses using global observations of bird richness across urbanization levels and seasons. We use eBird data to measure species richness and the European

Commission Global Human Settlement Layer to quantify urbanization, generating a dataset of over 66,000 points with a measure of species richness and urbanization including occurrences of over 10,000 bird species. Additionally, we used species-level data on habitat and diet breadth to examine how specialization varies across latitudes and among urbanization levels, as these aspects of niche breadth are important to the urban tolerance of bird species (K. L. Evans et al., 2011; Neate-Clegg et al., 2023; Sol et al., 2017). Our approach will further understanding of how this novel ecosystem is disrupting biodiversity patterns at global scales.



Figure 1. Hypotheses for the effects of urbanization on the latitudinal diversity gradient in birds year round (question 1; H1, H2, and H3) and between seasons (question 3; H4 and H5). The main plots are the expectations for the latitudinal diversity gradient in urban, suburban, and natural areas and the insets are the expected proportion of natural richness (green dotted line) in urban and suburban areas at each latitude, calculated by dividing the richness in urban and suburban areas by the natural richness at that latitude. H1) Urbanization will have variable effects on diversity, therefore adding noise to the pattern but not affecting the latitudinal diversity gradient overall. H2) Urbanization will cause the same proportional loss of richness across latitudes, so less species will be lost at higher latitudes because there are less species there, causing a slight dampening of the latitudinal gradient. H3) Urbanization will cause a greater proportional loss of species richness at lower latitudes because there are more specialists in the tropics, and urban areas are filtering out specialist species at higher rates, causing a further dampening of the gradient. H4) The latitudinal diversity gradient will be steeper in winter than in summer because birds are migrating towards the tropics, but at any given latitude, the proportional loss of species richness in urban and suburban areas will be the same between seasons. H5) The latitudinal diversity gradient will be steeper in winter than in summer and the difference in richness at high absolute latitudes will be lower in the winter because birds are using cities as buffers from winter harshness. In summer, richness will remain lower in urban areas because birds are not as urban-tolerant.

#### METHODS

#### 1. eBird dataset

To estimate bird species richness around the globe we used the eBird basic dataset (version ebd\_relMar-2023). eBird is a citizen science database with millions of records worldwide, where users submit 'checklists' of birds seen on an outing (Sullivan et al., 2014). We used the R package 'auk' (Strimas-Mackey et al. 2023a) to filter the full dataset according to the Cornell Lab of Ornithology eBird best practices protocol (Strimas-Mackey et al. 2023b). We subset the data by the following criteria: 1) checklists were "complete", meaning the observer indicated that they recorded all bird species seen during their outing; 2) checklists were from outings where birding was the primary activity (i.e. followed the "stationary" or "traveling" protocols); 3) the distance traveled during the outing was less than 5 km so that the geolocated point was not far from the bird sighting; 4) the duration of the checklist was less than 5 hours to reduce variability in sampling effort between checklists. We included checklists recorded between 2016 and 2022 to limit the bird sightings to a time period relevant for the urbanization data.

#### 2. Classifying urbanization level

To classify the degree of urbanization, we used the 2020 Global Human Settlement data (GHS) developed by the European Commission (Schiavina et al. 2022). The Settlement Model Layer (GHS-SMOD) classifies urbanization at a 1 km<sup>2</sup> resolution based on population and the population of nearby grid cells. It classifies each cell into one of three categories based on urbanization classifications from the UN statistical commission (Dijkstra et al., 2021): 'urban center' (urban) or grid cells with a density of at least 1500 inhabitants per km<sup>2</sup>, 'urban cluster' (suburban) or cells with a density of at least 300 inhabitants but fewer than 1500, and 'rural' or any cells that don't meet the former criteria.

Grid cells designated as "rural" based on the GHS classification could still have relatively high levels of human modification (e.g. agriculture, resource extraction, etc.) and we wanted to capture the latitudinal gradient in natural areas. We therefore classified 'natural' areas in our study as 'rural' areas that also have low human modification according to the Global Human Modification layer (GHM). The GHM, developed by the NASA Socioeconomic Data and Applications center, is a 1 km<sup>2</sup> resolution raster that maps a cumulative measure of human modification ranging from 0-1; with 1 being the highest modification (Theobald et al., 2020). Values are calculated from five anthropogenic stressors: human settlement, agriculture, transportation, energy production, and electrical infrastructure. Each cell value is assigned based on the estimated proportion that is modified and weighted by the intensity of the modification. To capture 'natural' areas we removed all 'rural' cells that had a modification greater than 0.5. To test how our choice of threshold affected the results, we also ran all analyses with a modification threshold of 0.25 and 0.75. We also removed all cells that were classified as water and cells that had missing values for urbanization.

#### 3. Calculating bird species richness

We estimated species richness by aggregating eBird checklists into the 1 km<sup>2</sup> raster cells of the GHS layer and calculating the total number of species observed in each cell. Because urban areas have a more limited latitudinal range than natural areas, we removed all natural cells that were outside of the latitudinal range of the urban data to avoid model extrapolation at high absolute latitudes (i.e. removed all cells north of 70° or south of  $-55^{\circ}$ ).

Because measures of species richness are highly dependent on sampling effort, we partially removed the influence of sampling effort by using a threshold number of checklists to improve the accuracy of richness values. We wanted to use a threshold number of checklists that

would capture most of the diversity, even in cells with the highest richness values, so we determined how many checklists were needed to reach a sampling coverage of 95% in the 500 cells in our dataset with the highest species richness. Measures of sample coverage fit a model to the species accumulation curve to determine how likely it is that a new sample will yield a new species, so a 95% sampling coverage means that there is a 5% chance that an additional sample will detect a new species. We estimated the number of checklists needed to reach a sampling coverage of 95% in the 500 richest cells using the 'iNEXT' R package (Hsieh et al. 2022). Checklists do not give reliable estimates of abundance, so we converted occurrences to incidence-frequency data to input into iNEXT. For each checklist, we assigned each species in the cell a 0 or 1 based on whether it was recorded in that checklist (presence = 1), summed frequencies over all checklists in the cell, and estimated coverage from the relative frequency of incidences using iNEXT. This yielded 500 estimates of the number of checklists needed to reach 95% coverage for each cell, and we took the 95<sup>th</sup> percentile of this distribution, which gave a threshold of 83 checklists per cell. We removed all cells that had lower than 83 checklists. This yielded 66,639 cells with both a measure of species richness and an urbanization score (33,485 cells in natural areas, 19,494 cells in suburban areas, and 13,660 cells in urban areas; Fig. 2A), which we used for further analyses. To test for an effect of our choice of minimum threshold on the results, we also calculated the number of checklists needed to reach 90% and 98% sample coverage, took the 95th percentile of this distribution, and ran all analyses with these lower and higher thresholds, respectively.

4. Analyses

#### a. *Overall latitudinal diversity gradient*

To examine the effect of urbanization on the latitudinal diversity gradient (question 1), we fit a linear model with species richness as the response variable and latitude, urbanization, and their

interaction as the predictors. Species richness was square root transformed to meet assumptions of normality in the residuals. We also included hemisphere and the triple interaction between hemisphere, latitude, and urbanization to account for potential differences in the effect of urbanization on the latitudinal diversity gradient between hemispheres. Diversity varies with elevation and precipitation, so we included these as covariates in our model. Elevation of the center point of each grid cell was extracted using the 'elevatr' package (Hollister et al. 2023) and mean annual precipitation was extracted from the WorldClim bioclimatic variables (Fick & Hijmans, 2017). Although we only included grid cells with sampling effort greater than a minimum threshold of 83 checklists, we included the number of checklists (log transformed) as a continuous fixed effect in the model to account for any remaining positive relationship between richness and sampling effort in cells above the threshold. We used the 'marginaleffects' package (Arel-Bundock 2023) to calculate marginal effects averaged over predictor variables. Thus the model was: sqrt(species richness) ~ absolute latitude x urban x hemisphere + precipitation + log(number of checklists) + elevation.

Spatial autocorrelation can increase the likelihood of type 1 error, so to account for the effects of spatial autocorrelation in the residuals, we spatially thinned the data and re-ran the model 1000 times, verifying that there was no residual spatial autocorrelation using the Moran's I test statistic in the 'spdep' package (Bivand & Piras, 2015). We spatially thinned the data by overlaying a 10 km<sup>2</sup> raster grid, randomly sampling one data point in each cell, and running the model. We repeated this 1000 times, which yielded 1000 estimates of the slope of the latitudinal diversity gradient across urbanization levels, from which we took the mean. To provide a conservative estimate of confidence around the mean, we used the maximum upper confidence intervals and minimum lower confidence interval among all runs.

#### b. Seasonal data

To explore differences in the latitudinal gradient in urban areas between seasons (question 3), we filtered the data for checklists recorded during the summer (June-August in northern hemisphere and December-February in the southern hemisphere) and the winter season (December-February in the northern hemisphere and June-August in the southern hemisphere). We chose these months to capture species' breeding and overwintering habitats and try and remove migration times. We calculated species richness independently in the summer and the winter for each grid cell. We again calculated the minimum number of checklists needed to reach 95% sampling coverage in the 500 richest cells (taking the 95th percentile of the distribution), which yielded a threshold of 62 checklists for summer and 73 checklists for winter. Fewer checklists were needed than the year-round data because it is a shorter time period and fewer checklists were needed in summer because most of the richest cells are in the tropics, which have lower richness in summer due to migration. We removed cells with fewer checklists, and natural cells that were outside of the latitudinal range of the urban cells, which was 66° N and -55° S. We were left with 20,570 cells in the summer (10,505 natural, 5,622 suburban, 4,443 urban) and 21,651 cells in the winter (8,753 natural, 7,526 suburban, 5,372 urban). We ran the same linear model as the full annual data, but with a 4-way interaction between latitude, urbanization, season, and hemisphere to test 1) whether the latitudinal diversity gradient was different between seasons (latitude x season) and 2) whether the effect of urbanization on the latitudinal diversity gradient was different between seasons (latitude x urbanization x season). We again thinned the data by iteratively sampling from a 10 km<sup>2</sup> raster grid and fitting the model to one data point from each season in each cell. We resampled and ran the model 1000 times and averaged the model fits for the latitudinal gradient across urbanization levels and seasons, taking the maximum upper confidence interval and minimum lower confidence interval in the suite of models.

#### c. Specialization

To examine whether a greater proportion of specialist species were filtered out of urban environments at low latitudes (question 2), we obtained species-level data on habitat and diet specialization. We used an index of habitat breadth calculated by Ducatez et al. (2014) where habitat breadth increases with the number of IUCN habitats in which the species occurs and the diversity of other taxa with which it co-occurs (i.e. a generalist species occurs in habitats that vary considerably in species composition). We derived an estimate of diet breadth from the 'EltonTraits' database (Wilman et al., 2014), which contains the proportion of a species' diet across ten diet classes. We calculated diet breadth using the Gini index, a measure of inequality ranging from 0, representing complete generalization (i.e. equal percentage of the diet in each class), to 1, representing complete specialization (i.e. 100% of the diet in one class). The Gini index has previously been used as a measure of specialization in birds (Morelli et al., 2019; Santangeli et al., 2022). We then subtracted the Gini index values from one so that larger values represented wider diet breadth. Of the 10,723 species in the analysis, 8,367 had an estimate of habitat breadth and 6,902 had an estimate of diet specialization.

To test predictions that species at low latitudes are more specialized on average, and that a greater number of specialist species are lost from urban areas at low latitudes than high latitudes, we compared mean specialization values across bird species found in four latitudinal bins: tropical (0° to 23.44°), subtropical ( 23.44° to 35°), temperate (23.44° to 50°) and subpolar (50° to 70°). To test whether birds that were found in urban areas were more specialized than birds not present in urban areas, we classified birds as "urban" and "non-urban" based on whether there were occurrences in urban cells in that latitudinal band. Then, we ran ANOVAs with habitat or diet breadth as the main response variable and urban category, latitudinal band, and their interaction as the predictors. Habitat and diet breadth were log transformed to meet assumptions of normality in model residuals. We ran the same model for the seasonally-divided data, adding an additional interaction for season, so there was a triple interaction between urban category, latitudinal band, and season.

#### RESULTS

We found that the latitudinal diversity gradient was significantly weaker in urban and suburban areas, exhibiting a two-fold and one-third reduction in the slope, respectively, compared to natural areas (Fig 2B; absolute latitude x urbanization F-value = 277.33, P < 2.2E-16). Urban areas had 28% lower species richness globally (129 species in natural areas vs 92.6 in urban; urbanization F-value 5131.3, p < 2.2E-16), but this loss of richness was proportionally higher at lower latitudes (Fig. 2A). At the equator, urban areas had, on average, 36% lower richness than natural areas, while at 60°, urban areas had 20% lower richness. Suburban areas had 18% lower species richness than natural areas globally (129 species in natural areas vs. 106 species in suburban), but also had a greater proportional richness decrease at lower latitudes, containing 25% lower richness than natural areas at the equator and 16% lower richness at 60°. Model thinning to remove spatial autocorrelation had a negligible impact on the slope and intercepts of the latitudinal gradient, but did increase the size of the confidence intervals so that the slope of the latitudinal gradient in urban and suburban areas was no longer significantly different. Although the slopes of the latitudinal gradients among urbanization levels were somewhat affected by the choice of sampling effort and human modification thresholds, the main takeaways were the same; the latitudinal gradient was dampened in urban and suburban areas in all sensitivity analyses, and a greater proportion of richness was lost at the tropics (Fig. S8).

When analyses were scaled up to 5km<sup>2</sup>, the latitudinal gradient was still dampened in urban and suburban areas, but interestingly, suburban areas had lower richness than urban areas (Fig. S7).



**Figure 2.** Map of sampling coverage and the latitudinal diversity gradient in urban, suburban, and natural areas. A) Global map of natural (green), suburban (pink), and urban (black) cells included in the model. B) The latitudinal diversity gradient in urban, suburban, and natural areas. Each point is a raster cell, colored by the urbanization score and each line is the model fit from the thinned models with confidence intervals. C) The proportion of natural diversity (green dotted line) in urban and suburban areas, calculated by dividing the model predictions for diversity in suburban and urban areas by diversity in natural areas at each latitude.

We found evidence that the disproportionately large effect of urbanization on richness at lower latitudes was driven by a greater loss of specialist species in urban areas in the tropics. Species that were excluded from urban areas had narrower habitat (F-value = 1333.04, p < 2.2E-16) and diet breadths (F-value = 52.21, p < 2.2E-16) than species that were found in urban areas (Fig. 3). Habitat breadth increased with latitude, and the difference in habitat breadth between urban and non-urban species was largest at the equator, as indicated by a significant interaction between latitude zone and urbanization category (Fig. 3; latitude zone x urbanization category F- value = 30.48, p < 2.2E-16). Diet breadth differed between latitude zones (latitude zone F-value = 52.21, p < 2.2E-16), but the difference in diet breadth between urban and non-urban species did not vary with latitude (Fig. S4; latitude zone x urbanization category F-value = 1.74, p = 0.16). Suburban areas showed similar patterns, as diet and habitat breadth were consistently higher in birds that were found in suburban areas compared to birds that were only found in natural areas (Fig. S5). The correlation between habitat and diet breadth was weak (cor = 0.13), suggesting that species that are generalized in their diet niche are not necessarily generalized in their habitat niche and these latitudinal patterns of specialization are driven by different bird species.



**Figure 3.** Density distribution and means of habitat breadth values in each latitudinal zone. The density plots are the distribution of habitat breadth values for 8,753 species that are present in urban areas (blue) and not present in urban areas (i.e. only present in natural areas; grey) in that latitudinal bin. The points are the ANOVA means with confidence intervals. Euler plots show the proportion of species that are in urban areas (black), and not in urban areas (blue). They are scaled by the number of species in each latitudinal bin. The species that are only present in urban environments (not natural) are delineated by a blue outline. The "urban only" species are included in the "urban species" part of the density distribution. The rest of the "urban species" are also present in natural areas in that latitudinal bin.

The effect of urbanization on the latitudinal diversity gradient differed between seasons (Fig. 4). The latitudinal gradient was steeper in summer than winter across all three urbanization levels (Fig. 4; absolute latitude x season F-value = 3079.99, P < 2.2e-16). Additionally, the latitudinal gradient was dampened in urban and suburban areas in both summer and winter (Fig.

3; absolute latitude x urbanization F-value = 411.42, P < 2.2e-16). In fact, the latitudinal diversity gradient appeared to be erased in the summer, as the decline in richness with latitude in urban areas was not significantly different from 0. However, this was only the case in the northern hemisphere; a negative latitudinal diversity gradient was still present in the southern hemisphere (Fig. S3). In summer, suburban areas had a slight latitudinal gradient, but the slope was not significantly different than in urban areas.

Urbanization had a larger effect on richness in the summer than the winter; in summer urban areas had 33% lower species richness than natural areas globally, while in winter urban areas had 24% lower species richness (Fig. 3; Urbanization x season F-value = 316.09, P = 2E-16). This was also the case in suburban areas but to a lesser extent; as they had 21% lower richness than natural areas globally in summer, and 17% lower richness in winter. Urbanization had a greater effect on richness at low latitudes in both seasons. During summer, at the equator, urban areas had a 44% lower richness than natural areas, while at 60° urban areas had 28% lower richness. During winter, at the equator, urban areas had 40% lower richness than natural areas. However, in the winter, urbanization appeared to no longer have a negative impact on richness at higher latitudes, as urban and suburban areas had equal richness to natural areas above 50° N. Model thinning to account for spatial autocorrelation did not change the slope of the latitudinal gradient or the interpretation of the results. The use of different thresholds for sampling coverage and human modification did not change the results (Fig. S9). The results were similar when analyses were scaled up to 5km<sup>2</sup>, except, again, suburban areas had lower richness than urban (Fig. S7). In both seasons, the greater loss of species richness at low latitudes appeared to be partially driven by the disproportionate loss of specialist species (Fig. S6) and seasonality did not have a large effect on environmental filtering by specialization (Table S2; Fig. S6).



**Figure 4.** The latitudinal diversity gradient in summer (left) and winter (right) in urban, suburban, and natural areas. Each point is a raster cell, colored by the urbanization score, and the lines are the model fits from the thinned models with confidence intervals.

#### DISCUSSION

Urbanization causes a two-fold weakening of the latitudinal diversity gradient in birds. Our evidence suggests this dampening effect is partially driven by a loss of specialist species in urban areas at low latitudes, as more species near the equator have narrow diet and habitat niches and these species are disproportionately lost from urban areas. Additionally, the latitudinal gradient is steeper in the winter compared to the summer for all urbanization levels. Furthermore, mean species richness is indistinguishable between urbanization levels at high latitudes in the winter. These findings support previous work on the effect of urbanization on the latitudinal diversity gradient at smaller spatial scales and within seasons (Filloy et al., 2015; Murthy et al., 2016), but further extends the inference to the global scale and across seasons. Additionally, our work builds on findings that generalist species are more urban-tolerant (Callaghan et al., 2019, 2020) and leverages an established macro-ecological pattern in generalism (the latitude nichebreadth hypothesis) to provide a mechanism for the greater effect of urbanization on richness at lower latitudes. Together, our findings demonstrate that urbanization is disrupting global biogeographic patterns.

The effect of urbanization on bird species richness is altered by seasonality. The latitudinal gradient is stronger in winter across urbanization levels, likely due to migratory patterns. Additionally, the effect of urbanization on richness differs between seasons, potentially due to seasonal variation in the urban tolerance of birds. Globally, the loss of richness in urban areas is lower in summer than winter, and this effect is especially apparent at higher latitudes, where richness is equal or greater in urban areas than surrounding natural areas, supporting previous findings that birds are more prevalent in cities in the winter (Callaghan et al., 2021). This reduced effect of urbanization on richness at higher latitudes in the winter could be due to species moving into urban areas from the surrounding regions or remaining in urban areas during the winter rather than migrating to lower latitudes, as urbanized areas at northern latitudes can be important overwintering areas for bird species (Jokimäki & Kaisanlahti-Jokimäki, 2012) and birds are more likely to remain year-round in urban areas (Bonnet-Lebrun et al., 2020). Urban areas can serve as refuges at higher latitudes because they buffer the effects of winter harshness by providing a warmer climate and increased food availability, and urbanization can increase overwintering survival in a number of species (Chace & Walsh, 2006; Suhonen et al., 2009;

Sumasgutner et al., 2023). However, to our knowledge, this is the first study to support this winter refuge hypothesis by finding no effect of urbanization on richness at mid to high latitudes.

The seasonal variation in our findings potentially resolves a previous contradiction in the literature about the effect of urbanization on the latitudinal diversity gradient in birds. One study found that urbanization eliminated the diversity gradient in the spring, which we also observed in our summer analysis (Filloy et al., 2015). In contrast, another study concluded that urbanization did not affect the richness or the slope of the gradient during the winter within the range of 30-55° N (Murthy et al., 2016). Our study does not fully agree with this finding, as we did detect differences in richness and the slope of the latitudinal gradient between non-urban and urban areas at those latitudes during the winter, but these differences in richness were much less pronounced than in the summer. Our results underscore the necessity of considering seasonality when analyzing biogeographic patterns and the effect of anthropogenic stressors.

We found that specialist species were disproportionately filtered out of urban environments at low latitudes. This latitudinal pattern in the exclusion of specialist species from urban areas has important implications for community assembly in urban environments. There is ample evidence that generalist species are better suited to urban environments (Bonier et al., 2007; Callaghan et al., 2019, 2020), and support for the hypothesis that species at low latitudes are more specialized on average is well documented (Granot & Belmaker, 2020; Salisbury et al., 2012; Saupe et al., 2019; Sunday et al., 2010). Our study combines these two hypotheses and provides evidence that the effect of urbanization on species richness varies geographically due to latitudinal patterns in specialization. We observed a larger difference in habitat specialization between urban and non-urban species at lower latitudes. Indeed, previous work shows that habitat breadth is most important as a predictor of urban tolerance in tropical areas, likely
because many tropical birds are specialized on forest habitats that are rarely found in urban environments (Neate-Clegg et al., 2023). Species present in urban environments also had consistently wider diet breadths, supporting previous studies showing that it is an important trait shaping urban tolerance (Callaghan et al., 2019; Neate-Clegg et al., 2023; Patankar et al., 2021). However, this effect was not as strong as habitat breadth, potentially because our measure of diet breadth was coarse and most species had a relatively narrow diet breadth with little variation. Interestingly, although birds in urban areas had consistently wider habitat and diet niches, our measures of habitat and diet breadth were not strongly correlated, suggesting that different bird species were driving these patterns. Additionally, there were still a number of species with specialized diet and habitat niches present in urban areas in our data. Measuring diet and habitat breadth does not provide a complete picture of the traits shaping urban tolerance, as there are many traits that promote species persistence in urban environments (K. L. Evans et al., 2011; Patankar et al., 2021). Nevertheless, our findings underscore the importance of niche generalization in determining a species' ability to thrive in urban environments, with implications for community assembly of birds in urban settings.

We observed a significant decrease in richness at low latitudes in the summer compared to the winter across urbanization levels (Fig. 3). This seasonal decrease in richness was most evident in natural areas, with a nearly two-fold difference on average (Fig. 3). This seasonal richness decrease supports previous findings (Somveille et al., 2013) and has been attributed to migratory patterns, as many birds leave tropical areas to breed. However, the seasonal decline in tropical richness observed here may not be entirely due to migration. Migrant species typically make up a small proportion (i.e. less than 20%) of the species pool at low latitudes (Somveille et al., 2013), making it unlikely that nearly half of tropical species would leave the region entirely

in the summer months. Our observations of lower richness could be driven by a lower density of birds in tropical areas in the summer, as billions of bird individuals migrate to northern latitudes to breed every year (Bauer & Hoye, 2014; Dokter et al., 2018; Hahn et al., 2009). Additionally, our observed richness decrease could be due to decreased detectability during the summer months due to seasonal changes in weather, behavior, and structural aspects of the forest (C. C. de O. e Silva et al., 2017). For example, in the Amazon rainforest, bird species are more detectable in the dry winter months than the wetter summer months due to changes in behavior and structural aspects of the forest (C. C. de O. e Silva et al., 2017).

We restricted the checklists for seasonal analyses to June-August and December-January to try and capture birds in their breeding and overwintering habitats. However, it is likely that we also captured species sighted during migration. Many birds use urban areas as migratory stopovers (La Sorte et al., 2014), but might not be able to breed or overwinter in urban areas. Therefore, we may be overestimating the number of birds that use urban areas as habitat for a significant portion of the year. This also applies to our cumulative annual measure of species richness, as we defined an urban bird as any bird that was sighted in an urban area, so the number of birds that use urban habitats for a significant period of time is likely lower. However, a larger negative impact of urbanization on richness would strengthen the patterns we observed.

Despite a similar dampening effect of urbanization on the latitudinal gradient between hemispheres, we found a steeper latitudinal gradient in the southern hemisphere across urbanization levels (Fig. S2), contrary to previous findings suggesting no difference in gradient strength (Hillebrand, 2004; Kinlock et al., 2018). However, due to limited data, it is challenging to draw definitive conclusions about whether the latitudinal gradient in bird diversity is genuinely stronger in the southern hemisphere or if our results merely reflect a bias in data

coverage toward the northern hemisphere. While our results were averaged between hemispheres, only 8% of our dataset originated from the southern hemisphere. Sampling in citizen science databases such as eBird is often biased toward countries in the global north, particularly the United States and Europe, overemphasizing biogeographic patterns in these regions (Martin et al., 2012). Additionally, although we found that the latitudinal diversity gradient was steeper in winter than in summer across urbanization levels in the northern hemisphere, there was no seasonal difference in the slope of the gradients in the southern hemisphere (Fig. S3). This lack of seasonal variation in the latitudinal diversity gradient is likely because there is considerably lower richness of migratory species in the southern hemisphere compared to the northern hemisphere due to reduced land mass and milder climate seasonality at high absolute latitudes (Somveille et al., 2013).

We sought to characterize global diversity patterns across latitudes and various levels of urbanization. However, imbalances in data coverage and historical and structural aspects of urbanization might impact our findings. Biases in where citizen science data are collected may cause systematic overestimation of diversity in urban areas. People are more likely to submit checklists in areas in or near urban developments. This was particularly true in 2020 during the COVID-19 pandemic, when there was a shift toward more observations in human dominated environments (Hochachka et al., 2021). Although we attempted to account for differences in sampling effort, this bias toward where humans are could cause us to overestimate diversity in or near urban areas compared to less-sampled rural areas. However, a systematic overestimation in diversity in urban areas is conservative to our findings, as that would mean that urbanization has a larger impact on richness than we observed in our study. Second, cities are often located near large bodies of water, so a given datapoint from an urban area may be more likely to be near

water than a given datapoint from a natural area. Therefore, richness may be higher in cities due to the of the presence of water birds. Additionally, some groups of marine birds follow an inverse latitudinal gradient (Dufour et al., 2024), which could cause systematic overestimation of richness in mid to high latitude cities, and contribute to the decrease in the proportional loss of richness at those latitudes. Future studies should look at how the effect of urbanization on the latitudinal gradient varies between avian orders.

Patterns of participation in citizen science may also covary with patterns in urban attributes that could affect our results. For instance, individuals in higher-income countries are more likely to participate in citizen science (Pocock et al., 2017, 2019), and urban areas in lower income countries tend to have different urban attributes, including denser population, smaller area, and shorter building height (Jedwab et al., 2021). The emphasis on cities with a certain urban structure could potentially bias our results, as city structure and socioeconomic factors can affect biodiversity patterns both within and among cities (Beninde et al., 2015; Kinzig et al., 2005). Although we did capture a variety of urban forms across continents in our study, our bias toward data-rich areas could limit the generalizability of our results on a global scale. Future research should examine how patterns in urban structure affect biogeographic patterns of species richness in urban areas.

Urbanization can be seen as a global experiment in understanding the impact of land use change and extensive habitat alteration on biogeographic patterns. Our findings demonstrate that urbanization dampens the latitudinal gradient by selectively filtering out specialist species, particularly in tropical regions, indicating consistent geographic patterns in the influence of urbanization on species diversity. Moreover, these patterns exhibit seasonal variation, underscoring the influence of seasonality on species' use of cities. Despite a decline in species

richness compared to areas with less human modification, urban environments worldwide still harbor significant regional diversity and provide important habitats for species worldwide. With the ongoing trend of increasing urbanization, careful urban planning is necessary to mitigate biodiversity loss and enhance human health and well-being.

## FINAL CONCLUSION AND SUMMARY

Urbanization is rapidly expanding across the globe; an increasing fraction of the population is moving into urban areas and more and more land is being converted into cities (Jiang & O'Neill, 2017; Li et al., 2022). Urbanization transforms habitats and has huge impacts on biodiversity (Aronson et al., 2014; Batáry et al., 2018; Garaffa et al., 2009; McKinney, 2008). Because of the importance of urban areas to humans and the benefits of urban biodiversity to human health and wellbeing, there has been a rise of studies on urban ecology (McDonnell, 2011; Wu, 2014). However, there is still a lack of knowledge on how urbanization affects biodiversity patterns at a global scale, even though urbanization is a global phenomenon. Here, we explored how urbanization is affecting one of the most well-known and ubiquitous biodiversity patterns, the latitudinal diversity gradient. We used birds as a focal system, as they are a data-rich group with a wealth of biodiversity and occurrence data worldwide. We hypothesized that there would be a loss of species richness in urban areas, and that this effect would be greatest at low absolute latitudes, causing a dampening of the pattern of the latitudinal diversity gradient. We used eBird and a global raster layer of urbanization to look at bird richness patterns across latitudes in urban, suburban, and natural areas, and between seasons.

We found that urbanization dampened the latitudinal diversity gradient, and had a greater effect on richness at lower absolute latitudes. We attributed this dampening effect to a greater

number of species being filtered out of urban environments at low latitudes, as species near the equator had narrower diet and habitat niches and these specialized species are filtered out of urban environments at higher rates. Additionally, we found that the latitudinal gradient was steeper in the winter than in the summer across urbanization levels due to migration. We found evidence that urbanization had a positive effect on species richness at higher latitudes during the winter, potentially because species are taking advantage of increased temperatures and food resources in urban areas in temperate zones that have greater seasonal fluctuations. Together, these findings indicate that urbanization is affecting biodiversity patterns at a global scale, the effects of urbanization on species richness dependent on geography and the distribution of species traits, and that these patterns are highly variable between seasons.

Urban ecology has become increasingly popular, as cities are incredibly important to humans and biodiversity in cities directly impacts human health and wellbeing (Sandifer et al., 2015). However, urban macroecology, or the effect of cities on broad scale ecological patterns and processes, is a much less researched field. Urban areas can serve as a fascinating experiment in broad-scale and replicated habitat alteration, and studying how this affects ecological patterns can tell us about our impact on these processes or even give us a better understanding of mechanisms. Our study builds on previous work examining how urbanization affects ecological patterns in birds (Filloy et al., 2015; Murthy et al., 2016), extending it to a global scale. Furthermore, we formulate and test hypotheses about geographic variation in the effect of urbanization on richness. The study of urban macroecology represents a promising avenue for understanding our effect on our environment and mitigating biodiversity loss in the places that most of us call home.

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## SUPPLEMENTARY MATERIALS

**Table S11.** Model results for the linear model of the effect of urbanization on the latitudinal diversity gradient, with the full year data (model A) and the seasonal data (model B). Model A) The significance of absolute latitude shows that there is a latitudinal gradient, the significance of urbanization shows that there is an effect of urbanization on the latitudinal gradient, and the significance of the interaction between absolute latitude and urbanization shows that urbanization affects the slope of the latitudinal diversity gradient. Model B) The significance of absolute latitude and season shows that the gradient is different between seasons. The significance of the three-way interaction between absolute latitude, urbanization and season shows that the effect of urbanization on the latitudinal diversity gradient is different between seasons.

Model A: Linear model of the effect of urbanization on the full year-round latitudinal diversity gradient $\sqrt{species \ richness} \sim absolute latitude x urban x hemisphere + biome + log(number of checklists) + elevation$ (df = 66,620, R <sup>2</sup> =0.38)					
Variable	Estimate	Std. Error	T value	P value	
(Intercept)	6.34	0.074	86.23	< 2E-16	
Absolute latitude	-0.06	0.0011	-53.645	< 2E-16	
Urbanization (Suburban)	-2.02	0.068	-29.51	< 2E-16	
Urbanization (Urban)	-3.07	0.066	-46.78	< 2E-16	
Hemisphere (Southern)	1.48	0.094	15.847	< 2E-16	
Precipitation	0.000016	0.000015	1.028	0.30	
Log(number of checklists)	1.48	0.0090	156.97	< 2E-16	
Elevation	0.0003	0.000014	-21.32	< 2E-16	
Absolute latitude x urbanization (suburban)	0.021	0.0018	11.71	< 2E-16	

Absolute latitude x urbanization (urban)	0.036	0.0017	20.860	< 2E-16	
Absolute latitude x hemisphere (southern)	-0.078	0.003	26.018	< 2E-16	
Urbanization (suburban) x hemisphere (southern)	0.028	0.020	0.139	0.88	
Urbanization (urban) x hemisphere (southern)	-1.152	0.019	-5.983	2.2E-09	
Absolute latitude x urbanization (suburban) x hemisphere (southern)	0.011	011 0.0063		0.09	
Absolute latitude x urbanization (urban) x hemisphere (southern)	0.022	0.006 3.659		0.0003	
Model B: Linear model of effect of urbanization on the latitudinal diversity gradient by season         √species richness       ~ absolute latitude x urban x season x hemisphere + biome + log(number of checklists) + elevation         (df =42,192, R <sup>2</sup> =0.38)					
Variable	Estimate	Std. Error	T value	P value	
(Intercept)	6.01	0.1	54.50	< 2E-16	
Absolute latitude	-0.036	0.0019	-19.03	< 2E-16	
Urbanization (Suburban)	-2.59	0.013	-20.18	< 2E-16	
Urbanization (Urban)	-3.26	0.018	-27.7	< 2E-16	
Season (winter)	2.91	0.099	29.48	< 2E-16	
Hemisphere (southern)	2.8	0.017	16.8	< 2E-16	
Precipitation	-0.00004	0.000018	-2.15	0.03	
Log(Number of checklists)	1.135	5 0.013 8		< 2E-16	
Elevation	-0.00039	0.00039 0.000017		< 2E-16	
Absolute latitude x urbanization (suburban)	0.027	0.0032	8.49	< 2E-16	
Absolute latitude x urbanization (urban)	0.034	0.0029	11.53	< 2E-16	
Absolute latitude x season (winter)	-0.11	0.0025	-44.61	< 2E-16	
Urbanization (suburban) x season (winter)	0.39	0.17	2.36	0.02	
Urbanization (urban) x season (winter)	-0.26	.26 0.16 -1.64		0.1	
Absolute latitude x hemisphere (southern)	-0.97	0.0051 -18.9		< 2E-16	
Urbanization (suburban) x hemisphere (southern)	-0.00046	0.036	-0.001	0.99	
Urbanization (urban) x hemisphere (southern)	-1.19	0.33	-3.67	0.0002	

Season (winter) x hemisphere (southern)	-3.32	0.24	-13.9	< 2E-16
Absolute latitude x urbanization (suburban) x season (winter)	0.012	0.0043	2.82	0.0047
Absolute latitude x urbanization (urban) x season (winter)	0.036	0.0041	8.82	< 2E-16
Absolute latitude x urbanization (suburban) x hemisphere (southern)	0.022	0.011	2.01	0.044
Absolute latitude x urbanization (urban) x hemisphere (southern)		0.0099	3.542	0.0004
Absolute latitude x season (winter) x hemisphere (southern)	0.12	0.0082	14.24	< 2E-16
Urbanization (suburban) x season (winter) x hemisphere (southern)	0.1	0.054	0.18	0.85
Urbanization (urban) x season (winter) x hemisphere (southern)	0.69	0.49	1.423	0.15
Absolute latitude x urbanization (suburban) x season (winter) x hemisphere (southern)	-0.03	0.017	-1.78	0.074
Absolute latitude x urbanization (urban) x season (winter) x hemisphere (southern)	-0.047	0.015	-3.091	0.002

Table S2. Results of ANOVA models of habitat breadth (model C) and diet breadth (model D) for each urbanization category (birds in urban areas or not in urban areas) and latitudinal zone and the effect of seasonality on these results (model E and F). Model C) The significance of latitudinal zone indicated that species in different latitudinal zones have different habitat breadth values (habitat breadth increases with latitude). The significance of urbanization category indicates that species that are found in urban areas have a wider habitat breadth on average than species that are not found in urban areas. The significant interaction between latitude zone and urbanization category indicates that the difference in habitat breadth between urban and nonurban birds differs between latitudinal zones (this difference is largest at low latitudes). Model D) Both latitudinal zone and urbanization category are significant, but the interaction between latitudinal zone and urbanization category is non-significant, indicating that the difference in habitat breadth between urbanization categories does not differ between latitudinal zones. Model E) Seasonality does not have a large effect on the habitat breadth patterns, as the term is nonsignificant. The triple interaction is slightly significant, meaning that the difference in habitat breadth values between urban and non-urban birds and how it relates to latitudinal zones is affected by seasonality. Model F) Season is significant, so diet breadth values are slightly different between seasons.

Model C: ANOVA of habitat breadth values across latitude bins Log(habitat breadth) ~ latitude zone x urbanization category					
Variable	Df	Sum sq.	Mean sq.	F value	P value
Latitude zone	3	1042	347.4	580.13	< 2E-16
Urbanization category	1	798	798.2	1333.04	< 2E-16
Latitude zone x urbanization category	3	55	18.3	30.48	< 2E-16
Model D: ANOVA of diet breadth values across latitude bins Log(diet breadth) ~ latitude zone x urbanization category					

Variable	Df	Sum sq.	Mean sq.	F value	P value	
Latitude zone	3	0.94	0.32	52.21	< 2E-16	
Urbanization category	1	0.51	0.51	85.01	< 2E-16	
Latitude zone x urbanization category	3	0.03	0.006	1.74	0.16	
Model E: Seasonal ANOVA of habitat breadth values across latitude bins Log(Habitat breadth) ~ latitude zone x urbanization category x season						
Variable	Df	Sum sq.	Mean sq.	F value	P value	
Latitude zone	3	1526	508.7	858.38	< 2E-16	
Urbanization category	1	1468	1468.4	2477.74	< 2E-16	
Season	1	1	0.9	1.55	0.21	
Latitude zone x urbanization category	3	83	27.6	46.62	< 2E-16	
Latitude zone x season	3	1	0.5	0.82	0.49	
Urbanization category x season	1	1	1.1	1.91	0.17	
Latitude zone x urbanization category x season	3	5	1.6	2.73	0.042	
Model F: Seasonal ANOVA of diet breadth values across latitude bins Log(Diet breadth) ~ latitude zone x urbanization category x season						
Variable	Df	Sum sq.	Mean sq.	F value	P value	
Latitude zone	3	2.04	0.68	109.92	< 2E-16	
Urbanization category	1	1.01	1.01	163.39	< 2E-16	
Season	1	0.03	0.03	4.77	0.029	
Latitude zone x urbanization category	3	0.033	0.034	5.47	0.00094	
Latitude zone x season	3	0.011	0.011	1.73	0.16	
Urbanization category x season	1	0.0028	0.0028	0.45	0.50	
Latitude zone x urbanization category x season	3	0.0034	0.0034	0.55	0.65	



**Figure S1.** Map of data points for seasonal analyses in summer and winter, with the number of points in each urbanization category and season. Each point has a measure of species richness and an urbanization score. Green points are categorized as natural, pink as suburban, and black as urban.



**Figure S2.** Differences in the latitudinal diversity gradient between the northern (n = 61,690) and southern (n = 4,949) hemisphere. Each point is a raster cell, colored by the urbanization score and each line is the model fit from the thinned models with confidence intervals. Insets are the proportion of natural diversity in urban and suburban areas, calculated by dividing the model predictions of species richness in urban and suburban areas by richness in natural areas.



**Figure S3.** Differences in the seasonal latitudinal gradient between northern and southern hemispheres and between summer (top) and winter (bottom). The points are the raw data colored by urbanization level and the points are the model fits of thinned models with confidence intervals. The effect of urbanization on the slope of the latitudinal gradient is different between seasons in the northern hemisphere but not the southern hemisphere.



**Figure S4.** Density distribution and means of diet breadth values in each latitudinal zone. The density plots are the distribution of diet breadth values for 6,902 species that are present in urban areas (blue) and not present in urban areas (i.e. present in natural areas only; gray) in that latitudinal bin. The numbers are the number of species in that latitudinal bin and the points are the ANOVA means with 95% confidence intervals.



**Figure S5.** Density distribution and means of habitat and diet breadth values in each latitudinal zone of species suburban and non-suburban species. The density plots are the distribution of diet breadth values for species that are present in suburban areas (pink) and not present in suburban areas (i.e. only found in natural areas; blue) in that latitudinal zone, with the number of species in each latitudinal zone. The points are the ANOVA means with 95% confidence intervals. For the ANOVA model with habitat breadth (left), latitudinal zone (F-value = 580.9, P < 2.2E-16), urban category (F-value = 921.3, P < 2.2E-16), and their interaction (F-value = 19.6; P = 1.13E-12) were significant. For the ANOVA model with diet breadth (right), latitudinal zone (F-value = 53.22, P < 2.2E-16) and urban category (F - value = 66.67, P = 3.53-15) were significant but their interaction was not, meaning that the difference in diet breadth between suburban and non-suburban species did not differ with latitude.



**Figure S6.** Seasonal density distributions and means of habitat diet breadth values in each latitudinal zone. A) Distribution and means of habitat breadth values in the summer and winter for species that are present in urban areas (blue) and not present in urban areas (gray) in that latitudinal bin. The numbers are the number of species in that latitudinal bin and the points are the ANOVA estimated means with 95% confidence intervals. B) Distribution of diet breadth values in the summer and winter for species that are present in urban areas (blue) and not present in urban areas (blue) and blue areas (blue) and blue areas (blue) and blue areas (blue) and blue areas (blue) areas (blue areas (blue) areas (blue area



**Figure S7.** Analyses scaled up to  $5\text{km}^2$  to look at the effects of scale on the results. Suburban areas were removed because the sample size was low at the larger spatial scale. Raster cells were aggregated to  $5\text{km}^2$  and categorized based on whether the aggregated cell contained more than 70% of a certain urbanization level. Aggregated cells that did not have 70% or more of one urbanization category were removed. We ran the same models for full year data and seasonal data, with the same predictors. A) Model results at  $5\text{km}^2$  for the year-round data in natural (n = 14,610), suburban (n = 268), and urban (n = 2264) areas. Points are the raw data and lines are the model fits. **B**) Model results at  $5\text{km}^2$  for the seasonal data for winter (natural n = 3282, urban n = 1399) and summer (natural n = 3811, urban n = 1120).



**Figure S8.** Sensitivity analyses to test for the effects of the thresholds on the results of the linear model. Top left) Results using a sampling coverage of 98% instead of 95%, and removing any cells with less than 198 checklists (instead of 83; n=30,736). With the use of a higher sampling threshold, the natural gradient is steeper and the urban gradient more dampened compared to our original model, while the suburban gradient is unaffected. Top right) Results using a sampling coverage threshold of 90%, and removing any cells with less than 44 checklists (n = 143,762). With the use of a lower sampling threshold, the natural gradient is less steep and the urban gradient is steeper, decreasing the effect of urbanization on the gradient. The suburban gradient is unaffected. Bottom left) Results when we removed all natural cells with a human modification greater than 0.25 (instead of 0.5), so that natural cells represent areas with only very little human
modification. This caused the natural gradient to be steeper than our original analysis, but did not affect the gradient in urban and suburban areas. Bottom right) Results when we removed all natural cells that had a human modification greater than 0.75, allowing for natural cells to still be included in the analysis if they had high levels of human modification. This made the natural gradient less steep than our original analysis, but did not affect the gradient in urban and suburban areas.



**Figure S9.** Sensitivity analyses to test for the effects of the chosen thresholds on the results between seasons. Top left) Results using a sampling coverage of 98% instead of 95%, and removing any cells with less than 198 checklists (n = 30,736). The natural gradient became steeper in both seasons but the urban and suburban gradient were unaffected. Top right) Results using a sampling coverage threshold of 90%, and removing any cells with less than 44 checklists (n = 143,762). The natural gradient is less steep than the original model and suburban and urban areas became slightly steeper. Bottom left) Results when we removed all natural cells with a human modification greater than 0.25 (instead of 0.5). The natural gradient became steeper than the original model but the urban and suburban gradients were unaffected. Bottom right) Results

when we removed all natural cells that had a human modification greater than 0.75. The natural gradient became less steep than the original model but the urban and suburban gradients were unaffected.



**Figure S10.** Generalized additive model (GAM) results for the full year-round data. Lines are model fits averaged over predictors, colored by urbanization level. <u>Model:</u> Species richness ~ s(absolute latitude, by = urbanization) + hemisphere + precipitation + log(number of checklists) + elevation.