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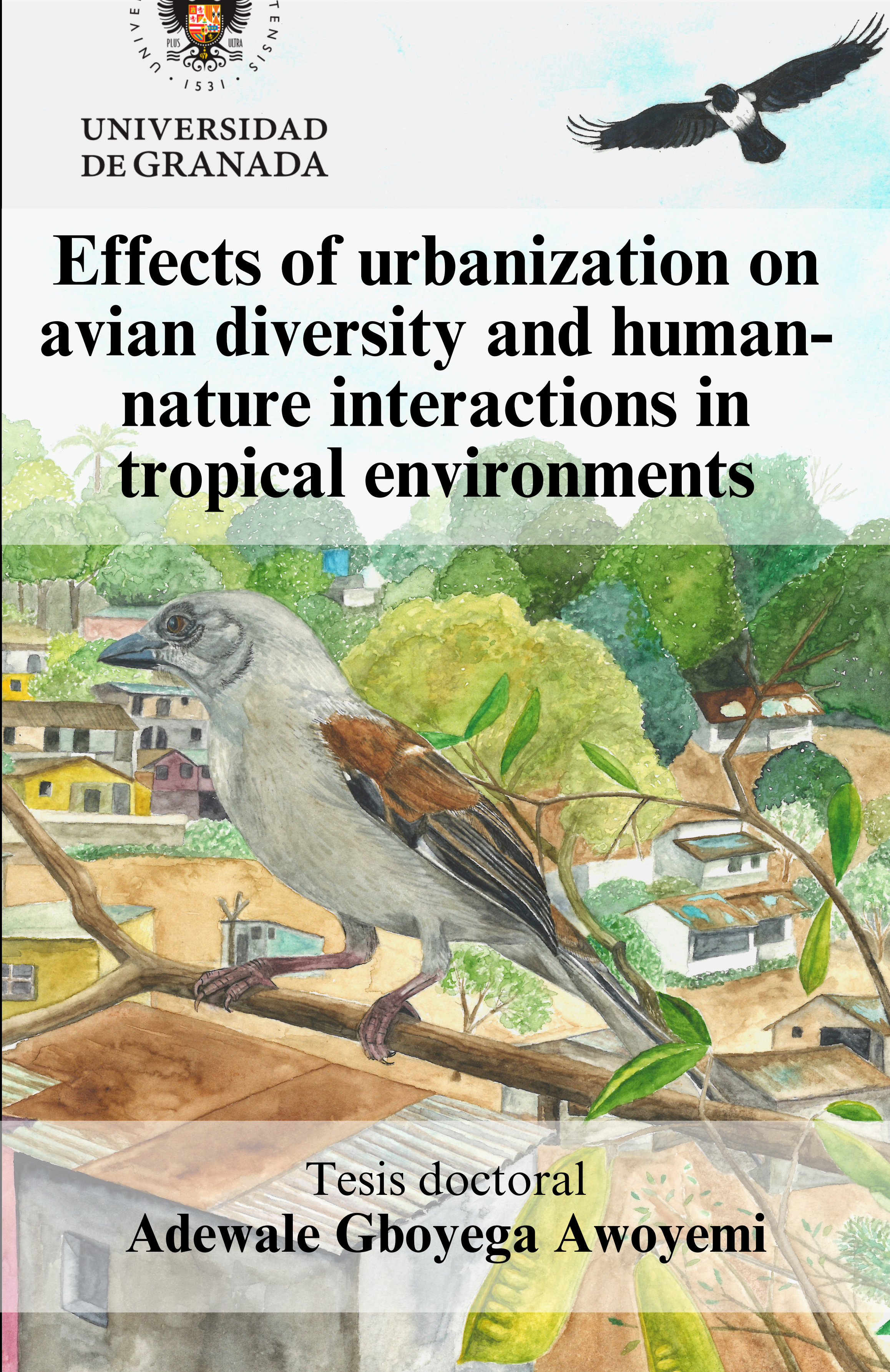
Effects of urbanization on avian diversity and human-nature interactions in tropical environments



Tesis doctoral

Adewale Gboyega Awoyemi

Programa de doctorado Biología Fundamental y de Sistemas
2025

EFFECTS OF URBANIZATION ON AVIAN DIVERSITY AND HUMAN-NATURE INTERACTIONS IN TROPICAL ENVIRONMENTS

EFECTOS DE LA URBANIZACIÓN EN LA DIVERSIDAD DE AVES Y LAS INTERACCIONES HUMANO-NATURALEZA EN AMBIENTES TROPICALES

By

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UNIVERSIDAD
DE GRANADA

Programa de Doctorado Biología Fundamental y de Sistemas

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Effects of urbanization on avian diversity and human-nature interactions in tropical environments

Doctoral Thesis Presented by Mr. Adewale Gboyega Awoyemi to qualify for a Doctorate Degree from the University of Granada, Spain

Memoria de Tesis Doctoral Presentada por el Licenciado D. Adewale Gboyega Awoyemi para optar al grado de Doctor por la Universidad de Granada, Spain

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To Omobamidele, Adetomi, Adetola, Adeshina and Adeola Awoyemi

“Africa’s urbanization is a double-edged sword: it can bring economic growth, but also devastating environmental costs.”

Dr. Jane Goodall,

Reason for Hope: A Spiritual Journey, 1999

Contents

Summary

Urbanization is a rapidly expanding global phenomenon that poses significant threats to biodiversity. Despite its importance, the impacts of urbanization on biodiversity in certain regions remain understudied. Recent studies have highlighted the need for more research on the topic, particularly in Africa, where unprecedented urbanization overlaps with vast biodiversity. Thus, this thesis investigated the impacts of urbanization on socioecological systems in the Afrotropics, providing data useful in achieving sustainable urban development in line with SDG Goal 11 (Sustainable Cities and Communities) in the region.

This thesis began with a comprehensive systematic literature review to assess the current state of urban ecology in Africa (Chapter 1). The review revealed a striking knowledge gap, with only 795 relevant papers published in the last century (1920—2020), much less than those from other continents. Notably, a disproportionate number of these studies (40%) were conducted in South Africa, indicating a significant geographical bias in our current knowledge on the topic. This review found that research efforts are driven by economic wealth (GDP) and the importance of conservation in African urban ecology. However, the review also exposed a surprising oversight: the Afrotropics, which is the most urbanized and biodiverse-rich African region, is not a primary focus of study. Furthermore, most urban ecology studies in Africa were conducted in a single city (55%), with substantial knowledge gaps persisting across taxonomic groups, scientific fields, and ecoregions. To partially address these important gaps, this thesis focused on investigating different research questions in multiple cities in Nigeria (Chapters 2—5), a typical Afrotropical country experiencing rapid urbanization. These additional chapters investigated the impacts of urbanization on bird taxonomic, functional and phylogenetic diversity (Chapters 2—3), avian-mediated regulating ecosystem services, including pest control, seed dispersal, pollination, and scavenging (Chapter 4), and human-nature interactions (Chapter 5).

The results of these studies unequivocally demonstrated that urbanization has profound negative impacts on bird diversity and ecosystem services in the Afrotropics. Compared to non-urban areas, urban areas exhibited significantly lower bird taxonomic diversity (Chapter 2) and reduced provisioning of essential ecosystem services provided by wildlife, including pest control, seed dispersal and pollination (Chapter 4). Scavenging was the only bird-mediated ecosystem service enhanced by urban development (wet season). Furthermore, certain urban attributes, such as the presence of vehicles and pedestrians, were found to compromise bird phylogenetic divergence and ecosystem service provision, particularly pollination and seed dispersal. However, the results also highlight the potential for targeted conservation efforts to mitigate these negative impacts. Notably, the presence of water bodies and specific vegetation types, such as canopy and bush cover, can significantly enhance multiple components of bird diversity and crucial bird-mediated regulating ecosystem services (Chapters 2 and 4). By preserving and restoring these key habitat features, it may be possible to reverse the decline of bird diversity and the associated regulating ecosystem services in Afrotropical cities, particularly seed dispersal and pollination.

Chapter 3 presents a novel application of machine learning and remote sensing techniques in estimating local habitat variables influencing bird diversity components across urban and non-urban areas. This study revealed that the Modified Chlorophyll Absorption Ratio Index (MCARI) is the most effective indicator of taxonomic and phylogenetic bird diversity in the Afrotropics. In contrast, the Normalized Difference Water Index 2 (NDWI2) and Soil Adjusted Total Vegetation Index (SATVI) were found to be the best predictors of functional diversity and phylogenetic divergence, respectively. Interestingly, the Normalized Difference Vegetation Index (NDVI), a commonly used predictor across regions and topics, ranked relatively low (25th percentile) in most cases. These results recommended the use of these alternative predictors (MCARI, NDWI2 and SATVI) rather than the NDVI in predicting bird biodiversity in urban and non-urban areas of the Afrotropics. This is likely due to NDVI's limitations, including scaling issues, saturation in high-biomass areas, and sensitivity to soil brightness, which can compromise its accuracy in diverse Afrotropical environments. The remote sensing approach employed in this study offers a potentially more efficient and cost-effective method for estimating local habitat variables compared to traditional manual estimation techniques. By leveraging machine learning algorithms and remotely sensed data, this approach can help reduce the labor, expense, and investigator error associated with manual data collection.

In addition to the ecological impacts, urbanization also has significant social implications. By investigating the extinction of experience concept among urban dwellers in Nigeria, Chapter 5 found that most citizens had little or no contact with nature. The main reasons cited for this disconnection were lack of time, money, and nearby natural areas. The study also found that respondents with higher nature contact were more connected to nature, and that the perception of neighborhood safety was an important factor promoting nature contact. Furthermore, the study also found that respondents living in Lagos, and those with lower levels of income and education, showed greater dissociation from nature. These findings could be useful to fight against the worrying extinction of experience in the region, providing potential factors to consider and implement in future urban development plans in the Afrotropics.

Overall, the Chapters of this thesis highlight the need for more research on the impacts of urbanization on biodiversity and ecosystem services in the Afrotropics. They also emphasize the importance of promoting nature contact and experience among urban dwellers, particularly in regions with rapid urbanization such as the study area (i.e. Nigeria). By addressing these knowledge gaps and promoting nature experience, we can work towards creating more sustainable and resilient urban ecosystems that will benefit both people and the environment.

Resumen

La urbanización es un fenómeno global en rápida expansión que plantea importantes amenazas a la biodiversidad. A pesar de su importancia, los impactos de la urbanización sobre la biodiversidad aún no se han estudiado lo suficiente en ciertas regiones. Estudios recientes destacan la necesidad de realizar más investigaciones sobre el tema, particularmente en África, donde una urbanización sin precedentes se solapa con una gran biodiversidad. Esta tesis, por tanto, se centra en el estudio de los impactos de la urbanización en los sistemas socio-ecológicos del África tropical, proporcionando datos útiles para lograr un desarrollo urbano sostenible en línea con el Objetivo de Desarrollo Sostenible 11 (Ciudades y Comunidades Sostenibles) en la región.

Esta tesis comienza con una exhaustiva revisión sistemática de la literatura para evaluar el estado actual de la ecología urbana en África (Capítulo 1). La revisión reveló una sorprendente falta de información sobre el tema, con solo 795 artículos publicados en el último siglo (1920-2020), muchos menos que en otros continentes. Además, un gran número de estos estudios (40%) se realizó en Sudáfrica, lo que indica un importante sesgo geográfico en nuestro conocimiento actual sobre el tema. Esta revisión encontró también que los esfuerzos de investigación sobre ecología urbana en África están asociados con la riqueza económica (PIB) y el estado de conservación de los ecosistemas. Sorprendentemente, la revisión también expuso que el Afrotrópico, la región africana más urbanizada y rica en biodiversidad, no está prácticamente estudiada. Además, este primer capítulo identificó que la mayoría (55%) de los estudios de ecología urbana en África se realizaron en una sola ciudad, y que existen importantes lagunas de conocimiento con respecto a ciertos grupos taxonómicos, campos científicos y ecorregiones. Para abordar parcialmente estas importantes lagunas, esta tesis se centró en investigar algunas de las principales preguntas sobre el tema a través del estudio de múltiples ciudades de Nigeria (capítulos 2 a 5), un típico país afrotropical que experimenta una rápida urbanización. De manera muy resumida, estos capítulos investigaron los impactos de la urbanización en la diversidad taxonómica, funcional y filogenética de las aves (Capítulos 2 y 3), los servicios ecosistémicos reguladores mediados por las aves, incluido el control de plagas, la dispersión de semillas, la

polinización y el consumo de carroña (Capítulo 4), y las interacciones entre humanos y naturaleza (Capítulo 5).

Los resultados de estos estudios demostraron inequívocamente que la urbanización tiene profundos impactos negativos en la diversidad de aves y los servicios ecosistémicos en el Afrotrópico. En comparación con las áreas no urbanas, las áreas urbanas exhibieron una diversidad taxonómica de aves significativamente menor (Capítulo 2) y mostraron menores niveles de servicios ecosistémicos esenciales proporcionados por los organismos silvestres, incluido el control de plagas, la dispersión de semillas y la polinización (Capítulo 4). El consumo de carroña fue el único servicio ecosistémico mediado por las aves que mejoró en relación al desarrollo urbano (estación lluviosa). Además, se identificaron ciertas características urbanas, como la presencia de vehículos y peatones, que afectan negativamente a la diversidad filogenética de las aves y la prestación de servicios ecosistémicos, en particular la polinización y la dispersión de semillas. Sin embargo, los resultados también resaltan el potencial que pueden tener ciertas actividades de conservación para mitigar estos impactos negativos. En particular, la presencia de masas de agua y algunos tipos de vegetación específicos, como la cobertura arbórea y arbustiva, pueden mejorar significativamente múltiples componentes de la diversidad de aves así como varios de los servicios ecosistémicos de regulación que proporcionan (Capítulos 2 y 4). Al preservar y restaurar estas características clave del hábitat en las ciudades del África tropical, se podría revertir la reducción en la diversidad de aves y los servicios ecosistémicos reguladores en la zona, en particular la dispersión de semillas y la polinización.

El Capítulo 3 presenta una aplicación novedosa de técnicas de aprendizaje automático y teledetección para estimar las variables del hábitat local que influyen en los distintos componentes de la diversidad de aves en áreas urbanas y no urbanas. Este estudio reveló que el índice de absorción de clorofila modificado (MCARI) es el indicador más eficaz de la diversidad taxonómica y filogenética de aves en el Afrotrópico. Por el contrario, se encontró que el Índice de Diferencia Normalizada de Agua 2 (NDWI2) y el Índice de Vegetación Total Ajustado del Suelo (SATVI) eran los mejores predictores de la diversidad funcional y la divergencia filogenética, respectivamente. Curiosamente, el Índice de Diferencia Normalizada de Vegetación (NDVI), un predictor comúnmente utilizado en todas las regiones y temas, obtuvo una clasificación de idoneidad relativamente baja (percentil 25) en la mayoría de los casos. Estos resultados apoyan el uso de estos predictores alternativos (MCARI, NDWI2 y SATVI) en lugar del NDVI para predecir la diversidad de aves en áreas urbanas y no urbanas del África tropical. Es probable que esto se deba a las limitaciones del NDVI, incluidos problemas de escala, saturación en áreas de alta biomasa y sensibilidad al brillo del suelo, que pueden comprometer su precisión en diversos ambientes del Afrotrópico. El uso de la teledetección en este estudio ofrece un método potencialmente más eficiente y rentable para estimar las variables del hábitat local en comparación con las técnicas tradicionales de estimación manual en campo. Al aprovechar los algoritmos de aprendizaje automático y los datos de detección remota, este enfoque puede ayudar a reducir el esfuerzo de trabajo de campo, los gastos y los errores de los investigadores asociados con la recopilación manual de datos.

Además de los impactos ecológicos, la urbanización también tiene importantes implicaciones sociales. Al investigar el concepto de extinción de la experiencia entre los habitantes urbanos de Nigeria, el Capítulo 5 encontró que la mayoría de los ciudadanos de esta región tenían poco o ningún contacto con la naturaleza. Los principales motivos citados para esta desconexión fueron la falta de tiempo, dinero y espacios naturales cercanos. El estudio también encontró que los encuestados con mayor contacto con la naturaleza estaban más conectados con la naturaleza y que la percepción de seguridad del vecindario era un factor importante que promovía el contacto con la naturaleza. Además, el estudio también encontró que los encuestados que vivían en Lagos y aquellos con niveles más bajos de ingresos y educación mostraban una mayor disociación con la naturaleza. Estos hallazgos podrían ser útiles para luchar contra la preocupante extinción de la experiencia en la región, proporcionando elementos adicionales a considerar e implementar en futuros planes de desarrollo urbano en el Afrotrópico.

En general, los capítulos de esta tesis destacan la necesidad de realizar más investigaciones sobre los impactos de la urbanización en la biodiversidad y los servicios ecosistémicos en el África tropical. También enfatizan la importancia de promover el contacto y la experiencia con la naturaleza entre los habitantes urbanos, particularmente en regiones con rápida urbanización como es el área de estudio (Nigeria). Al abordar estas lagunas de conocimiento y promover la experiencia en la naturaleza, podemos ayudar a crear ecosistemas urbanos más sostenibles y resilientes que beneficiarán tanto a las personas como al medio ambiente.

General introduction

Urbanization's impacts on socioecological systems

Urbanization, the conversion of natural areas into built environments, is one of the greatest global environmental challenges of recent decades (Seto et al., 2012; United Nations, 2016). This human-induced landscape change is tightly linked with humanity's rapidly increasing population and rural-urban migration (Oyeleye, 2013; United Nations, 2019). For instance, approximately 50 % of the global human population (i.e., 6.2 billion) lived in urban areas at the start of the 21st century (Grimm et al., 2008; United Nations, 2024). It is also predicted that urban areas will continue to expand in the near future, with grave consequences for socioecological systems (Angel et al., 2011; Seto et al., 2012; United Nations, 2018).

Broadly speaking, an urban area is a contiguous patch of built-up land greater than 1 km^2, and dominated by human-constructed features like buildings (>10 buildings/ha), high human density (>1600 inhabitants/km^2), roads, and vehicles (Marzluff et al., 2001; Niemelä, 1999; Nilon et al., 2003; Schneider et al., 2010). In contrast, non-urban habitats consist of extensive wilderness and vegetation cover, interspersed with agricultural landscapes (MacGregor-Fors, 2011; Marzluff et al., 2001). Thus, the burgeoning field of urban ecology investigates the "interaction of organisms, built structures and the physical environment where people are concentrated" (Forman, 2014). This scientific field tests overarching hypotheses at the interface of urbanization and socioecological systems, particularly investigating drivers of biodiversity, human-nature interactions and the ecosystem services provided by urban nature (e.g., Arjona et al., 2023; Cox & Gaston, 2015; Ibáñez-Álamo et al., 2020; Reynolds & Howes, 2023; Soga et al., 2015). This holistic approach is necessary given that actions targeted at minimizing human footprints while conserving urban nature still need the support of urban dwellers (Miller & Hobbs, 2002). The field of urban ecology will ultimately enhance the achievement of inclusive, safe and sustainable urban development in line with SDG Goal11 (United Nations, 2015).

To start with, the interrogation of urbanization's impacts on biodiversity has received considerable attention relative to other socioecological systems such as human-nature interactions and ecosystem service provisioning (Hagen et al., 2017; Ibáñez-Álamo et al., 2017; Lin & Grimm, 2015; Magle et al., 2012; Wu, 2014). These studies also show how research effort favor certain taxa, regions and biodiversity components (i.e., taxonomic, functional or phylogenetic diversity). Regarding taxa, urban ecology research effort expended on biodiversity focused more on higher plants and animals than microorganisms (Donaldson et al., 2017; Shwartz et al., 2014) despite their relevance in stabilizing ecosystems (Epp Schmidt et al., 2019; Thompson et al., 2017).

In relation with geography, most urban ecology studies are concentrated in Global North regions (e.g.; Europe and North America) relative to those in the Global South, particularly Africa and Asia (e.g., Marzluff, 2016; Shackleton et al., 2021). This implies a significant mismatch worthy of scientific attention given that the Global South is the most impacted by urban development while simultaneously holding the greater proportion of the Earth's biological diversity (Gatti et al., 2015; Seto et al., 2012). The need for more urban ecology studies from the Global South is not far-fetched. This region consists of underdeveloped and developing countries mainly located in Africa, Latin America, Asia, and Oceania (Dados & Connell, 2012; Shackleton et al., 2021). The Global South has peculiar biophysical and socioeconomic characteristics (e.g., high rate of urbanization, unemployment, and poverty, and issues of security, governance and health) compared to the Global North (World Cities Report, 2020). Thus, urban ecology theories from the Global North do not always fit the Global South, and several authors have advocated for more Global South urban ecological studies (e.g., Okpala, 1978; Shackleton et al., 2021).

Perhaps, the Afrotropics remains the most understudied Global South region regarding urban ecology (Shackleton et al., 2021). For instance, while investigating drivers of urban taxonomic diversity is not uncommon in the Afrotropics (Adegbola et al., 2024; Afrifa et al., 2022), comparing taxonomic diversity between urban and adjacent non-urban habitats are scarce despite the capability of such an approach to provide nuanced understanding of urbanization's impacts on biodiversity (Chamberlain et al., 2017). From an applied perspective, citizens' interactions with nature are also low in urban environments of this region (Lee et al., 2022), and an understanding of the reasons for this disconnect is crucial to develop mitigating interventions (Shackleton et al., 2021). This need for applied urban ecology studies from the Afrotropics also extends to regulating ecosystem services. The few (< 50) papers published on the topic for the whole African continent focused on South Africa and few ecosystem services (i.e., pollination and regulation of water flow and runoff) (du Toit et al., 2018; Reynolds & Howes, 2023), highlighting the need for additional studies overcoming this important lack of knowledge.

In relation with biodiversity components, there is a scientific consensus showing that urbanization generally reduces taxonomic diversity, the presence of species in an area (Magurran, 2004), through a process known as the biotic homogenization (Aronson et al., 2014; McKinney, 2006, 2008). However, much less is known with respect to functional and phylogenetic diversity despite its potential relevance for conservation decisions (Cadotte et al., 2011, 2012; Tucker et al., 2017). The former focus on how the functional traits of species influence ecosystem services and functioning (Mouchet et al., 2010; Reynolds & Howes, 2023) while the later provides information on the evolutionary richness or divergence of all species in a given community assemblage (Faith, 1992; Helmus et al., 2007). This bias is even more crucial in cities where urbanization exerts differing impacts on the various components of biodiversity (Dylewski et al., 2023; Ibáñez-Álamo et al., 2020; Leveau et al., 2020). Some key research questions here are: (1.) How will urban planners and conservationists simultaneously conserve the various components of biodiversity in urban centers? (2.) What are the local influential variables that could enhance the various components of urban biodiversity? Answering these questions is key to proposing tailored interventions that could mitigate the loss of biodiversity due to urban development in general, and particularly on the African continent. Moreover, the impact of urbanization on functional and phylogenetic diversity is poorly understood in the Afrotropics (Hagen et al., 2017; Ibáñez-Álamo et al., 2017) and, thus, demanding additional investigations.

From a more applied point of view, several studies report how local attributes (e.g., impervious surfaces, numbers of vehicles and pedestrians, tree canopy, and the coverage of bush, grass, water) affect biodiversity in urban areas worldwide (e.g., Adegbola et al., 2024; Ibáñez-Álamo et al., 2020; Wood & Esaian, 2020). These local urban attributes could not only help to understand the patterns and processes of urban ecosystems but also allow specific recommendations for city planners and conservation practitioners (Arjona et al., 2023; Aronson et al., 2014; Shackleton et al., 2021). In this same context, recent advances show that employing remotely sensed spectral indices (e.g., NDVI and EVI) is more comprehensive and less laborious in capturing how site characteristics influence biodiversity than the field-based estimation of those local influential variables (Benedetti et al., 2023; Leveau et al., 2020). This remote sensing approach could be important in Africa, where socio-economic constraints limit urban ecology studies (see Shackleton et al., 2021).

Urbanization-induced biodiversity loss has far-reaching consequences for both the environment and human well-being (Liang et al., 2019; Moore et al., 2003). One of such negative effects corresponds with the alteration of ecosystem services provided by organisms (e.g., wildlife, vegetation); known as the tangible (e.g., food, water) and intangible (e.g., climate regulation, pest control) benefits people derive from nature (Pinho et al. 2017). Regulating ecosystem services (RES) are disproportionately impacted, with urbanization favoring scavenging over other essential services like seed dispersal, pollination, and pest control (Chamberlain et al., 2017; Fattorini, 2011; Schneiberg et al., 2020; Wenzel et al., 2020). Despite these findings, research on this topic is largely skewed towards Global North countries, with a striking knowledge gap in African regions (Shackleton et al., 2021). To date, fewer than 50 studies have investigated this issue on the entire African continent (du Toit et al., 2018), highlighting the need for more comprehensive and inclusive research.

The disruption of ecosystem services not only compromises human well-being but also exacerbates the disconnection between people and nature. Urbanization's potential to limit natural areas and excursion opportunities can lead to the "extinction of experience" (Pyle, 1993), where people become increasingly disconnected from nature. While research has investigated the components and mechanisms driving this phenomenon, it is heavily biased towards Global North countries (Barragan-Jason et al., 2022; Bashan et al., 2021; Pett et al., 2016), leaving important knowledge gaps in our understanding of human-nature interactions in regions of the Global South. This knowledge gap is concerning, as it leaves us with a limited understanding of human-nature interactions in Global South regions like the Afrotropics.

This thesis employed different scientific approaches to bridge some of the most relevant knowledge gaps regarding Afrotropical urban ecology. To start with, Chapter 1 incorporated the systematic literature review to determine the state of African urban ecology and identify critical knowledge gaps in the last century (1920–2020). The remaining four chapters tested how urbanization shapes various socioecological systems in the Afrotropics using Nigeria, the most populous African country that is rapidly urbanizing (Seto et al., 2012; World Bank, 2021), as the study area. Accordingly, Chapter 2 delved into how urbanization affects avian taxonomic, functional and phylogenetic diversity across habitats (i.e., urban *vs.* non-urban), seasons (i.e., dry *vs.* wet), and vegetation zones (i.e., rainforest *vs.* savannah), and tested the effects of local influential variables (e.g., impervious surfaces, numbers of vehicles and pedestrians, tree canopy, and the coverage of bush, grass, water) estimated in the field. Chapter 3 complemented Chapter 2 by using satellite data (i.e., remotely sensed multispectral indices like NDVI, EVI) to predict how urbanization affects avian taxonomic, functional and phylogenetic diversity across the habitats and vegetation zones. This approach is necessary given social unrest that hamper biodiversity monitoring in some Afrotropical areas (Ojukwu, 2011; Otu et al., 2018). In addition, this remote sensing approach provides more accurate data, and is less laborious, expensive and prone to investigators' errors compared to the manual or field-based estimation of local influential variables (Ghosh et al., 1995; Gorrod & Keith, 2009; Morrison, 2016). From an applied perspective, Chapter 4 interrogated variations in bird-mediated regulating ecosystem services (i.e., pest control, fruit dispersal, pollination and scavenging) across the seasons, habitats, and vegetation zones. Lastly, Chapter 5 examined human-nature interactions in Afrotropical urban areas. Birds were the focal species used to investigate Chapters 2—5 because their composition changes between seasons and vegetation zones (e.g., Brown et al., 1982; Morelli et al., 2021), and have a well-validated phylogeny (e.g., Jetz et al., 2012). Birds are also commonly used in human dimension studies investigating drivers of human-nature interactions and ecosystem services in urban areas (e.g. Cox & Gaston, 2015; Reynolds & Howes, 2023).

Overall, this thesis will identify critical knowledge gaps in African urban ecology and expand our understanding on how urbanization shapes different biodiversity components, human-nature interactions and regulating ecosystem services (Fig. 1). Thus, it can provide very much needed data for sustainable urban development in the region and beyond.

Thesis aims

To identify knowledge gaps in African urban ecology and investigate how urbanization affects socioecological systems across Afrotropical environments and seasons.

Thesis objectives

1. To determine the status of African urban ecology in the last century (1920–2020).
2. To study the effects of urbanization on bird taxonomic, functional and phylogenetic diversity across Afrotropical habitats, vegetation zones and seasons.
3. To examine how remotely sensed multispectral indices predict urbanization’s impacts on bird taxonomic, functional and phylogenetic diversity across Afrotropical habitats and vegetation zones.

4. To study how urbanization influences avian-mediated regulating ecosystem services (pest control, fruit dispersal, pollination and scavenging) across Afrotropical habitats, vegetation zones and seasons.
5. To investigate drivers of human-nature interactions in Afrotropical urban habitats.

Objetivos de la tesis

1. Determinar el estado de la ecología urbana africana en el último siglo (1920-2020).
2. Estudiar los efectos de la urbanización en la diversidad taxonómica, funcional y filogenética de las aves en distintos hábitats, zonas de vegetación y estaciones del trópico africano.
3. Examinar cómo los índices multiespectrales basado en datos satelitales predicen los impactos de la urbanización en la diversidad taxonómica, funcional y filogenética de las aves en los hábitats y zonas de vegetación del trópico africano.
4. Estudiar cómo la urbanización influye en los servicios ecosistémicos reguladores mediados por las aves (control de plagas, dispersión de frutos, polinización y consumo de carroña) en hábitats, zonas de vegetación y estaciones del Afrotrópico.
5. Investigar los determinantes de las interacciones entre los humanos y la naturaleza en los hábitats urbanos del África tropical.

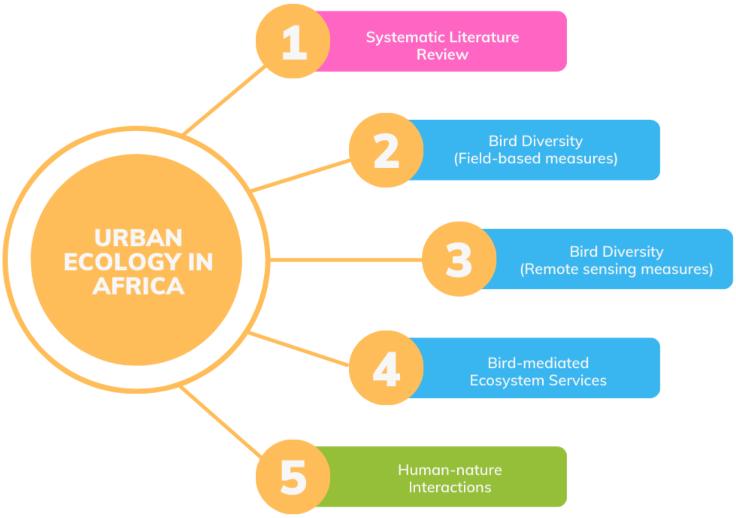

Figure 1: An overview of the thesis objectives.

General methodology

Study area

Chapter 1 is a systematic literature review that covered 58 countries making up the entire African continent (United Nations, 2024; World Cities Report, 2020). The literature search, covering 1920—2020, was performed in Web of Science, Google Scholar, and Scopus on 8 March 2021. The resulting papers were screened with Rayyan (https://www.rayyan.ai/), a web-based semi-automation App (Olofsson et al. 2017; Ouzzani et al., 2016), and followed the highly recommended Preferred Reporting Items for Systematic Reviews and meta-analyses (PRISMA Statement) (Abreha, 2019; Moher et al. 2009) indicated in Figure 1 of Chapter 1. Additional data were collected from different global databases, including the Global Biodiversity Information Facility (GBIF, 2021; accessed May 2022), World Wildlife Fund for Nature (WWF: Olson et al., 2001), Africapolis for urbanization intensity (OECD/SWAC, 2020; accessed 9th June 2021) and the United Nations for socio-demographic details (United Nations, 2018).

Data for the remaining Chapters were taken from Nigeria. This country is situated in the Afrotropical belt, experiencing the distinct climatic variations of wet (April—September) and dry (October—March) seasons (Ezealor, 2001; OECD/SWAC, 2020). In Nigeria, annual rainfall intensity (4,000 mm—600 mm) and duration decrease northwards from the southern coast compared with the mean annual temperature (8°C—40°C) (Ezealor, 2001). These climatic variations shape Nigeria’s vegetation physiognomy and bird composition (Barshep et al., 2022; Elgood et al., 1994). Thus, the southern Nigerian sites visited for this study support dense evergreen forests of tall trees with thick undergrowth (termed “rainforest”) in comparison with the northern sites dominated by grasses interspersed by small-medium sized trees (termed “savannah”) (Ezealor, 2001).

General field procedure

Data were collected from paired urban and non-urban habitats of eight Nigerian cities evenly distributed across the rainforest (Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos) vegetation zones (see Fig. 1 of Chapter 2). In general, each urban area (e.g., Fig. 2) consisted of a contiguous patch of built-up land greater than 1 km^2, and dominated by human-constructed features like buildings (>10 buildings/ha), high human density (>1600 inhabitants/km2), roads, and vehicles (Marzluff et al., 2001; Niemelä, 1999; Nilon et al., 2003; Schneider et al., 2010). The paired non-urban habitat (e.g., Fig. 3), always situated in an adjacent area, was characterized by extensive wilderness/vegetation cover interspersed with agricultural matrix and sparsely settled villages (MacGregor-Fors, 2011; Marzluff et al., 2001). Any urban or non-urban site in this study was located at least 20 km away from each other to grant the independence of their avian communities (Liker et al. 2008).

Figure 2: Drone shot of Ibadan, a typical urban center where data were collected in Nigeria. Credit: IITA Communications Office.

Fieldwork for Chapters 2—4 was carried out in paired urban and non-urban habitats of either all or some of the eight Nigerian cities (depending on the Chapter) distributed across the rainforest (Ado, Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos) vegetation zones (Fig. 1). This mainly involved the use of the point count method (Bibby et al., 2000; Sanllorente et al., 2023) for recording birds and local influential variables estimated manually in the field (i.e., impervious surfaces, numbers of vehicles and pedestrians, tree canopy, and the coverage of bush, grass, water) or via remote sensing (e.g., 29 variables including NDVI, EVI etc.).

Figure 3: Drone shot of the Olokemeji Forest Reserve, a typical non-urban habitat where data were collected in Nigeria. Credit: IITA Communications Office.

This methodology has been previously used by multiple studies (Benedetti et al., 2023; Leveau et al., 2020; Reynolds & Howes, 2023; Sanllorente et al., 2023). For Chapters 2—4, fifty points (i.e., 25 urban vs 25 non-urban) were randomly selected (Møller et al., 2012) in each of the eight cities, equally distributed across the rainforest (Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos). Each point was marked with a GPS to ensure data collection was from the same location throughout the entire study. Data for Chapters 2 and 4 were collected across the dry (November 2020—January 2021) and wet (August—September 2021) seasons, while Chapter 3 utilized only the cloudless data from the dry season (November 2020—January 2021). Data collection for Chapter 5 was restricted to the southern rainforest sites (i.e., Auchi, Calabar, Ibadan, Lagos) due to important security issues (kidnapping and banditry) in northern Nigeria at the time. During the wet season (August—September 2021), the four southern sites were visited for data collection for Chapter 5. The same field data, comprising bird counts, formed the basis for Chapters 2—5. Meanwhile, additional data were integrated into each chapter. The local influential variables (e.g., number of vehicles, canopy cover….) were incorporated to contextualize the bird count data for Chapter 2. To investigate Chapter 3, remotely sensed spectral indices (e.g., NDVI, EVI…) were added to the bird count data. For Chapter 4, diet information was extracted from Savitraits, serving as a proxy for ecosystem service provisioning by the sampled birds. Finally, structured questionnaires were administered to 600 respondents (300 women and 300 men), offering a socio-ecological perspective, were added to the bird count data and local influential variables.

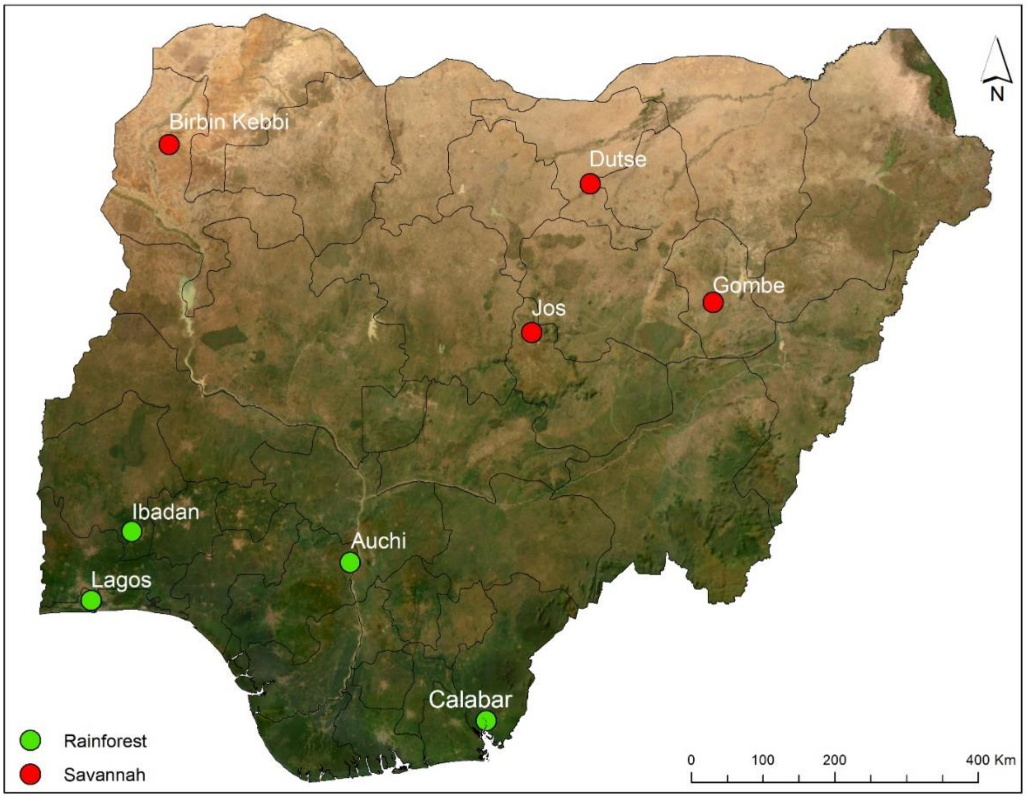

Figure 3: Distribution of study sites across the savannah and rainforest vegetation zones in Nigeria. At each city, data were collected in paired urban and non-urban sites.

Chapter 1

Status of urban ecology in Africa: A systematic review

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Abstract

Urbanization is an extreme human activity and is expanding worldwide, consequently increasing the attention of scientists across research areas of urban ecology. Recent studies have warned of the lack of information from certain regions, particularly Africa, which is rapidly urbanizing. Thus, we did a detailed literature search to determine the state of knowledge in African urban ecology in the last century. We found 795 relevant papers from where data were collected and tested to understand geographic and ecological mismatches in research effort, allowing us to identify important knowledge gaps (e.g., taxonomy and scientific fields). We also tested the effect of current and future urbanization intensity, human population density, size and conservation status of ecoregions and Gross Domestic Product (GDP) on research effort. Our results suggest a low turnout of papers and a dearth of knowledge about African urban ecology. Studies were conducted in 72% of African countries, with South Africa alone accounting for almost 40% of all published papers. The studies were either conducted at the city (55%) or local/country (34%) level, suggesting the lack of transnational research collaboration. Interestingly, only country GDP and the size and conservation status of ecoregions significantly predicted the number of publications, suggesting that research effort is driven by economic reasons and the relevance of conservation in African urban ecology. We need to account for these biases to advance our understanding of the impacts of urbanization on African biodiversity.

Introduction

Rapidly expanding urbanization is a major threat to nature worldwide, leading to the reduction of biodiversity and alteration of species interactions and ecosystem services (Gaston, 2010; Mcdonald et al., 2008; McKinney, 2006; United Nations, 2016). The impacts of urbanization could be even worse in the near future due to the geometric progression of human population. According to the United Nations (2019), the global human population density will increase from 60 humans/km^2 in 2020 to 78 humans/km^2 in 2050, while the global urban land cover will increase from 824,200 km^2 to 1,145,698 km^2 during the same period (Angel et al., 2011). Thus, research on urban ecology is imperative to achieve sustainable development, allowing for the understanding of ecological processes in urban areas and providing necessary data for urban planning, landscape design, policy formulation and biodiversity conservation (Corbyn, 2010; Moragues-Faus & Carroll, 2018).

Given the availability of various definitions of urban ecology, we follow the scientific proposition that incorporates the ‘interaction of organisms, built structures and the physical environment where people of urbanization, the concept of social and ecological integration (inclusiveness) has been proposed to enhance biodiversity in urban areas (e.g., Haase et al., 2017). For instance, Ferketic et al., (2010) demonstrated the usefulness of inclusiveness in promoting conservation justice in Cape Town (South Africa), thereby influencing the ecology of the city, and an understanding of such a nexus is useful to design resilient and sustainable urban areas (Childers et al., 2015; Grimm et al., 2008).

The globally recognized multi-disciplinary fields and the embedded scientific topics in urban ecology have attracted increasing attention from researchers (e.g., Anderson et al., 2013; Cilliers et al., 2013; Girma et al., 2019). However, several papers have highlighted important knowledge gaps across regions, taxa and scientific topics (e.g., Magle et al., 2012; Tóth et al., 2020; van der Walt et al., 2015). Probably, one of the most important mismatches between urban ecology research effort and the urbanization process is the lack of knowledge on the topic from the most rapidly urbanizing continents of South America, Asia and Africa (Ibáñez-Álamo et al., 2017; Seto et al., 2012; Shackleton et al., 2021). As identified in these studies, geographic biases impede the full comprehension of the real impacts of urbanization on nature. Future studies conducted in appropriate areas will therefore be useful to determine ameliorative strategies needed to promote the co-existence of humans with nature, thereby enhancing urban habitats and the associated biodiversity, which is in line with the 11th Sustainable Development Goal of the United Nations (2021).

Literature reviews provide an opportunity for summarizing the state of evidence-based knowledge applied in many fields (e.g., Ibáñez-Álamo et al., 2017; Magle et al., 2012). Broadly, this involves the incorporation of published literature in any given field (Garousi et al., 2019). However, the generalization and application of findings from literature reviews in decision-making have been a subject for debate, mainly due to transparency, objectivity, repeatability and credibility (Sánchez-Tójar et al., 2020). Since traditional approaches to literature reviews are prone to errors (Grant & Booth, 2009), rigorous methodological approaches have been developed and applied more recently in the field of urban ecology (e.g., Cilliers et al., 2018; Kendal et al., 2020; Ibáñez-Álamo et al., 2017), allowing for an important advancement in our understanding of the effect of urban areas on organisms.

In the present study, we conducted a systematic literature review to determine trends in urban ecological research conducted in Africa. Relative to other regions such as Asia, Europe and North America (Forman, 2016; Lin & Grimm, 2015; Magle et al., 2012; Wu et al., 2014), there have been few attempts aimed at synthesizing the state of knowledge in African urban ecology (e.g., Cilliers et al., 2013; Shackleton et al., 2017; Lindley et al., 2018; du Toit et al., 2018). Our aims were to (i) analyze the current status of research effort on urban ecology in this continent, (ii) identify research gaps (geographic, taxonomic and ecological) and (iii) provide recommendations and insights on future prospects. Additionally, (iv) we investigated the potential association of urban ecology research effort with some factors previously associated with the number of scientific publications. On the one hand, we tested whether the number of publications in the field (i.e., urban ecology) per country could be influenced by human population density, economic wealth, as well as the current or future urbanization prospects. Given the positive association between human population density and the degree of urbanization (e.g., Gao & O’Neill, 2021; Qizhi et al., 2016), we would expect that countries with high human population density would hold the majority of studies in urban ecology. Furthermore, if urban ecology research effort is driven by the intensity of urbanization, based on the scientific reasoning of geographic focus areas of particular interest, we could predict a positive association of the number of publications on this topic in those countries currently more urbanized or with the highest rate of urban expansion (i.e., future urbanization). Although the relationship between urbanization and economic growth is often contested (e.g., Chen et al., 2014; Moomaw & Shatter, 1996), we would expect that wealthier countries (i.e., higher Gross Domestic Product –GDP–) are those concentrating the majority of urban ecological studies as increased funding positively influences publication rates (Man et al., 2004). On the other hand, we also tested whether the number of publications in the field could be influenced by the conservation status and size of African ecoregions. Previous reviews have pointed out the positive association between the conservation status of study sites and research effort (e.g., de Lima et al., 2011). Thus, if research effort is based on conservation oriented reasons, we would expect that threatened ecoregions will be more studied. In addition, since smaller areas generally support lower species richness (see Rantalainen et al., 2005), we would expect that larger ecoregions will provide more study opportunities for researchers specializing in different species and scientific topics, and will therefore be more studied. Considering the marked differences between Global North and Global South urban settings (Shackleton et al., 2021), we acknowledge that there could be other factors (e.g., climate severity, colonial history or high diversity in human-nature interactions) shaping the urban ecology research effort in Africa, which is considered part of the Global South. However, we did not include them because of the difficulty of extracting such information and to avoid overparameterization of models. Findings of this study will provide additional information about African urban landscapes that should generate interest among researchers, conservation practitioners and policymakers.

Methods

Bibliographic search and paper screening

We performed a literature search in Web of Science, Google Scholar and Scopus on 8 March 2021 using different combinations of 89 relevant keywords within the article titles, abstracts and keywords, covering the period 1920–2020. The search string containing research focus (23 keywords; e.g., ecology, biodiversity and wellbeing) and urban terms (5 keywords; e.g., urban, city and town) were matched with region (Africa and country name). We performed independent searches for each of the 58 countries and autonomous territories in the continent. A detailed description of these search terms, and the relevant Web of Science categories (41) and Scopus study fields (10) selected can be found in Table S1. The relevance of the use of such comprehensive keywords has been demonstrated by previous studies (e.g., Raji & Downs, 2021; Roy et al., 2012; Tan & bin Abdul Hamid, 2014).

We then uploaded all detected papers on Rayyan (https://www.rayyan.ai/) for screening. Rayyan is a web-based App that uses a semi automation process to screen paper's preliminary pages with a high degree of precision (Olofsson et al., 2017; Ouzzani et al., 2016). Its adaptability and many functions allow the detection of duplicates, verification, collaboration and decisions in systematic reviews (Abreha, 2019; de Keijzer et al., 2016). In the present study, both authors independently performed the paper selection process by activating the "blind function" in Rayyan and reached a consensus thereafter. Our selection process followed the Preferred Reporting Items for Systematic Reviews and meta-analyses (PRISMA Statement) (Abreha, 2019; Moher et al., 2009), which is presented in Fig. 1. Based on article titles and abstracts, we first excluded duplicates, non-African studies and investigations carried out outside urban settings. We also excluded papers on human diseases, climate change, pollution and agriculture when they were exclusively focused on clear different disciplines, such as malaria studies exclusively focused on the medical science (e.g., Kigozi et al., 2020) or agricultural papers investigating different crop varieties without any socio-ecological, biodiversity or human dimensions focus (e.g., Kent et al., 2001). Several systematic reviews already exist on these disciplines (e.g., Fayiga et al., 2018; Hulme et al., 2001; Orsini et al., 2013). The remaining articles were then screened and those that met the following criteria were retained for data extraction: (1) urban landscape, ecological and sociological studies, (2) journal articles published in English, (3) peer-reviewed as a first step towards quality control (Beninde et al., 2015; Raji & Downs, 2021), and (4) biodiversity conservation studies (including pet animals and introduced species).

Data extraction and categorization

We extracted the following data from each included paper: title, year of publication, journal, country of study and study sites. We then classified each paper based on type (field study, review or perspective) and scale, which included city (conducted in a single city), local (involving more than one city in a country), regional (involving more than one African country) and global (involving more than the African continent). Further, we followed the classification of Magle et al. (2012) to allocate each paper to one of the following scientific fields, including animal behavior, community ecology, conservation, human dimensions, human-wildlife conflict, landscape ecology, population ecology, wildlife disease and wildlife management. For taxonomic studies, we extracted information on the kingdoms and classes of focal species based on the classification of the Global Biodiversity Information Facility (GBIF) (GBIF, 2021; accessed May 2022).

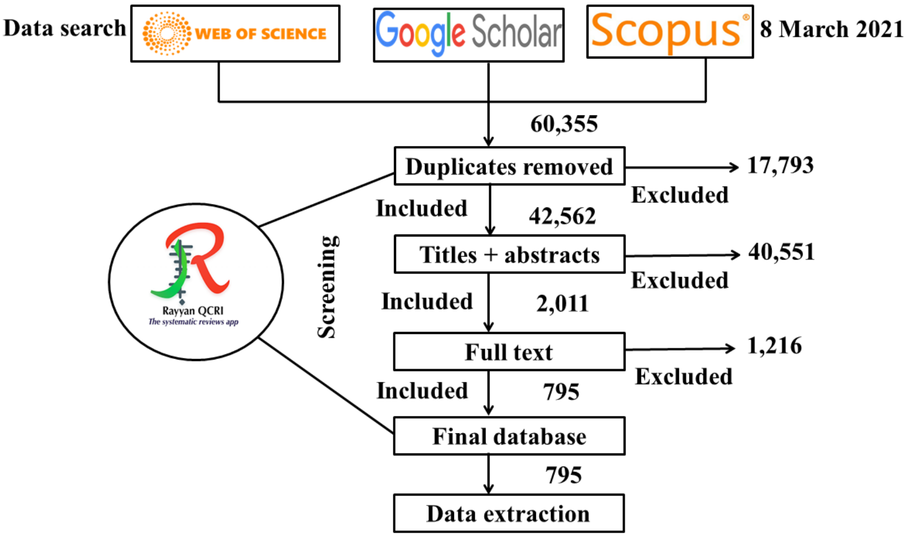

Figure 1. PRISMA flow diagram for determining the state of urban ecology in Africa using the Rayyan Software.

With the exception of reviews and perspectives, we obtained the coordinates of all 1405 African study sites included in the selected papers by using Google Earth. This ensured conformity and completion given that the coordinates of some sites were either not originally provided in the papers or were presented in different formats. We then obtained information on all terrestrial ecoregions found in Africa from the World Wildlife Fund for Nature (WWF: Olson et al., 2001). Further data on the ecoregions, including size, conservation status and the biome they are located in, were also collected (Burgess et al., 2004). In addition, we obtained data on urbanization intensity and urban land cover (2015) across the continent, as well as the total population (2015) and total land area of each studied country from Africapolis (OECD/SWAC, 2020; accessed 9th June 2021). Urban land cover was used as a proxy for country urbanization intensity, while the total population was divided by the total land area to obtain the population density of each country. We then overlaid the study sites across ecoregions and urbanization intensity, as well as urbanization intensity across ecoregions, using QGIS (version 3.24 Tisler). Africapolis is the single most important and comprehensive geospatial database on cities and urbanization dynamics in Africa, which incorporates data on demography, satellite and aerial imagery and other cartographic sources (OECD/SWAC, 2020). To investigate urbanization prospect based on the urban land cover, data on the average annual rate of change of the percentage urban expansion by country (2015–2050) were integrated (United Nations, 2018). The Gross Domestic Product (GDP 2020; US$) of each studied country was also extracted from the National Accounts Section of the United Nations Statistics Division (accessed 6th May 2022).

Statistical analyses

All analyses were carried out using R Version 1.4.1717 (R Core Team, 2016). We performed descriptive statistics using the number of published urban ecological studies to determine temporal and spatial trends in urban ecological knowledge across years, countries, study scales, scientific fields, journals, and taxonomic kingdoms and classes.

We first used the number of published urban ecological studies (hereafter: research effort) per country as the response variable to test the effect of urbanization intensity, urbanization prospect, human population density and GDP using general linear models (LM). We used the "performance" package to check for multi-collinearity among the independent variables (Bernat-Ponce et al., 2021; Lüdeck et al., 2021) and tested the normality (Shapiro & Wilk, 1965) of the dependent variable ($p < 0.05$). The independent variables had low correlation (Variance Inflation Factor < 5) and, consequently, were all included in the models, but research effort was log-transformed to obtain reasonably normally distributed residuals from final models, and models that did not violate LM assumptions when examined visually as diagnostic plots (Crawley, 2013). Using the stepwise backward selection method (Crawley, 2013), variables with the highest p values were removed and the procedure repeated until the best model was selected as the one with the lowest Akaike Information Criterion value (Burnham & Anderson, 2002). Statistical significance was set at p value < 0.05. We also conducted a sensitivity analysis (Moher et al., 2009) due to the disproportionate weight of South African studies in our database, causing outliers. Of the overall 710 field studies that mentioned the 42 African countries represented here, 313 (44 %) were from South Africa. The second model therefore incorporated the same variables as the first but without South African papers.

Secondly, we tested for mismatches in the distribution of research effort across ecoregions. Note that this information could not be combined with the one collected at the country level and thus requires for an additional model to be tested. Given that research effort was not normally distributed ($p < 0.05$) even after log-transformation, we built a separate model using Poisson Logistic Regression to test if the size and conservation status of ecoregions (factor: Critical, Endangered, Vulnerable, Relatively Stable or Relatively Intact) influence research effort. We then conducted a Tukey post-hoc test for a pairwise comparison across the different categories of conservation status using the package "emmeans" (Manley et al., 2015; Yvoz et al., 2020).

Results

Our search string detected a total of 60,355 papers out of which 17,793 duplicates were removed. The output of the remaining processes of Rayyan screening led to the retention of 795 papers considered in this review (Fig. 1). Out of them, 691 (87 %) were field studies, 90 (11 %) reviews and 14 (2 %) perspectives, all of which were published in 377 journals (Table S2). The first urban ecology studies focused on Africa date back from the 1970s (Okpala, 1978; Hugo, 1979), but the publication rate on the topic was slow (<10 papers/year) until 2006 when an exponential growth started, culminating in 126 papers published in 2020 (Fig. 2). From a geographical point of view, we found studies from 72 % of the countries that make up the African continent (42 out of 58 countries and autonomous territories; Fig. 3).

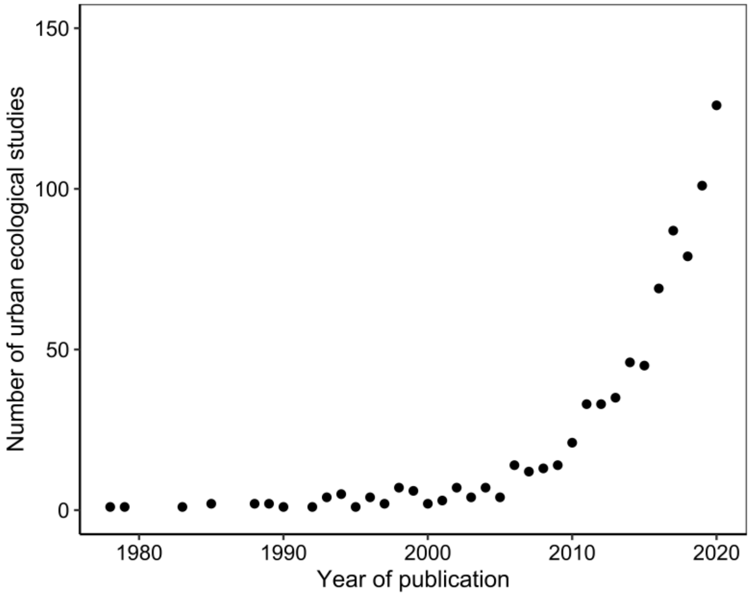

Figure 2. Urban ecology research effort (number of urban ecological studies) across years.

However, a single country (South Africa) published 4 out of every 10 papers on the topic (N = 313), with the highly-urbanized and biodiversity-rich countries of tropical regions of the continent recording little (<40 papers; e.g., Democratic Republic of the Congo and Kenya) or even no urban studies (e.g., Angola and Liberia; Figs. 3 and 4) for the period of study (1920–2020). Furthermore, papers found in our literature search showed that most urban ecological research in Africa (89 %) was performed within countries, either focused on a single city (N = 434; 55 %) or conducted locally (N = 270; 34 %). We identified very few international research as only 4 % of the studies were carried out regionally (i.e., including more than one African country; N = 29) and only 8 % were coordinated at a global scale (i.e., including data from other continents too; N = 62).

The result of the LM analysis for all countries shows that research effort significantly increased with higher GDP, but not according to any other predictors (Table 2; Fig. 5). Contrary to our expectation, countries with higher human density and current or future urbanization prospects (up to 2050) have not been more studied (Table 1). In contrast, wealthier African countries have significantly investigated more on urban ecology (Table 1; Fig. 5). The same significant pattern was found for the sensitivity analysis (i.e., when South Africa was removed; Table S3).

Table 1: Results of a GLM exploring the predictors of the number of urban ecological studies published across all countries. The number of urban studies + 1 was log-transformed to achieve a normal distribution of residuals. The last model (F_{40} = 51.9, P < 0.001; AIC=100.57) incorporated only the significant variable and had an adjusted R^2 = 0.55.

	Estimate	SE	*t-value*	*p-value*
Intercept	1.41E+00	1.38E-01	10.22	<0.001
Gross Domestic Product	9.88E-12	1.37E-12	7.203	<0.001
Rejected variables				
Urbanization intensity	1.07E-01	1.20E-01	0.892	0.378
Human population density	-9.24E-04	9.68E-04	-0.955	0.346
Urbanization prospect	5.19E-02	3.69E-02	1.4	0.167

Regarding ecoregions, we found information from 75 out of the 119 ecologically relevant regions in Africa (Fig. 6a-b; Table S4). This implies 37 % of ecoregions without a single urban ecology study. The research effort at this respect is not homogeneously distributed and varies considerably depending on the biome (Table 2). Furthermore, 22 out of the 44 African ecoregions without urban ecology studies are classified as threatened (Table S4) (Burgess et al., 2004). The Poisson Logistic Regression shows that research effort significantly increased in larger and more threatened ecoregions (Table 3). Urban areas in critical, endangered and vulnerable ecoregions have been more intensively studied (Fig. 7).

Our review also showed important taxonomic biases in the study of urban ecology in Africa. We found information on studies focusing on seven kingdoms, with Animalia and Plantae being the most studied so far (Fig. 8). This result also highlights our limited understanding of other organisms, including Archaea, Bacteria, Chromista, Fungi and Protozoa, which when combined accounted only for 5 % of the studies. The number of studied classes was considerably higher in Animalia (27) than Plantae (9), with Aves (N = 138; 34 %) and Mammalia (N = 95; 23 %) accounting for the majority of studied animal groups (Fig. 9). Regarding plants, the most commonly studied classes were Magnoliopsida (N = 253; 66 %) and Liliopsida (N = 94; 24 %).

Table 2: Urban ecology research effort (i.e., studied ecoregion/total ecoregion %) across African biomes and ecoregions.

Biome	Total ecoregion	Studied ecoregion	Research effort (%)
Temperate Coniferous Forests	1	1	100
Mangroves	5	4	80
Tropical and Subtropical Moist Broadleaf Forests	30	23	77
Mediterranean Forests, Woodlands, and Scrub	7	5	71
Tropical and Subtropical Grasslands, Savannas, Shrublands, and Woodlands	24	16	67
Montane Grasslands and Shrublands	16	10	63
Flooded Grasslands and Savannas	10	6	60
Deserts and Xeric Shrublands	23	9	39
Tropical and Subtropical Dry Broadleaf Forests	3	1	33

From a more conceptual point of view, we found variation in research effort among scientific fields (Fig. 10). The main focus of urban ecology in Africa seems to be applied studies given that conservation and human dimensions studies were the two most commonly investigated fields, with 41 % of all papers falling into these two categories. The scientific fields of wildlife management, wildlife disease and human-wildlife conflict were the least studied, accounting for merely 6 % of the total publications represented in this review. Our data showed that pattern approaches (e.g., Population, Community or Landscape Ecology) are more common than mechanistic studies (e.g., Animal Behavior) in Africa (Fig. 10). The first animal behaviour studies were published in the early 1990s, investigating insects (Paillette et al., 1993) and birds (Van Zyl, 1994). But the focus on this discipline has considerably increased since 2015, with 64 % of all Africa urban ecology studies on animal behavior published after this year (Table S2). Despite this increasing interest, there is still an important taxonomic bias, and only 44 % of the 27 animal classes were represented in animal behaviour studies, including Mammalia (38), Aves (47), Reptilia (7), Amphibia (6), Insecta (5), Gastropoda (2), Actinopterygii (2), Arachnida (1), Clitellata (1), Entognatha (1), Malacostraca (1) and Sarcopterygii (1).

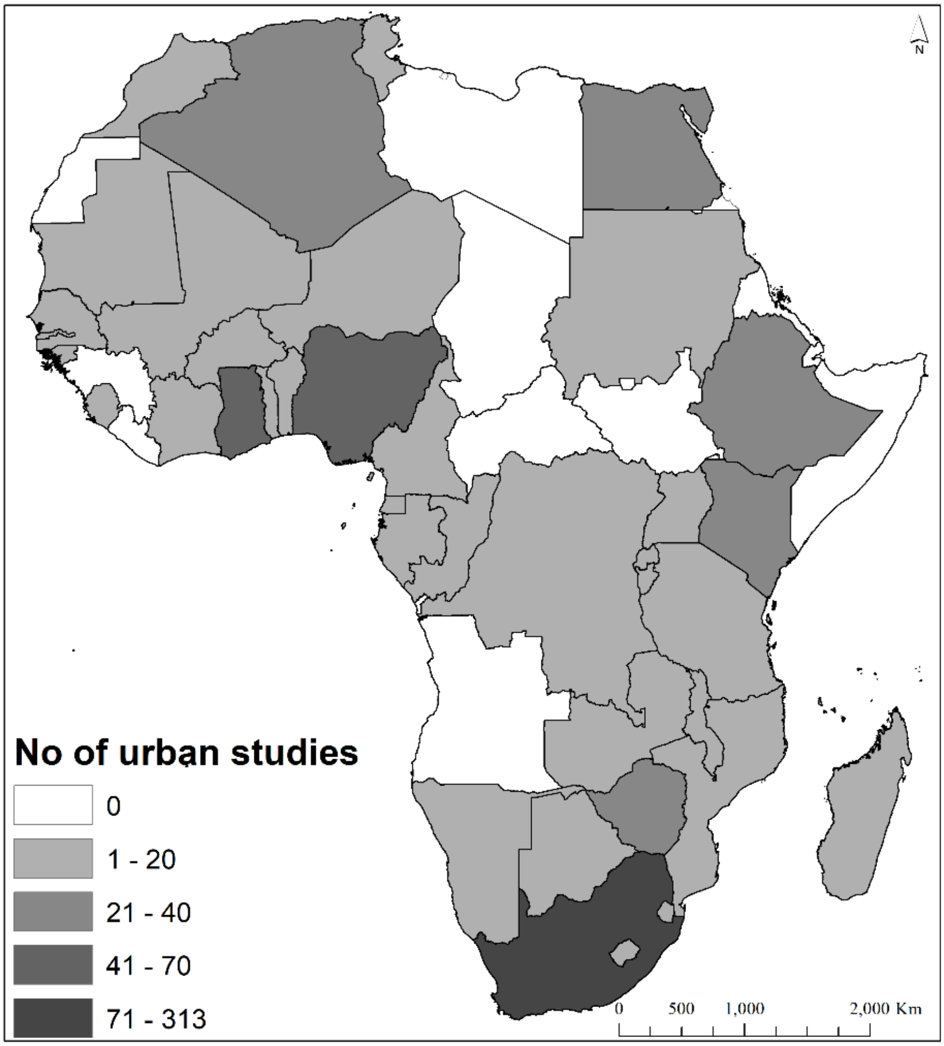

Figure 3. The distribution of urban ecological studies across African countries.

Table 3: Results of a Poisson Logistic Regression exploring the relationship between the number of published urban studies and the conservation status and size of ecoregions. Conservation status is a factor with 5 levels (Critical, Endangered, Relatively Intact, Relatively Stable, Vulnerable) and size is a continuous variable. Critical has been set as the intercept in the model.

	Estimate	SE	z-value	*p-value*
Intercept	2.99E+00	4.50E-02	66.467	**<0.001**
Endangered	2.44E-01	6.46E-02	3.782	**<0.001**
Relatively Intact	-2.33E+00	2.13E-01	-10.971	**<0.001**
Relatively Stable	-1.13E+00	9.02E-02	-12.524	**<0.001**
Vulnerable	-2.62E-02	1.10E-01	-0.239	0.811
Size	5.45E-07	4.69E-08	11.609	**<0.001**

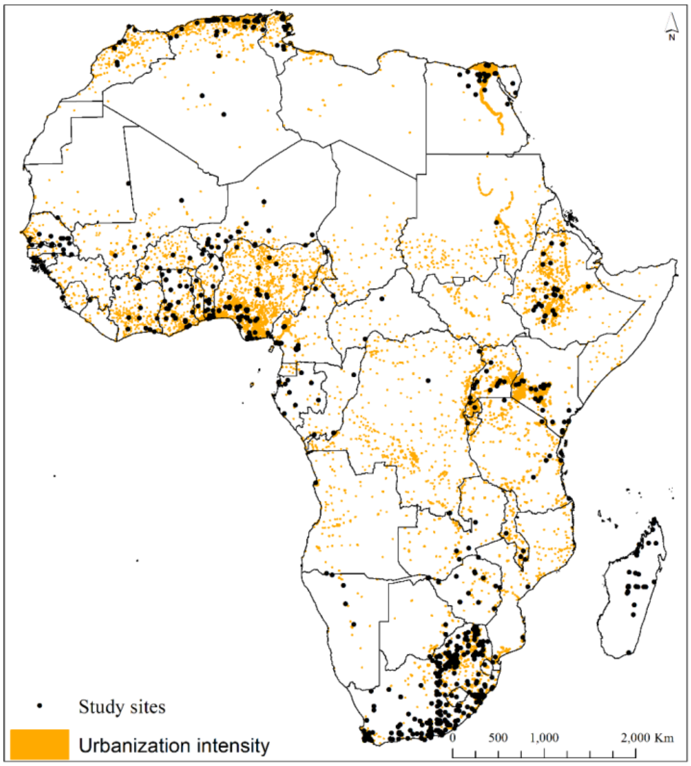

Figure 4. The distribution of urban ecological study sites superimposed on urbanization intensity.

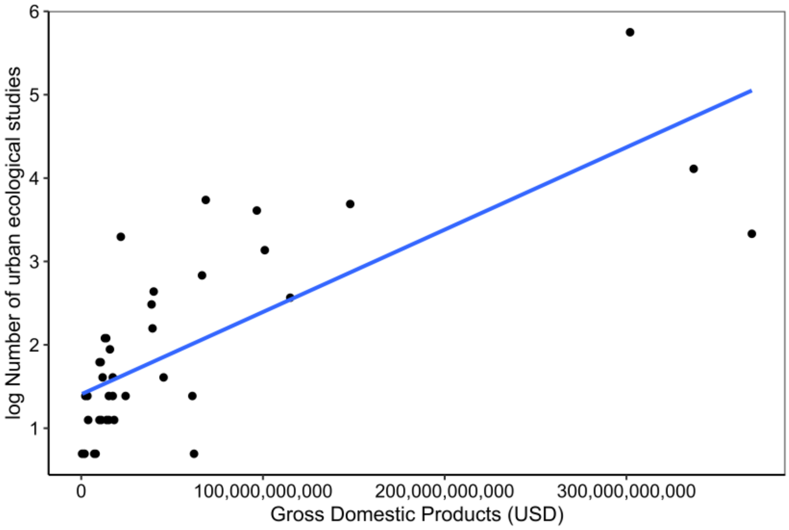

Figure 5. Relationship between urban ecology research effort (number of urban ecological studies) across all countries and Gross Domestic Products (USD). Note that the y-axis is on a logarithmic scale and that there are several overlapping point.

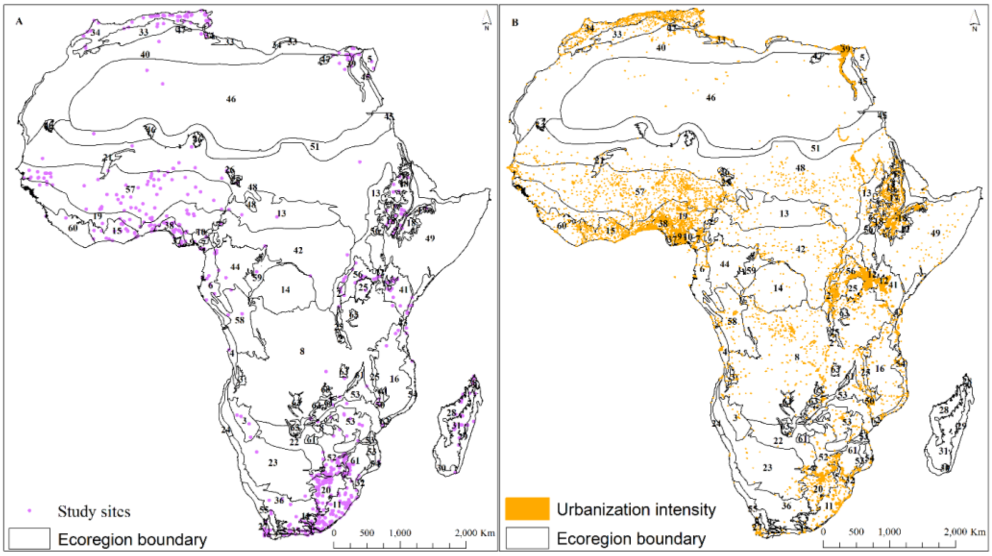

Figure 6. Map of the African terrestrial ecoregions showing the distribution of urban ecological study sites (a) and urbanization intensity (b). The maps were simplified to facilitate interpretation. Thus, we retain outlines of relatively large ecoregions >10,000 km^2 and those including study sites. However, the names of all ecoregions, their corresponding numbers in the map and additional details (e.g., size) are included in Table S4.

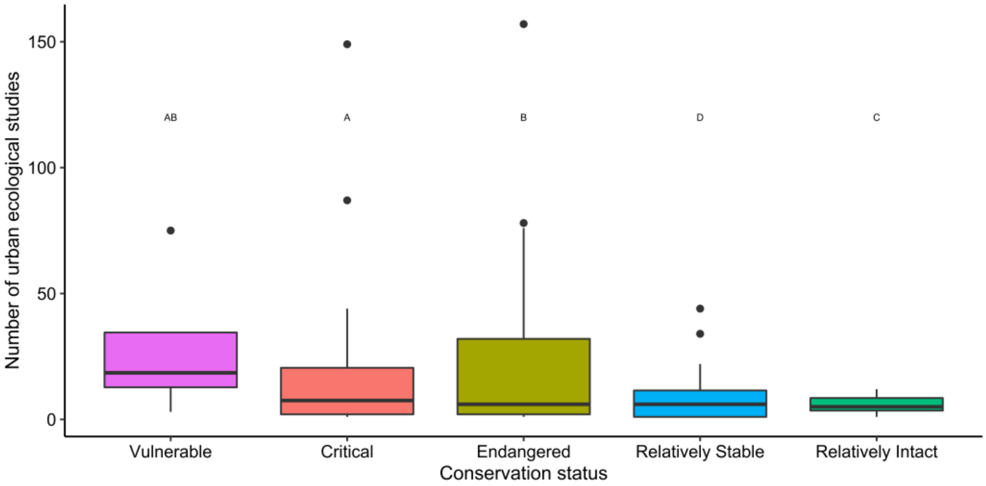

Figure 7. Urban ecology research effort (number of urban ecology studies) across the conservation categories of ecoregions. Box-plots show median, quartiles, 5- and 95- percentiles and extreme values. Different letters indicate significant differences (P < 0.01) between conservation status according to Tukey post-hoc tests using the package “emmeans” (Manley et al., 2015; Yvoz et al., 2020).

Discussion

Spatio-temporal patterns in knowledge

Our literature search shows almost 800 urban ecology papers for the entire African continent. According to a recent review investigating the top 20 countries publishing on urban ecology (Shackleton et al., 2021), this number is lower than the number of publications from medium-sized European countries, such as Germany (2,479) or Spain (1,864), and much lower than the research effort identified for the United States (12,728), China (6,655) or Australia (2,900). This suggests that urban ecology research in Africa is still considerably low compared to other regions of the World (e.g., Europe, North America, Asia or Australia), matching previous findings that already indicated the African continent was the least studied regarding urban ecology (e.g., Magle et al., 2012 stated that Africa accounted for 2.8 % of published papers on urban wildlife ecology in 2010). It is interesting to note that despite the exponential growth in research effort during the last 15 years, mimicking the global trend on the topic (Lin & Grimm, 2015), Africa has not increased its relative contribution to the field like other regions (e.g., Asia) that were also underrepresented a decade ago (Magle et al., 2012; Wu et al., 2014; Shackleton et al., 2021). The overall number of urban ecology papers in Africa does not seem to be associated with a delayed start in the discipline. Our review shows that African urban ecology started at the end of 1970s around the same time that this discipline started in other regions of the World (McDonnel, 2011; Wu, Xiang, & Zhao, 2014). We cannot be completely sure that there have not been earlier publications in non-English languages, but probably the first African paper explicitly mentioning the concept of urban ecology corresponded to Okpala's study (1978). This pioneering investigation focused on socio-economic aspects from Lagos (Nigeria), already highlighting the potential conflict of trying to apply European or American urban ecology theory to the African case, an argument that is still valid within the Global North and Global South framework (Shackleton et al., 2021). The current underrepresentation of African urban ecology is particularly worrying as most African urban settings are considered as clear representatives of the Global South urban settings, integrating particular biophysical and socio-economic contexts (Shackleton et al., 2021).

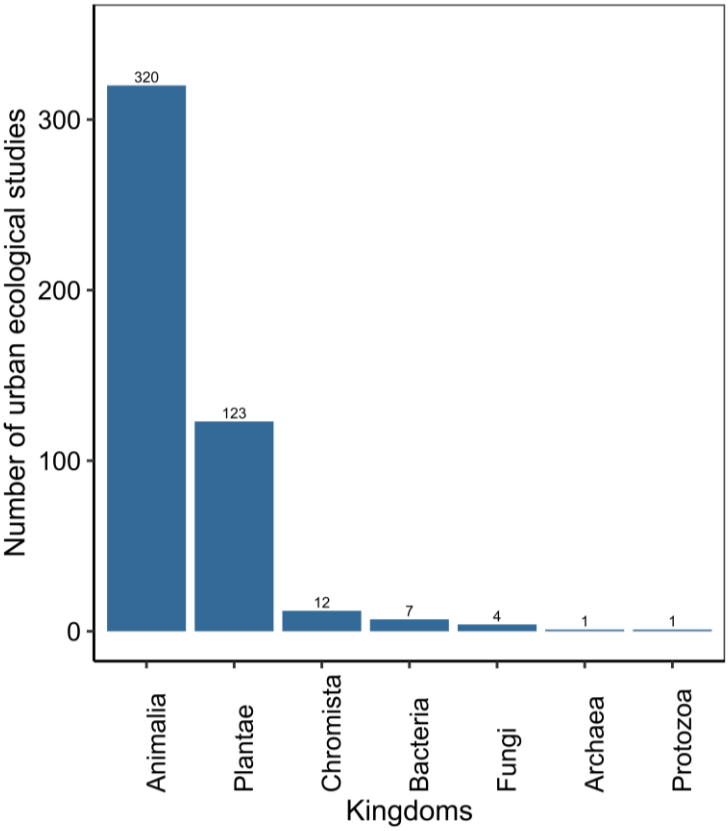

Figure 8. Urban ecology research effort (number of urban ecological studies) across taxonomic kingdoms.

Thus, the lack of knowledge at this respect impedes us to complement our understanding of urban ecology, which is based on the more traditional Global North perspective. There could be other different reasons explaining the low number of publications from Africa. The lack of local capacity/experts in the field is one of them. This factor has been previously highlighted as a key difference between the Global North and Global South urban settings that could influence the lower level of urban ecology research effort in the latter (Shackleton et al., 2021). According to the UNESCO's database for the period 2015–2020 (UNESCO, 2020; accessed 30 Oct 2022), the number of researchers per million of inhabitants in Northern (732.4) and, particularly, Sub-Saharan Africa (97.4), is considerably lower than in other egions of the planet, such as North America (4,544.8), Europe (3,010.4) or Oceania (3,510.5).

This low ratio of skilled people has been demonstrated to influence research effort in Africa regarding other fields such as ornithology (Cresswell, 2018). Therefore, we encourage funding bodies to finance the education of local urban ecologists and researchers to overcome this potential restriction. Another potential reason explaining the low research effort is partially linked to the previous one: the lack of investment in Research and Development (R&D) in Africa compared to other continents. Despite the African Union aims at reaching to the 1 % of GDP invested in R&D (United Nations. Economic Commission for Africa 2018), current data indicate that it is 0.64 % and 0.34 % for northern and sub-Saharan Africa, respectively. This is quite far from the values of North American, European or Eastern Asian countries that reached a mean of 2.6 % in 2020. Matching the target proposed by the African Union will certainly help to increase the focus on multiple topics, including urban ecology. However, there are ways to improve knowledge on urban ecology in Africa even without the need of large economic investments. For example, the use of available databases, such as the various atlas projects, which have been successfully implemented in the continent (Botts et al., 2011; Lee & Nel, 2020). Other repositories, such as the Global Biodiversity Information Facility, laboratories, herbaria and museums in and outside of Africa are also useful tools to advance our understanding of the ecology of African urban areas and biodiversity as some recent studies have already shown (e.g., Cohen et al., 2021; Fishpool & Collar, 2018). This approach could also be implemented in collaboration with inhabitants of African urban areas through citizen science projects (e.g., iNaturalist or the Southern African Bird Atlas Project) that can serve to improve information on certain urban questions (e.g., animal distribution) as well as promote the connection between citizens and nature (Reynolds et al., 2021). Engaging citizens could also be instrumental to help increase the urban governance in the Global South, including Africa (Shackleton et al., 2021), and ultimately promote additional support for urban ecology studies in this continent.

Our review also shows that research effort is not homogeneously distributed within the African continent. From a political point of view, there is an important variation among African countries in their urban ecology research effort. One single country (South Africa) stands out as it is responsible for almost 40 % of published papers on the topic. This is so despite only representing 4 % of African territory and 1.02 % of all urban areas in the region (OECD/SWAC, 2020). This high rate of urban ecology publications matches previous information indicating that South Africa is very active in the field at the global level (Shackleton et al., 2021). This does not seem to depend on its number of researchers per million of inhabitants (411.6) or its R&D investment (0.62 % of GDP), which is lower than the mean for Northern Africa (UNESCO, 2020), an area that not even combining all its countries reaches half the number of papers published in South Africa. This country started publishing urban ecology papers at the earliest stages in Africa (Hugo, 1979), so it is possible that this long-term publication period is behind its uniqueness. Another possibility could be that several South African cities (e.g., Cape Town and Durban) are located in biodiversity hotspots of global importance (Cilliers & Siebert, 2012). Alternatively, given that Global North urban principles do not always apply to Global South urban areas (Okpala, 1978; Shackleton et al., 2021), there could be a special interest by funders and/or researchers from this country to acquire first-hand knowledge of direct application to South-African urban settings. For instance, some universities from this country (e.g., Witwatersrand) have strategically focused on global change research, including urban ecology (Scholes et al., 2013) or have developed specific institutes for the study of 'urbanism from an African perspective' (e. g., The African Centre for Cities, from the University of Cape Town in South Africa; <https://www.africancentreforcities.net/about/acc-at-uct/>). Independently of the reasons for this important outlier, urban ecology research effort varies considerably within African countries. We identified that 28 % of these countries did not publish a single urban ecology study and thus, they completely depend on urban knowledge obtained elsewhere that sometimes might not be really useful for their local situations.

Our analyses show that the number of publications per country on the topic is not associated with current or future urbanization. This result contradicts our initial prediction; however, it could be well understood from a Global South perspective. African countries, like other countries from this group, have several particularities compared to those from the Global North (Shackleton et al., 2021). One of them is the extremely high urbanization rate. Africa is the continent of the World with the most intense urbanization (Cohen, 2006; Seto et al., 2012), with many African countries experiencing urbanization rates above 4 % (e.g., Mali, Nigeria, Angola or Mozambique), an order of magnitude higher than those from other regions of the planet (World Bank, 2021). This factor leads to unplanned urbanization (Zhang, 2016) and compromises sustainable urban development in the continent by impeding the implementation of ecologically-sound practices (Cohen, 2006) and hence potentially explaining the mismatch between urbanization and urban ecology research effort.

Furthermore, we found that the human population density of a country was not significantly associated with the number of publications on urban ecology either. The reasons for this lack of association could be the same as explained before for the current and future urbanization prospects as these are positively correlated with human population density (e.g., Gao & O'Neill, 2021; Qizhi et al., 2016). However, this predictor could also be associated with other potential factors that might prevent investing resources and effort in investigating about urban ecology. For example, there is an increase in people living in extreme poverty in Africa, with more than half of the urban population living in slums and informal settlements (World Cities Report, 2016). Highly populated areas also require a higher infrastructure investment, which is particularly needed in Africa (Zhang, 2016). Thus, socio-economic priorities combined with an insufficient capacity of urban governance (Zhang, 2016; Shackleton et al., 2021) could prevent finding the initially expected effect of human population density. Considering all these results and factors, particularly the uncoupled distribution between urban ecology knowledge and future urban prospects, we would recommend local authorities, funding bodies and researchers to make an effort in the study of the areas that soon will be transformed into urban landscapes. This is particularly important in the tropical African belt given that it will concentrate the greatest urban expansion in the future (Seto et al., 2012), but also holds the largest biodiversity of the continent (Cazzolla Gatti et al., 2015).

Interestingly, our results indicate that the number of published urban ecological studies depended on economic factors (i.e., GDP). This association has been found in other cross-sectional (e.g., Doi & Takahara, 2016; Fisher et al., 2011) and longitudinal studies (Vinkler, 2008). This economic indicator is in addition significantly associated with a higher rate of influential publications within their subject area (Bornmann et al., 2014). However, other investigations showed that R&D investment rather than per capita GDP is positively associated with research productivity in different continents (Meo et al., 2013, 2014). It is possible that GDP is a better predictor of R&D in Africa than in other regions, thus potentially explaining the obtained finding. This influence of economic factors on urban ecology research effort is crucial given the link between cities and economic wealth (Zhang, 2016), which could lead us to think that as urbanization progresses in Africa, the better their economies will be and consequently more research on urban ecology could be made. This scenario seems unlikely as this association between economic and urban growth is decoupled in the African continent (Cohen, 2004), which does not warranty this increasing research effort in the future.

Other factors not considered in our analyses could also explain the country-wide variation in urban ecology research. For example, political instability could play an important role for the lack of studies on the topic in certain countries such as Western Sahara, South Sudan or Libya. The fact that the majority of published studies were conducted locally within a single city or country (e.g., Koricho et al., 2020; Lindley et al., 2018; Muleya & Campbell, 2020) suggests the need for investigation of local/national cases for the application of specific solutions. However, it also highlights the lack of transnational collaboration among African countries. This low level of international research both within Africa and with countries from other continents is particularly important considering that: (1) it impedes the generalization of findings at the continental and global scale, and (2) reduces the number of substantive contributions to scientific progress (Bornmann et al., 2014). Therefore, we recommend funders and researchers alike to strengthen or promote the creation of new international networks or institutes on African urban ecology as well as encourage urban ecologists of the continent to participate in other global actions, networks (e.g., the Urban Biodiversity Research Coordination Network) or societies (e.g., Society for Urban Ecology) that are already running.

The geographic variation in research effort could also be linked to conservation aspects. Conservation research in Africa is particularly relevant and prolific in the global context (Doi & Takahara, 2016). There are still some controversies on whether conservation status is significantly and positively associated with research effort at the species level (e.g., Brooke et al., 2014; Ducatez & Lefebvre, 2014; Ibáñez-Álamo et al., 2017), but countries with a higher level of environmental protection activity investigate more in ecology (Doi & Takahara, 2016). Our results match this finding given that urban ecology research effort is significantly associated with the conservation status of African ecoregions. The ecologically relevant regions belonging to the most threatened categories (Critical, Endangered and Vulnerable) showed the highest number of publications on the topic. This is logical considering the previously described restricted R&D investment in Africa that would divert the current available resources towards areas of conservation concern. Despite this, we found that about half (50 %) of African ecoregions without a single published study on the topic are classified as threatened, and urbanization is considered a leading threat in the area (Burgess et al., 2004), suggesting the need for additional studies to determine the ecological effects of urbanization and propose suitable conservation actions. On the other side, the significant effect of ecoregion size fitted our initial expectations as larger ecoregions would support higher biodiversity levels (Rantalainen et al., 2005) and consequently a higher likelihood of being investigated. As larger and more threatened ecoregions were significantly more studied in the continent, there is a need to expend greater research effort on smaller and relatively stable ecoregions (e.g., East African Montane

Moorlands and Lake Chad Flooded Savanna), which are more likely to suffer unnoticed fragmentation from urbanization and other anthropogenic land use changes as also indicated by previous studies (e.g., Beyer, Venter, Grantham, & Watson, 2020; Burgess, Hales, Ricketts, & Dinerstein, 2006; McDonald et al., 2008). Particularly surprising is the lack of studies from the majority (77 %) of ecoregions from the Tropical and Subtropical Dry Broadleaf Forests biome. These ecoregions mainly correspond with large areas of Madagascar, a megadiverse country (<https://www.biodiversitya-z.org/content/megadiverse-countries> accessed 30 October 2022) with the lowest percentage of urban land cover in the whole continent (0.04 %; OECD/SWAC, 2020). In contrast, other forested biomes are quite well represented, which makes sense considering that forests, especially those from Western Africa, support higher biodiversity and endangered species, thus promoting a more intense ecological research effort (Doi & Takahara, 2016).

Gaps in knowledge according to taxonomy and scientific fields

Our review also offers interesting information on the current methodological and conceptual orientation of urban ecological research in Africa. From a methodological point of view, we found an important taxonomic bias in the study of urban ecology in Africa similar to those previously reported (e.g., Callaghan et al., 2020; Shwartz et al., 2014). This taxonomic bias has a strong effect in our urban ecology knowledge given that the impact of urbanization varies considerably depending on the type of organisms considered (McKinney 2008; Paul & Meyer, 2001). Our literature search offered studies focused on organisms belonging to seven kingdoms, although the majority of urban ecology research used either animals or plants as model systems. This result highlights our limited understanding of other organisms in the African urban context, including Archaea, Bacteria, Chromista, Fungi and Protozoa, which should be prioritized for future studies. This is justified by current literature highlighting their relevance in natural environments (e.g., Epp Schmidt et al., 2019; Kartzinel et al., 2019; Thompson et al., 2017). The uneven distribution of urban ecology research effort went down to lower taxonomic levels (e.g., classes). Among animals, birds and mammals were the two most studied groups. The publication bias towards these two classes in urban ecology is not restricted to Africa alone (Donaldson et al., 2017; Shwartz et al., 2014), and has also been identified in other study fields such as conservation biology (Lawler et al., 2006) and invasion ecology (Pyšek et al., 2008). Several reasons have been proposed to explain this bias for birds and mammals, such as body size (Brodie 2009) or conservation status of focal species (Donaldson et al., 2017). Regarding plants, flowering plants (Magnoliopsida and Liliopsida) dominate urban ecology research effort in Africa, replicating the patterns found by other research effort studies on plants (Richardson & Rejmanek, 2011; Stranga & Katsanevakis, 2021). In contrast with plants, with the richly diverse Magnoliopsida (Tracheophyta) relatively well studied (Cilliers & Bredenkampl, 1999; Moussa et al., 2020; van der Walt et al., 2015), the most diverse animal group of Arthropoda is clearly underrepresented in urban ecology and calling for additional scientific attention (reviewed here; McIntyre, 2000).

Urban ecology research effort in Africa also varied in terms of scientific disciplines. Conservation was the most studied scientific field. This result is in agreement with previous findings already highlighting the relevance of Africa in the study of environmental conservation and ecology (Doi & Takahara, 2016), and matches also with our initial result that indicates preference for ecoregions of conservation concern. Interestingly, a handful of such African conservation studies diagnosed different socio-environmental issues in urban areas and developed useful frameworks or plans for promoting nature conservation and sustainable urban development in the continent (e.g., Boon et al., 2016; Cilliers et al., 2004; Goosen & Cilliers, 2020; Rebelo et al., 2011). While these findings imply the availability of data that could be useful for promoting conservation actions, they are mostly restricted to South Africa. For an effective implementation of conservation actions, more studies are needed from unrepresented areas as they may help to discover local issues such as environmental injustice (Ernstson, 2013). The human dimension field is well-represented within African urban ecological research, which points to the relevance of multifaceted approaches in Africa, particularly regarding ecosystem services that complements conservation or ecological studies (e.g., population ecology or animal behavior). For instance, the majority of human dimension studies in our review indicate that people in African urban areas appreciate the socio-ecological services (Dipeolu et al., 2020; Rogerson & Rogerson, 2020) and economic benefits provided by urban biodiversity (Babalola et al., 2013; King & Shackleton, 2020). In a study by Popoola and Ajewole (2002), most Nigerian respondents were even willing to support the conservation of urban nature through personal funds. The conservation of urban biodiversity is tightly linked to public support (Miller & Hobbs, 2002), and thus, human dimension studies could be useful educational tools to reconcile urban development and nature preservation in the continent (McDuff, 2000). In addition, unlike in other regions where the important roles of urban biodiversity in enhancing ecosystem services and human well-being have been well documented (Brown & Grant, 2005; Dallimer et al., 2012; O’Sullivan et al., 2017), this interplay is much more complex in the African case (Wangai et al., 2016) usually not considering the ecosystem disservices that could be of critical importance in areas of the Global South (Davoren & Shackleton, 2021). In general, ecosystem services in Africa have been poorly studied (du Toit et al., 2018), although there is a clear effort in recent years to overcome this important gap (e.g., Dobbs et al., 2021; Escobedo, 2021; Shackleton et al., 2021; Wangai et al., 2016), including the evaluation of how different frameworks are applied to African urban settings (Lindley et al., 2018).

We identified that many urban ecology papers focused on Africa used pattern approaches either at the species or community level. Several reviews on urban ecology or specific aspects of urban ecology (e.g., urban ornithology) have also found similar results at the global level (Magle et al., 2012; Marzluff, 2016; Wu et al., 2014). As we have stated before, Africa is understudied in urban ecology, and we lack many basic information on even the presence/absence of certain organisms in cities of this continent. Some of the studies in these categories describe new species (e.g., Malonza et al., 2016; Smales et al., 2017), provide information on potentially problematic organisms (e.g., invasive species; Bigirimana et al., 2011; Hima et al., 2019) or provide much needed information on the distribution of organisms in African urban settings (e.g., Moussa et al., 2020; Muchayi et al., 2017). But some of these articles also used applied approaches by integrating human-nature interaction aspects. For example, Chamberlain et al. (2019) found evidence supporting the luxury effect in South Africa. This effect states that there is a positive correlation between wealth and biodiversity, and thus relates to environmental injustice issues (Reynolds et al., 2021). These pattern approach studies that also consider applied aspects and the particularities of Global South urban areas are excellent examples on how we can advance in our understanding of African urban ecology. Some researchers have highlighted the lack of urban ecology mechanistic studies in countries of the Global South compared to those from the Global North (Marzluff, 2016). Mechanistic studies would, for example, include animal behavior papers that could explain the observed patterns (e.g., feeding behavior explaining the presence of certain animals in cities). Africa has produced quite a lot of animal behavior studies centered in urban areas but most of them were observational (e.g., McPherson et al., 2016; Widdows & Downs, 2016), with only a handful of experimental manipulations (Cronk & Pillay, 2018; Patterson et al., 2016) that are much more powerful to identify cause-effect associations. Future studies should try to put more emphasis on experimental manipulations to fill in this important gap in our urban ecology knowledge.

Landscape ecology is still not as well studied as in other regions regarding urban areas (Magle et al., 2012; Wu et al., 2014), but it offers unique opportunities for the development of this field in Africa. On the one hand, landscape ecology studies in our database extensively utilized the Geographic Information System (GIS) for estimating land cover and habitat heterogeneity (e.g., Benza et al., 2016; Kowe et al., 2020). The use of GIS techniques could enhance better coverage of study sites (e.g., conflicting/dangerous/remote areas), helping to complete the missing geographic areas in urban ecology research detected in our review. These techniques require highly qualified personnel but provide useful information at minimal time and cost (Langat et al., 2019), thus, offering a good opportunity for capacity building in the continent while considering the economic restrictions in R&D of the region (see above). On the other hand, landscape ecology is an integrative discipline merging geospatial patterns, ecological and socio-economic processes and ecosystem services/disservices, thus favoring the interdisciplinary collaborations between sociologists, ecologists and geographers among others (Wu et al., 2014), thereby facilitating the establishment of much needed interdisciplinary collaborations in African urban ecology. For all these reasons, we expect that the field of urban landscape ecology will continue to increase as it has happened at the global scale (Magle et al., 2012).

Conclusions

This review shows that research effort on urban ecology is still low in Africa, with the exception of South Africa, particularly in the highly urbanized and biodiversity-rich areas of the continent. This continent is an important representative of the Global South, and thus the lack of information on the topic is an important impediment to try to overcome the traditional Global North perspective on urban ecology (Shackleton et al., 2021). In addition, the information presented here could be crucial to achieve the 11th Sustainable Development Goal in the rapidly urbanizing African continent (Cobbinah et al., 2015). Urban areas, if well-planned, can still provide substantial benefits for biodiversity, act as hotspots and habitat corridors for some threatened species (Ives et al., 2016; Kumdet et al., 2021) and serve important socio-ecological (Dipeolu et al., 2020; Rogerson & Rogerson, 2020) and economic benefits (Babalola et al., 2013; King & Shackleton, 2020). To our knowledge, this is the first general literature review of urban ecological studies for the entire African continent that follows rigorous, verifiable and repeatable methodological approaches recommended in recent times (Ibáñez-Álamo et al., 2017; Magle et al., 2012; Moher et al., 2009; Sánchez-Tójar et al., 2020). Previous methodologically-similar reviews of African urban ecology, though interesting and useful, either focused mainly on socio-ecological systems (e.g., Cilliers, 2019; Lindley et al., 2018) or specific aspects of African urban biodiversity (e.g., Güneralp et al., 2018; Roets et al., 2019; Trimble & van Aarde, 2014). The low research effort in African urban ecology seems to point to socioeconomic factors such as the low level of skilled people and reduced investment in R&D typical from this continent (e.g., Cresswell, 2018). We believe that this situation could be partially reverted if African countries follow the African Union recommendation of investing 1 % of their GDP in R&D, although other socio-economic needs (e.g., infrastructure, security, health issues) could make this change very difficult (Zhang, 2016).

Economic factors (GDP) rather than other urban indicators (e.g., urbanization intensity, human population density) are also crucial to explain urban ecology research effort within the continent. South Africa congregates many of the papers on the topic, while there are 16 African countries without urban ecology studies, providing clear targets for future investigations. The South African case could be useful to identify specific aspects that could be reproduced in other neighboring countries to try to boost urban ecology research. Thus, studies comparing different urban ecology aspects between South Africa and other African countries would be particularly interesting at this respect. In addition, it is especially worrisome the uncoupled nature between future urbanization prospects and urban ecology knowledge as local authorities will not count with valuable information to take scientifically-based actions. This lack of information has already been suggested as an important impediment to achieve sustainable urban development in Africa (Cobbinah et al., 2015; Patel et al., 2017).

In addition, greater research effort is expended on larger and threatened ecoregions. Threatened sites and species are usually prioritized for conservation actions (Brooks et al., 2006), and could influence research effort (e.g., de Lima et al., 2011). However, relatively stable ecoregions could suffer unnoticed effects of urbanization, which could be detrimental to certain biodiversity that may suffer regional extinction before being identified. This pattern has been previously reported in Africa (Ahrends et al., 2011), and could even be more severe in the future given the mismatches in the allocation of research effort across regions. This research bias towards threatened areas is partially linked to the fact that conservation studies dominate the urban ecology literature produced in the African continent. Our literature search also indicated that African urban ecology research is multidimensional with an important contribution to human dimension studies including those on ecosystem services and disservices. These studies have increased in recent years providing much needed information for the urban settings of this continent and ultimately helping to improve our understanding of the complex urban environment in which many different components interact (e.g., sociological, ecological, economical…).

Recommendations

We argue that for African urban ecology to provide more useful information for decision-making and promote sustainable development, future research should try to overcome the detected geographic, taxonomic and ecological biases. To help in this endeavor, we provide a list of the articles reviewed here as well as the journals of publication, where key stakeholders or researchers could obtain relevant data on the topic (Table S2).

Based on our review, we propose the following recommendations to promote urban ecology research in this continent: (1) strengthening collaboration and networking among researchers across regions and countries, as previously suggested in a more general context (McPhearson et al., 2016). This will allow for larger scale studies that will provide an additional and complementary perspective to city/local studies that tackle more specific problems. (2) Helping the education of local experts on urban ecological studies can be also instrumental to overcome some of the previously described publication biases on the topic (Shackleton et al., 2021). (3) Engaging with the citizenship through citizen science projects. This will allow the acquisition of additional scientific information at the same time as it promotes a better urban governance through participation of urban inhabitants. (4) Use of low-cost techniques like GIS or available databases (e.g., museums) to maximize the scientific outcome considering the economic restrictions of the region. We hope that this review will help to re-orientate our research effort on the topic and fill in some important knowledge gaps highlighted here to grant a balanced strategy between urban development and nature conservation in this unique continent.

Supporting Materials

Supplementary data to this article can be found online:
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Chapter 2

Associations between urbanization and avian communities in the Afrotropics: Evidence from taxonomic, functional and phylogenetic diversity

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Abstract

Urbanization negatively affects biodiversity worldwide, with the rapidly urbanizing Afrotropical area being understudied. Furthermore, most previous studies investigating this topic focused on taxonomic diversity while recent findings have highlighted the need to incorporate complementary diversity metrics. Thus, this study investigated how urbanization affects bird taxonomic, functional, and phylogenetic diversity in Nigeria, a country with one of the fastest rates of urbanization in the world. We conducted bird censuses at 400 points organized across eight paired comparisons (urban vs non-urban habitats), vegetation zones (rainforest vs savannah), and seasons (dry vs wet). Of the total 237 bird species recorded, 65 % were never encountered in urban areas, suggesting the negative effect of urbanization that was also supported by our statistical analyses. Taxonomic diversity was significantly higher in non-urban than urban habitats. This contrasted with the result on functional and phylogenetic diversity, which was higher in the urban than non-urban habitat. These relationships were similar across seasons, but more intense in the rainforest, revealing that birds in this vegetation zone are more vulnerable to urbanization than their savannah counterparts. We also found that water cover significantly promoted all avian diversity metrics analyzed during the dry season independently of urbanization. In contrast, canopy and bush cover mediated the effects of urbanization on some diversity components (i.e., functional and phylogenetic diversity). Our results highlight the significance of incorporating spatiotemporal patterns in related studies and provide much needed information for city planners and other urban stakeholders in the Afrotropics.

Introduction

The world is experiencing accelerated urban development (United Nations, 2016), which is predicted to increase the urban land cover from 824,200 km2 in 2020 to 1,145,698 km2 by 2050 (Angel et al., 2011). This dramatic land-use change mainly occurs in developing countries, such as those in the Afrotropical region (OECD/SWAC, 2020; Seto et al., 2012). Coincidentally, this region holds huge but declining biodiversity (Gatti et al., 2015), and is relatively understudied (Ibáñez-Álamo et al., 2017; Magle et al., 2012). Recent studies indicate that the fewer urban studies from the Afrotropics strongly correlate with low levels of local capacity and funding (e.g., Awoyemi & Ibáñez-Álamo, 2023). However, information on effects of urbanization on biodiversity is necessary to prevent or minimize biodiversity loss (e.g., Gaston, 2010; Ives et al., 2016; McKinney, 2006, 2008).

The various components of biodiversity (i.e., taxonomic, functional and phylogenetic diversity) offer complementary information useful in promoting biodiversity conservation (Tucker et al., 2017). Taxonomic diversity reveals the presence of species in an area (Magurran, 2004), while functional diversity shows how the functional traits of species influence ecosystem services and functioning (Mouchet et al., 2010; Reynolds & Howes, 2023). Moreover, phylogenetic diversity provides information on the evolutionary richness or divergence of all species in a given community assemblage (Faith, 1992; Helmus et al., 2007). Thus, recent studies have recommended the simultaneous investigation of taxonomic, functional, and phylogenetic diversity as the same process may affect them in varied ways

(Nava-Díaz et al., 2022). In general, urbanization negatively affects bird taxonomic diversity (e.g. Aronson et al., 2014; Ibáñez-Álamo et al. 2017). However, studies investigating the effects of urbanization on bird functional and phylogenetic diversity have found contrasting results across space and time (La Sorte et al., 2018; Lee et al., 2021; Morelli et al., 2021). These studies also show that urban habitat characteristics (e.g., built surfaces, pedestrians, water, bushes, grasses, or tree canopy) affect biodiversity components differently. Meanwhile, several literature reviews on functional diversity and evolutionary distinctiveness in urban areas have revealed the lack of studies from the Afrotropical region (e.g., Hagen et al., 2017; Ibáñez-Álamo et al., 2017). In fact, a recent review on African urban ecology highlighted that there have been no studies simultaneously investigating the impacts of urbanization on these three components of biodiversity (taxonomic, functional, and phylogenetic diversity) in the continent (Awoyemi & Ibáñez-Álamo, 2023). This lack of information could restrict our ability to tackle the increasing challenge posed by urbanization in the area.

Furthermore, most studies on urban ecology in Africa are city based, with each study conducting research in a single city (Awoyemi & Ibáñez-Álamo, 2023). Thus, if we really want to identify general patterns in the effect of urbanization on African biodiversity, we should consider potential variation between cities. In addition, the Afrotropics has a strong temporal variation associated with climate (e.g., dry or wet season) and vegetation (e.g., rainforest or savannah) that influence biodiversity in the region (Chapin, 1923; Sumasgutner et al., 2023). In Western Africa, for example, bird species richness is higher in the rainforest than in the savannah (Brown et al., 1982; Ezealor, 2001), while food is more abundant in the wet than the dry season (Siegfried, 1972; Sinclair, 1978). However, the influence of this spatiotemporal variation on the taxonomic, functional, and phylogenetic diversity of Afrotropical birds has not been explored in the context of urbanization (Awoyemi & Ibáñez-Álamo, 2023).

In this study, we assessed how urbanization affects the different components of biodiversity (taxonomic, functional and phylogenetic) in Nigeria. This country is a regional representative of the Global South with important biophysical and socioeconomic scenarios different from those of the more commonly studied Global North countries (Shackleton et al., 2021). Nigeria is one of the most densely populated countries in Africa with approximately 226 humans/km2 (United Nations, 2019). Due to this density and other factors, such as rural-urban migration for a better life (Oyeleye, 2013), Nigeria is projected to experience one of the largest urban expansions globally in the near future (OECD/SWAC, 2020; Seto et al., 2012). This makes it an ideal site to test the effect of urbanization on the continent's biodiversity.

Here, we used birds as a model group because they experience important community changes between seasons and vegetation zones (e.g., Brown et al., 1982; Morelli et al., 2021) and have a well-validated phylogeny (e.g., Jetz et al., 2012). By incorporating spatial (8 cities in 2 vegetation zones) and temporal (2 seasons) replicates, we (1) investigated differences in the three biodiversity components between habitats (urban vs non-urban), vegetation zones (rainforest vs savannah), and seasons (dry vs wet). Based on previous findings, we expect urban areas to hold significantly lower levels of taxonomic (e.g., Aronson et al., 2014; van Rensburg et al., 2009) and phylogenetic diversity (e.g., Ibáñez-Álamo et al., 2017) than the adjacent non-urban areas, which will contrast with the result on functional diversity (Hagen et al., 2017; Weideman et al., 2020). Given the higher vegetation cover in the rainforest than the savannah (Brown et al., 1982; Ezealor, 2001), we could expect a more intense reduction in biodiversity due to urbanization in the former than in the latter. We also (2) explored how local influential variables, such as pedestrians, bushes, water, and tree canopy affect diversity metrics in the region. The result of our study will provide crucial information for formulating conservation strategies in the Afrotropics and expand our knowledge on the effects of urban development on wild animals.

Methods

Study area and site description

Nigeria has a tropical climate with distinct wet and dry seasons. Annual rainfall and length of wet season generally decrease northwards from the coast (4,000 mm - 600 mm) (Ezealor, 2001). Variations in daily, monthly, and annual mean temperature are small in coastal and rainforest areas, but become greater further inland; thus, in the savannah part of Nigeria, temperatures over the year range from approximately 8°C to over 40°C (Ezealor, 2001).

The southern Nigerian sites visited for the present study are a typical representative of urban and non-urban rainforest locations. These sites are characterized by dense evergreen forest of tall trees with thick undergrowth and receive a mean annual rainfall of approximately 2,000 mm/annum occurring mainly from April to September (Ezealor, 2001). Meanwhile, the northern Nigerian sites are located within the northern Guinea and Sudan savannah vegetation zones, and thus, are classified here as savannah. These sites are characterized by grasses interspersed by small-medium sized trees, and receive annual rainfall of approximately 900 mm/annum occurring mainly between July and September (Ezealor, 2001).

We conducted fieldwork in paired urban and non-urban sites of eight Nigerian cities equally distributed across the rainforest (Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos) vegetation zones (Fig. 1). Here, we considered an urban area (city) as a contiguous patch of built-up land greater than 1 km2, and dominated by human-constructed features like buildings (>10 buildings/ha), high human density (>1600 inhabitants/km2), roads, and vehicles (Marzluff et al., 2001; Niemelä, 1999; Nilon et al., 2003; Schneider et al., 2010). In contrast, we considered the adjacent non-urban areas as places with extensive wilderness/vegetation cover interspersed with agricultural matrix and sparsely settled villages (MacGregor-Fors, 2011; Marzluff et al., 2001). Urban and non-urban sites in this study were situated at least 20 km away from each other to grant the independence of their avian communities following (Liker et al. (2008).

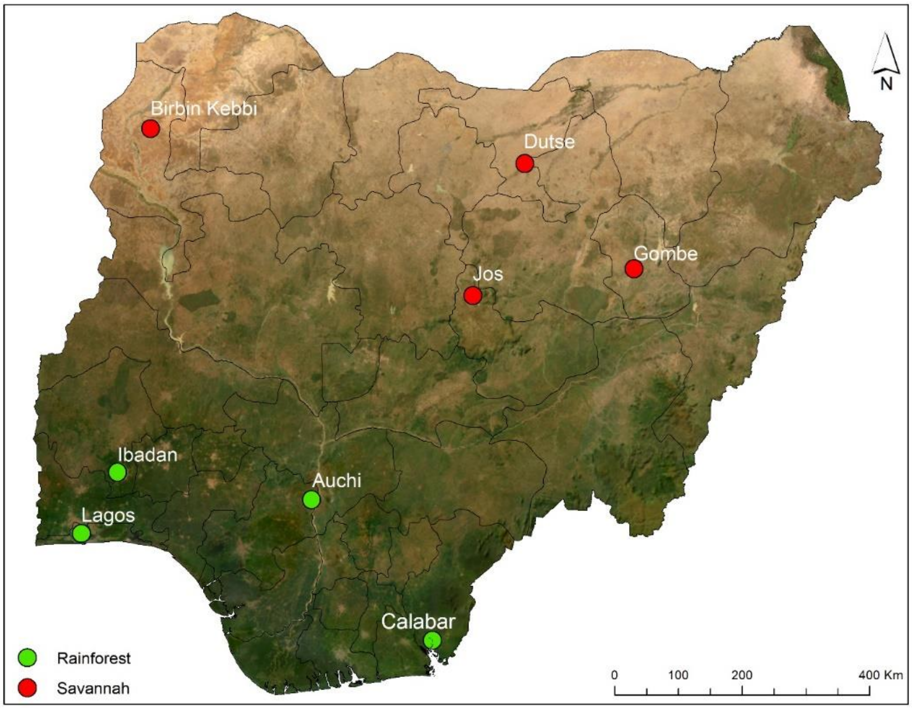


Figure 1: Distribution of study sites across the savannah and rainforest vegetation zones in Nigeria. At each city, data were collected in paired urban and non-urban sites.

Estimation of site characteristics and bird data collection

We used the point count method for bird censuses (Bibby et al., 2000). To ensure a widespread distribution of data that could be representative of the study area (Danjuma et al., 2012; Galbraith et al., 2015), we stratified each site (i.e., urban or non-urban site per city) into five areas stationed at the center and its four cardinal points (i.e., west, east, south and, north) similar to Ciski et al. (2019). We then randomly selected five points from each area. The selection of the areas and points were done using the "create random points tool" in ArcGIS. Each point was marked with a GPS to ensure data collection was from the same location.

During the dry season (November 2020-January 2021), we collected data from 50 selected points (i.e., 25 urban vs 25 non-urban) in each of the eight cities (Møller et al., 2012), totaling 400-point count stations across the two vegetation zones (i.e., 200 rainforest vs 200 savannah). Each point was separated from any other by at least 200 m to reduce potential effects of pseudo-replication (Adegbola et al., 2024; Morelli et al., 2017), and visited in the morning, up to 4 h after local sunrise. Point counts lasted 5 mins/point during which we recorded the numbers of individuals of each bird species and pedestrians seen or heard at 50-m radius of the point (e.g., Adegbola et al., 2024; Morelli et al., 2021). Thereafter, we estimated the following field-based environmental measures (to the nearest 10 %) at 50 m radius of each point, including canopy cover, bush cover, grass cover, water cover, and built surface. To reduce detection issues related to identification, data on bird species and estimation of the field-based environmental measures were collected only by AGA, an expert ornithologist with more than 10 years of experience working with birds of the region.

To determine the effects of seasonal variation, we repeated the above sampling procedure during the wet season (August-September 2021). However, due to security issues in northern Nigeria at that time, we were only able to perform this second round of point counts in the rainforest sites (i.e., 200 point-count stations).

Avian diversity and community metrics

For each season, we quantified three different components of avian diversity. (1) Taxonomic diversity (TAX) was estimated as bird species richness (BSR); calculated as the total number of bird species recorded at each sampling point (Magurran, 2004). (2) Functional diversity (FUN) was calculated using the Rao's Quadratic Entropy (Rao's Q), which complements the traditional taxonomic approach (de Bello et al., 2010), and is not positively correlated with BSR (Botta-Dukát, 2005). To calculate the Rao's Q, we used the avian niche trait categories provided by

Pearman et al. (2014). The calculation was based on bird traits related to their feeding and breeding ecology. We then collected the associated information for each detected bird species from general bird compilations, including the Birds of Africa (Brown et al., 1982; Fry & Keith, 2000; Fry et al., 1988; Fry & Keith, 2004; Urban et al., 1986; Urban & Fry, 1997), Birds of the World (Pearson, 2020) and Handbook of Avian Body Mass (Dunning, 2007). This compilation resulted in a trait table (Table S1) with 73 variables that describe the ecological niche of each bird species found. The variables include body mass, food types (13 variables), food acquisition behaviors (9 variables), substrate from which food was taken (9 variables), period of day during which a species foraged actively (3 variables), foraging habitats (20 variables) and nesting habitats (18 variables). All variables except the body mass were binomial (scored as either 0 or 1). The Rao's Q of each point was calculated using the function "dbFD" from the "FD" package for R (Laliberté et al., 2015). Finally, (3) Phylogenetic diversity was calculated using two different variables: Faith's phylogenetic diversity (PD; for estimating richness) and phylogenetic species variability (PSV; for estimating divergence) for each community assemblage (Faith, 1992; Helmus et al., 2007). This was based on the recommendation of Tucker et al. (2017) highlighting the significance of integrating complementary information on the total evolutionary history (PD), and the similarity of species within the assemblages. The PD and PSV were estimated by building a phylogenetic tree of the species in each point count. This tree was based on genetic data from all bird species (Jetz et al., 2012) provided in "BirdTree" (www.birdtree.org) and obtained using the "ape" v5.6 package for R (Paradis et al., 2004). Both metrics were estimated (i.e., average values of PD and PSV) using the function "pd'"and "psv" from the "picante" v1.8.2 package for R (Kembel et al., 2010).

Statistical analyses

Given our inability to collect data in the savannah during the wet season due to security issues, we carried out separate analyses for the dry (rainforest and savannah) and wet seasons (only rainforest). All statistical analyses were conducted with R Version 1.4.1717 (R Core Team, 2022).

Before modeling the diversity metrics, we carried out a series of initial checks in our databases. First, we checked for spatial autocorrelation across sampling points by performing a Mantel test (Legendre & Fortin, 2010; Mantel, 1967) based on a matrix of the geographic distance of the point count stations, and a matrix of differences in BSR, Rao's Q, PD or PSV, and applied the Monte Carlo permutations with 9999 randomizations (Ibáñez-Álamo et al., 2020). Across the dry and wet seasons, there were no significant spatial autocorrelation issues with any estimated diversity metric (all p values > 0.18). Thus, we considered our point counts as statistically independent observations in subsequent analyses. Second, we checked for multicollinearity among the independent variables using the “vif.mer()” function of the “performance” package in R (Bernat-Ponce et al., 2021; Lüdeck et al., 2021), and tested the normality of the dependent variables (Shapiro & Wilk, 1965). During the dry season, built surface, grass cover and the number of pedestrians had high multicollinearity issues (Variance Inflation Factor > 10) in relation to all the diversity metrics, and were thus excluded from subsequent modeling. During the wet season, the interaction of habitat with water cover, built surface and the number of pedestrians (excepting with PSV) had high multicollinearity issues (Variance Inflation Factor > 10) in relation to all the diversity metrics, and were thus excluded from subsequent modeling. Furthermore, we added BSR as an additional predictor while modeling PD (Morelli et al., 2021) as they positively correlated (e.g., for dry season; r (398) = 0.95, p <0.001). Third, we standardized all independent numerical variables by using the “scale” function and “optimx” package for scaling and centering (Morelli et al., 2021; Nash, 2017; Revelle, 2022).

We then used Generalized Linear Mixed Models (GLMMs) to determine variations in bird taxonomic (BSR), functional (Rao’s Q) and phylogenetic (PD and PSV) diversity in relation to vegetation zones (rainforest vs savannah), habitat types (urban vs non-urban), coverage of canopy, bush, water, and the number of pedestrians, modeled as predictors. The potential interactive effects of habitat types with other independent variables were tested by the corresponding two-way interactions. City (n = 8) was included as a random factor to account for possible consistent differences among them. We then used a stepwise backward selection method to simplify the models (Crawley, 2013; Marhuenda et al., 2014). Thus, variables with the highest p values were first removed, and the procedure repeated until the best model (containing significant effects) was selected as the one with the lowest Akaike Information Criterion value (Burnham, & Anderson, 2002). We set statistical significance at p value < 0.05, and calculated generalized R2 with the “rsq” package (v. 2.5) as a measure of model fit (Kong et al., 2022; Overs et al., 2023; Zhang, 2022). All candidate models for BSR as the response variable were fitted with Poisson distribution using the “glmer” function of the “lme4” package in R after having explored their distribution (Bates et al., 2015; Shapiro & Wilk, 1965). The models of functional and phylogenetic diversity were fitted using a Gaussian distribution (using the “lmer” function included in the lme4 R package) based on the same initial exploration. Further, we performed Tukey post-hoc tests for pairwise comparisons of the diversity metrics between urban and non-urban habitats using the package “emmeans” (Manley et al., 2015; Yvoz et al., 2020).

Results

We recorded a total of 8,738 birds of 237 species across the eight paired urban and non-urban habitats and seasons (dry season = 400-point counts and wet season = 200-point counts) throughout the surveys (Table 1; see Table S1 for the list of bird species and their functional traits). Of the eight studied cities, Jos recorded the highest number of bird species in the urban habitat during the dry season, while Ibadan registered the highest number of bird species during the wet season (Table 1).

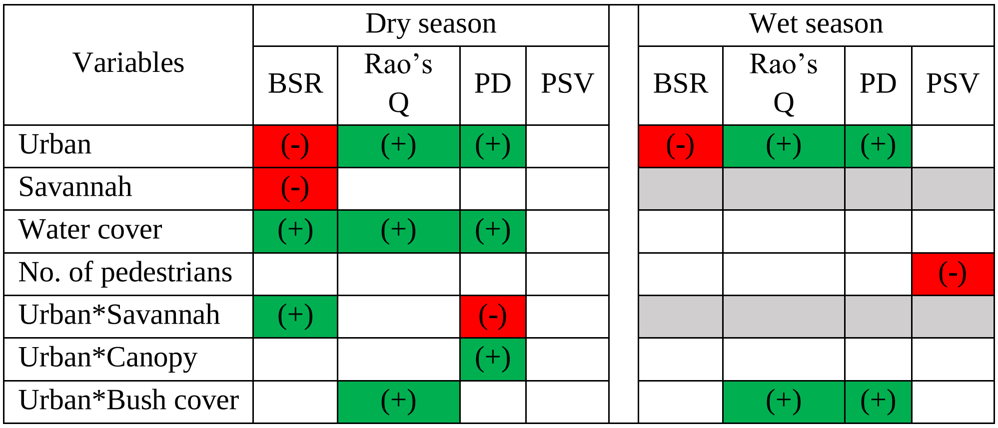
Table 1: Variation in bird species richness recorded across cities, seasons, and habitats in Nigeria, November 2020—September 2021. Note: Wet season surveys were conducted only in the four rainforest sites due to security issues in the savannah sites. The size of each city was obtained from Google Earth (accessed October 2020).

		Dry season		**Wet season**	
City	Size km^2	Urban	Non-urban	Urban	Non-urban
Auchi	35	20	66	21	80
Calabar	406	17	45	17	52
Ibadan	3,080	24	80	30	73
Lagos	1171	16	56	16	41
Birnin Kebbi	35	20	32		
Dutse	45	24	48		
Gombe	90	23	26		
Jos	260	31	49		
Mean	640.25	21.875	50.25	21	61.5
Standard Deviation	1,057.17	4.76	17.41	6.38	18.12

The urban habitat was dominated by laughing dove (*Streptopelia senegalensis*; present in 41 % of all urban point counts studied), common bulbul (*Pycnonotus barbatus*; 32 %), speckled pigeon (*Columba guinea*; 28 %), yellow-billed kite (*Milvus aegyptius*; 25 %) and red-eyed dove (*Streptopelia semitorquata*; 20 %). Meanwhile, common bulbul (39 %), green-backed camaroptera (*Camaroptera brachyura*; 25 %), vinaceous dove (*Streptopelia vinacea*; 23 %), green crombec (*Sylvietta virens*; 23 %), and little greenbul (*Andropadus virens*; 16 %) were the most commonly recorded species in the adjacent non-urban habitat. We found that 65 % (n = 154) of all species recorded were never encountered in urban areas (e.g., cassin's hawk-eagle *Aquila africana*, black-shouldered nightjar *Caprimulgus nigriscapularis*, ahanta francolin *Francolinus ahantensis*, oriole warbler *Hypergerus atriceps*, and chestnut wattle-eye *Platysteira castanea*).

Avian biodiversity during the dry season

We found significant interaction effects of habitat (urban *vs* non-urban), vegetation zone (rainforest *vs* savannah), and site-level indices on BSR, Rao's Q, PD, and PSV (Fig. 2; Table S2). Specifically, BSR was significantly lower in the urban than non-urban habitat across vegetation zones (habitat × vegetation zone interaction: Estimate ± SE = 0.44 ± 0.10, Z = 4.55, $p < 0.001$), although more intensely in the rainforest than the savannah (Fig. 3a). We also found significant differences between rainforest and savannah for non-urban areas (higher BSR in the former) but not for urban habitats (Fig. 3a). In general, the higher Rao's Q values in the urban than non-urban habitat (Table S2) were not significantly different across the vegetation zones (habitat × vegetation zone interaction: Estimate ± SE = -0.07 ± 8.34, t = -0.008, p = 0.99; Fig. 3b). Meanwhile, PD revealed contrasting results as this metric was significantly higher in the urban than non-urban habitat only in the rainforest (habitat × vegetation zone interaction: Estimate ± SE = -34.72 ± 12.45, t = -2.79, p = 0.006; Fig. 3c; Table S2). In contrast, we found no significant differences between urban and non-urban habitats for PSV (Estimate ± SE = 0.002 ± 0.002, t = 1.16, p = 0.25; Fig. 3d).



Variables	Dry season				Wet season			
	BSR	Rao's Q	PD	PSV	BSR	Rao's Q	PD	PSV
Urban	(-)	(+)	(+)		(-)	(+)	(+)	
Savannah	(-)				▨	▨	▨	▨
Water cover	(+)	(+)	(+)					
No. of pedestrians								(-)
Urban*Savannah	(+)		(-)		▨	▨	▨	▨
Urban*Canopy			(+)					
Urban*Bush cover		(+)				(+)	(+)	

Figure 2: Schematic presentation of main associations (from final models) between values of taxonomic diversity (estimated from bird species richness), functional diversity (estimated from Rao's Quadratic Entropy), phylogenetic diversity (estimated from Faith's Phylogenetic Diversity and phylogenetic species variability) calculated for avian communities across habitats (urban and non-urban) and seasons (dry and wet) in Nigeria, and different characteristics of the sites. Positive significant associations are indicated in green (+), while negative ones are highlighted in red (-). The grey color indicates untested associations because of our inability to

collect data in the savannah during the wet season due to important security issues in the area. These results were simplified to reflect only significant variables from the final models shown in detail in Tables S2-S3.

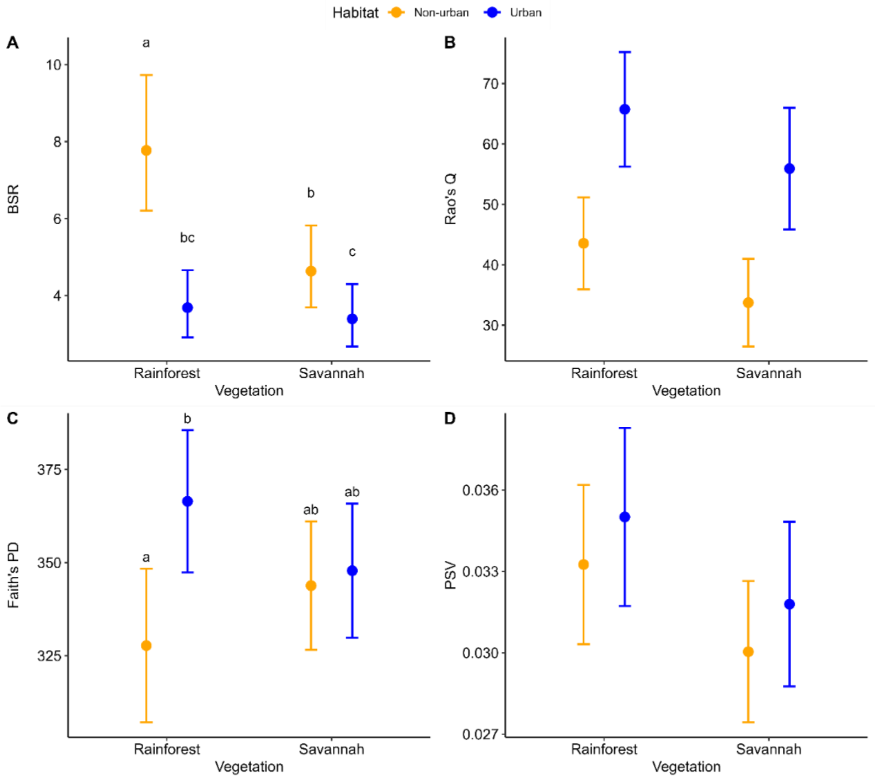


Figure 3: Mean ± 95% Confidence Interval across vegetation zones (rainforest *vs* savannah) and habitats (urban *vs* non-urban) for four avian diversity components estimated from across eight Nigerian cities during the dry season: (A) taxonomic diversity (bird species richness, BSR); (B) functional diversity (Rao's Q); (C) phylogenetic diversity (Faith's PD) and phylogenetic divergence (PSV). Significant associations ($P < 0.01$) are indicated with asterisks. For those diversity variables showing significant differences for the interaction habitat x vegetation zone (BSR and PD), different letters indicate significant differences according to Tukey post-hoc tests using the package "emmeans". The plots are based on model predictions.

Our results also show contrasting effects of local influential predictors (Fig. 2; Table S2). With the exception of PSV (Estimate ± SE = 1.12 ± 6.58, $t = 1.707$, $p < 0.089$; Fig. 2), water cover was in general, significantly (positively) associated with all the diversity metrics during the dry season (BSR: Estimate ± SE = 0.05 ± 0.02, Z = 2.139, p = 0.032; Rao's Q: Estimate ± SE = 4.70 ± 1.82, t = 2.58, p = 0.011; PD: Estimate ± SE = 5.99 ± 2.83, t = 2.12, p = 0.035; Fig. 2). On the contrary and also during this season, the number of pedestrians did not significantly influence PSV values as this variable was not retained in the final model (Table S2). PSV was the only diversity metric for which we could test this predictor during the dry season as it was excluded from the others due to multicollinearity issues. Furthermore, we found that habitat (i.e., urbanization) mediated the effect of some local variables during this season (Fig. 2). In this respect, bush cover significantly promoted Rao's Q (Estimate ± SE = 27.12 ± 6.85, t = 3.96, p < 0.001; Fig. 4a) while canopy cover did the same for PD values (Estimate ± SE = 21.23 ± 10.02, t = 2.12, p = 0.035; Fig. 4b) in urban habitats compared to more natural habitats.

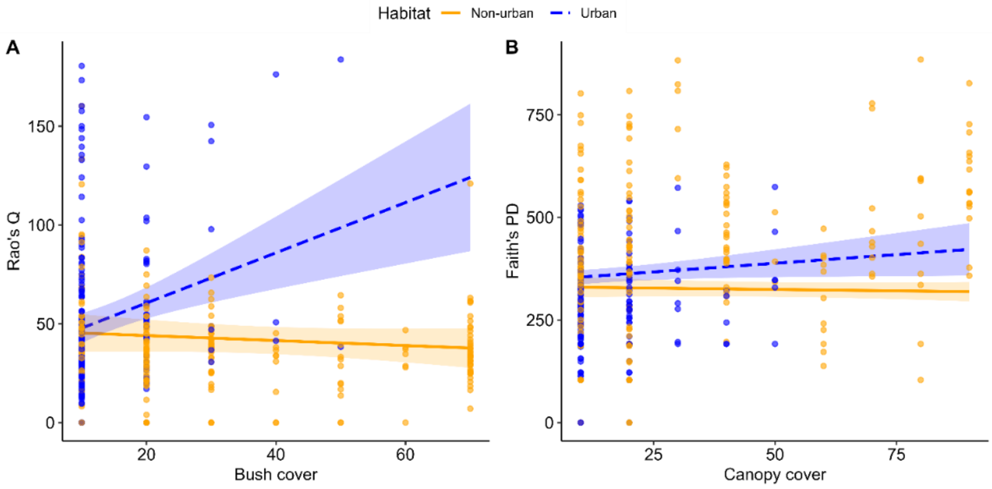


Figure 4: (A) The effect of bush cover by habitat (urban *vs* non-urban) on functional diversity (Rao's Q) during the dry season, and (B) the effect of canopy cover by habitat (urban *vs* non-urban) on phylogenetic diversity (Faith's PD) during the dry season. The plots are based on model predictions.

Avian biodiversity during the wet season

BSR was significantly higher in the non-urban than urban habitat (Estimate ± SE = -0.65 ± 0.11, Z = -6.14, p < 0.001; Table S3; Fig. 5a). This contrasts with the results of Rao's Q (Estimate ± SE = 26.13 ± 7.85, t = 3.33, p = 0.001; Table S3; Fig. 5b) and PD (Estimate ± SE = 50.24 ± 12.85, t = 3.91, p < 0.001; Table S3; Fig. 5c) that were significantly higher in the urban than non-urban habitat. We found no significant differences for PSV during this season (Estimate ± SE = 3.96 ± 2.85, t = 1.39, p = 0.17; Table S3; Fig. 5d).

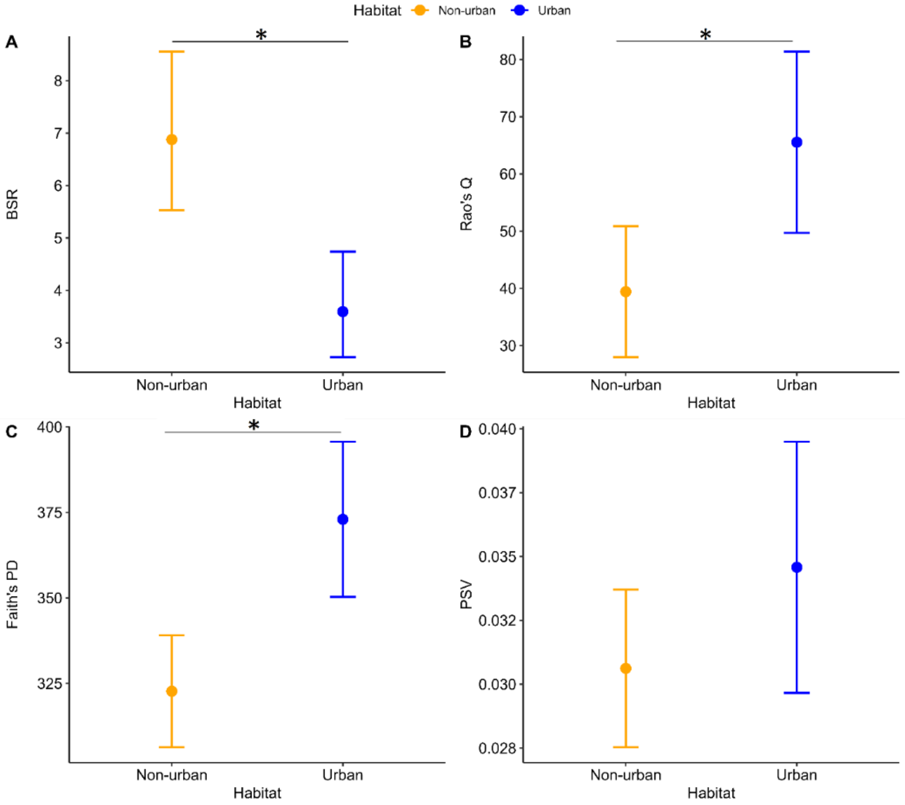


Figure 5: Mean ± 95% Confidence Interval for four avian diversity components estimated from across four Nigerian cities during the wet season: (A) taxonomic diversity (bird species richness, BSR); (B) functional diversity (Rao's Q); (C) phylogenetic diversity (Faith's PD); and (D) phylogenetic divergence (PSV). Significant associations ($P < 0.01$) are indicated with asterisks. The plots are based on model predictions.

Complementing our results for the dry season, the number of pedestrians significantly reduced PSV values during the wet season (Estimate ± SE = -2.28 ± 9.47, t = -2.411, p = 0.018). In this same context, habitat (i.e., urbanization) mediated the effect of only bush cover among local variables, significantly promoting Rao's Q (Estimate ± SE = 21.84 ± 10.12, t = 2.16, p = 0.032; Fig. 6a), and PD (Estimate ± SE = 40.44 ± 15.23, T = 2.655, p = 0.009; Fig. 6b) compared with non-urban habitats. No additional predictor significantly influenced avian diversity indices for the wet season (Table S3).

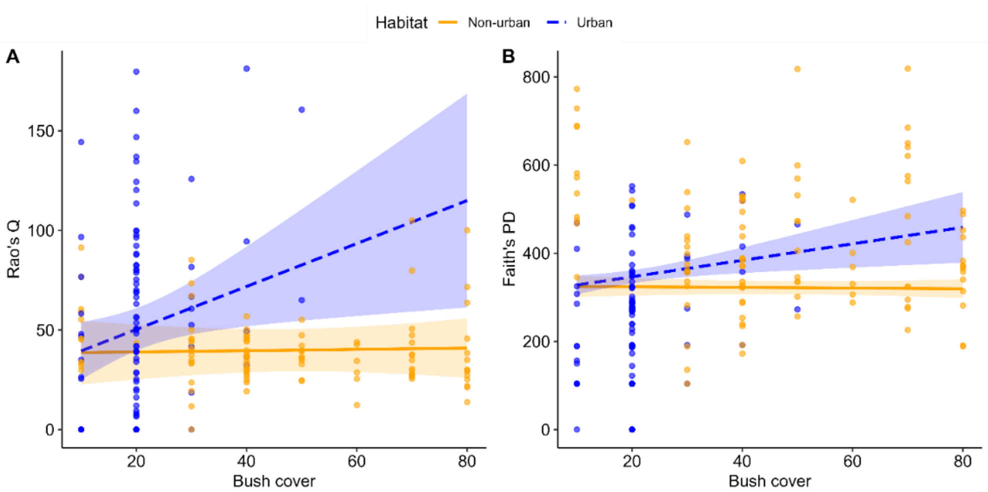


Figure 6: (A) The effect of bush cover by habitat (urban *vs* non-urban) on functional diversity (Rao's Q) during the wet season, and (B) the effect of bush cover by habitat (urban *vs* non-urban) on phylogenetic diversity (Faith's PD) during the wet season. The plots are based on model predictions.

Discussion

Our study showed that urbanization has a complex and multifaceted effect on avian diversity. This is because not all biodiversity components were similarly affected by this human-induced landscape change. This finding matches previous studies from other regions of the world (Devictor et al., 2010; Morelli et al., 2017), and suggests the need for the simultaneous study of multiple diversity components.

Variations in avian diversity across urbanization, seasons, and vegetation zones

We found that urbanization severely reduced avian taxonomic diversity, with the urban habitat supporting less than half the number of bird species recorded in the adjacent non-urban habitat. This is consistent with previous findings from other regions of the world, and based on other Afrotropical (e.g., Chamberlain et al., 2017) and Pantropical studies (e.g., Alexandrino et al., 2022). In addition, the similar numbers of bird species we recorded across the surveyed cities may have been due to their habitat similarities. Several authors (e.g., Clergeau et al., 2001; McKinney, 2006; Savard et al., 2000) have argued that human activities produce similar ecological structures, functions, and constraints that affect the associated biodiversity in urban areas worldwide (i.e., biotic homogenization).

Our results revealed that rainforest birds seem to be more affected by urbanization than their savannah counterparts. Urban habitats in the rainforest hold a much smaller proportion of their corresponding non-urban habitats than the urban vs. non-urban savannah comparison. This finding is critical for conservation prioritization. Although the rainforest is more productive than the savannah (Brown et al., 1982; Ezealor, 2001), it also concentrates a larger proportion of urban development in the area (OECD/SWAC, 2020; Seto et al., 2012). The rainforest sites investigated in our study are part of the “Western African Forests”, one of the 25 global biodiversity hotspots (Myers et al., 2000), highlighting the relevance of potential ecological alteration in this region. The extent of primary vegetation of the Western African Forests has been reduced to approximately 10% of its original size (1,265,000 km2), and urbanization is a leading threat in the area (Myers et al., 2000; OECD/SWAC, 2020; Seto et al., 2012). If the current urban expansion continues unabated, a greater number of bird species could be threatened.

Furthermore, the consistently lower taxonomic diversity we recorded in the urban than in the non-urban site during both the dry and wet seasons corroborates previous studies revealing that anthropogenic features (e.g., built surface, human density) rather than non-anthropogenic factors (e.g., climate, geography) are better predictors of the loss of taxonomic diversity in urban habitats (e.g., Aronson et al., 2014). However, this does not imply that future urban studies should not consider other variations as we found that they could be important in tropical regions (e.g., different reduction in BSR associated with urbanization between vegetation zones). Studies investigating taxonomic diversity of birds in urban areas have been previously conducted in Africa (Adegbola et al., 2024; Afrifa et al., 2022; Aouissi et al., 2017; Njoroge et al., 2014), but those comparing taxonomic diversity between urban and non-urban habitats are still scarce (Chamberlain et al., 2019; Lee et al., 2021). Thus, our study provides much-needed information to fill this important knowledge gap.

In general, functional diversity was higher in the urban than non-urban habitat independently of vegetation zone or season. Urban areas could offer more ecological niches than non-urban areas (Lokatis & Jeschke, 2022; Palacio, 2020), which could explain our findings as additional niches could enhance avian FD (Petchey & Gaston, 2002). For instance, the non-urban sites of the rainforest visited for this study comprised mainly of forest vegetation compared with the urban sites that included a mosaic of habitats, including parks, gardens, cemeteries, sanitary landfills, residential areas, and offices. Our result showing a higher phylogenetic diversity in urban than non-urban habitat supports this position. For instance, generalist birds (e.g., urban exploiters) capable of exploiting diverse habitat niches are more abundant in urban than non-urban areas that supports more specialist birds (Lee et al., 2021). Thus, this study pinpoints the need for additional studies investigating the specific urban attributes promoting avian functional diversity in the region.

The lower PD found in the non-urban than the urban habitat of the rainforest implies an increase in evolutionary richness due to urbanization. This result did not meet our expectations, particularly given the higher levels of taxonomic diversity (BSR) we recorded in the non-urban habitat independently of season. However, higher levels of BSR may not directly translate into higher PD for birds if the different species that dominate the community share similar evolutionary relationships (i.e., closely related species), leading to phylogenetic redundancy, a pattern found by other urban studies (e.g., Sanllorente et al., 2023). This is clearly represented with the example of the family Lybiidae for which we found six species in the non-urban habitat (*Lubius leucocephalus, Lybius vieilloti, Pogoniulus bilineatus, Pogoniulus chrysoconus, Pogoniulus scolopaceus*, and *Pogoniulus subsulphureus*), of which only two were registered in the urban habitat (*P. bilineatus* and *P. chrysoconus*). Additionally, some urban features (e.g., buildings, vehicles or pedestrians) could provide opportunities for some evolutionarily unique groups of species to colonize urban environments. In this sense, our study revealed nine distantly related species that could have boosted PD values in the urban habitat (*Accipiter badius, Apus affinis, Colius striatus, Euplectus hordeaceus, Falco alopex, Hirundo fuligula, Lagonosticta larvata*, *Necrosyrtes monachus*, and *Phoeniculus purpureus*), which were never recorded in the non-urban habitat during our survey. Meanwhile, the lack of significant differences in PD values between urban and non-urban habitats in the savannah contrasts with those obtained for the rainforest (dry season) and reinforces the importance of considering the vegetation zone in this kind of studies.

The results of our PSV indicated that urban birds in Nigeria are no more closely related to each other than non-urban birds independently of the vegetation zone. This finding contradicts those obtained by Morelli et al. (2021), highlighting the relevance of our study that focused on the understudied Afrotropics.

Effects of local influential features on avian diversity across urbanization, seasons, and vegetation zones

During the dry season, water cover was the crucial local variable promoting all the diversity metrics considered across habitats and vegetation zones. The positive associations we found between water cover and the three biodiversity metrics during this season could be due to enhanced availability of the diverse resources linked to water. For instance, water availability could attract bird species (e.g., waterbirds) seeking access to this restricted resource during the dry season. This is plausible given that this effect was lost during the wet season, when water or associated resources (e.g., seeds, flowers, leaves) were more readily available in Afrotropical environments. In addition, food becomes scarcer in Afrotropical environments during dry weather conditions (Siegfried, 1972; Sinclair, 1978), and water availability could ameliorate this situation.

Bush cover in the urban habitat significantly enhanced both functional (dry and wet seasons) and phylogenetic diversity (wet season) compared with more natural habitats. This contrast between habitats highlights the importance of bushes in Afrotropical cities, providing a clear conservation action that city planners and urban conservationists could implement. In fact, Clergeau et al. (2006) found that the functional group of bush-dwelling birds significantly decreased with increasing urbanization, further supporting our recommendation in this respect. Bushes in cities could provide additional nesting and feeding opportunities (e.g., Daniels & Kirkpatrick, 2006; Grant et al., 2006) that could also partially explain the observed positive association between urbanization and bird functional diversity found in this study. In addition, we could speculate that the species attracted by bushes are of different evolutionary lineages (e.g., *Corvus albus, Passer griseus*), which could explain the increase in phylogenetic richness during the wet season.

Similar to urban bush cover, tree canopy in Afrotropical cities could attract canopy-loving species from distantly related evolutionary lineages (e.g., *Poicephalus senegalus or Necrosyrtes monachus*), consequently explaining its positive association with the phylogenetic richness obtained during the dry season. Parrots and other species could look for feeding resources in the urban canopy as the dry season corresponds with the peak of fruiting in the region (Brugiere et al., 1999; Polansky & Boesch, 2013). In addition, urbanization selects against ground nesters (Croci et al., 2008; Jokimäki & Huhta, 2000), but urban trees could act as safe nest sites for other groups of birds. For example, during data collection, we observed some critically endangered hooded vultures *Nerosyrtes monachus* nesting at an urban park in Lagos. Hooded vultures are persecuted and traded for traditional belief-based practices (Williams et al., 2021), and urban sites could be a haven for this and related species due to relatively low perceived predation pressure. This adaptation to urban life has also been found in European birds (Møller, 2008).

Surprisingly, the number of pedestrians was not significantly associated with BSR, Rao's Q or PD (for those models incorporating the variable; see Tables S2 and S3). Studies conducted in other regions of the world, such as Europe or South America, have shown that increasing the number of pedestrians has negative impacts on bird taxonomic and functional diversity (Curzel et al., 2021; Ibáñez-Álamo et al., 2020; Sanllorente et al., 2023). This contradictory finding could be explained by the fact that birds from our study area deal better with humans. It could also suggest that other aspects beyond human activities (e.g., landscape organization) play a more important role for Afrotropical birds. Supporting these positions, our wet season result revealed that the number of pedestrians rather significantly decreased phylogenetic relatedness (i.e., PSV) independently of habitat. Thus, bird communities with more pedestrians seem to hold less closely related species as the fear of humans could exert a filtering effect on certain species (Braimoh et al., 2018).

Conclusions and recommendations

This study revealed that Nigerian urban areas hold a significantly lower richness in bird species compared with non-urban ones. This effect is more severe in the rainforest than in the savannah, highlighting the vulnerability of birds in this vegetation zone to the urbanization process. We also found contrasting results among biodiversity components, suggesting the need to investigate urban effects beyond BSR (see also Ibáñez-Álamo et al., 2020; Morelli et al., 2021). Despite our limitations, our findings indicate between-season consistency in the associations between urbanization and these different biodiversity indices.

Our study highlights the need to minimize the impacts of urbanization on biodiversity and recommends the following: (1) Replication of our study in other Afrotropical or even tropical areas to test the generality of our findings; (2) The need for city planners to integrate a combination of features that could promote biodiversity-friendly cities. In this context, our study showed that the integration of a mosaic of water bodies, bushes, and trees could boost avian diversity in Afrotropical urban centers, particularly during the dry season; (3) The use of alternatives for field-based predictors of avian diversity. A recent review on African urban ecology (Awoyemi & Ibáñez-Álamo, 2023) recommends the use of remotely sensed vegetation variables (e.g., Normalized Difference Vegetation Index) to overcome accessibility issues. We hope that our study and recommendations will promote sustainable urban development in the Afrotropics.

Supporting Materials

Supplementary data to this article can be found online:
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Chapter 3

Remotely sensed spectral indicators of bird taxonomic, functional and phylogenetic diversity across Afrotropical urban and non-urban habitats

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Abstract

Urban areas are quickly expanding around the world, promoting deep changes in biodiversity. However, certain biogeographic realms, like the Afrotropics, are clearly understudied despite urbanization overlapping with their biodiversity hotspots. A commonly highlighted reason for the lack of information from the Afrotropics has been the logistical problem associated with data collection in the field. Recent advances in satellite remote sensing imagery offer an excellent opportunity to revert this situation, enhancing the understanding of urban impacts on biodiversity. NDVI is the most commonly used remotely sensed spectral index (hereafter: indicator) despite several studies showing its limitations and advocating for the use of alternative indicators. Thus, this study identifies the best indicators of bird taxonomic, functional, and phylogenetic diversity in Afrotropical urban and non-urban areas. To do so, we sampled birds at 400 points equally distributed across eight Nigerian areas, two vegetation zones (rainforest vs savannah), and two habitats (urban vs non-urban), and extracted 29 indicators (mean and SD) at 50-m radius of each point (exact area of bird censuses). Random Forest Regressions and Generalized Linear Mixed Effect Models were used to identify the topmost ranked indicator of each avian diversity component, and its variation between urban and non-urban areas. MCARI was the best indicator of taxonomic and phylogenetic diversity, while NDWI2 and SATVI got the most support for functional diversity and phylogenetic divergence, respectively. In most cases, NDVI ranks very low (occupying the 25th percentile), not supporting its use for monitoring avian diversity in the Afrotropics. MCARI and NDWI2 showed different associations with taxonomic and functional diversity depending on the habitat, highlighting the need for considering urban areas differently while using these indicators. Our study provides useful tools to remotely monitor Afrotropical avian diversity, particularly in expansive, inaccessible or insecure areas, which could also be more cost-effective.

Introduction

Urbanization is a highly ranked human-driven landscape change exerting negative impacts on biodiversity worldwide (Angel et al., 2011; McKinney, 2006; Seto et al., 2012). Coincidentally, this human pressure is expanding more in low-medium income countries of the Global South often characterized with biodiversity hotspots (Mcdonald et al., 2008; OECD/SWAC, 2020). This overlap, together with an inadequate research capacity (Awoyemi & Ibáñez-Álamo, 2023; Beale, 2018), highlight the urgent need for an efficient monitoring technique that could provide data necessary to safeguard the dwindling biodiversity of the area (Garzon-Lopez et al., 2024; Schmeller et al., 2017). However, multiple studies conducted in the region have subjectively estimated different urban and vegetation characteristics (e.g., impervious surfaces, water, soil, vegetation and water; hereafter: field-based environmental measures) to examine their effects on the associated biodiversity (e.g., Chamberlain et al., 2017; John & Kagembe, 2022). Despite the relevance of this traditional methodological approach, such a field-based estimation is often laborious, expensive and prone to investigators' errors (Ghosh et al., 1995; Gorrod & Keith, 2009; Morrison, 2016). This is even more challenging when surveys involve repeated coverage of large, inaccessible or insecure sites (Casagli et al., 2017; Negash et al., 2023). Thus, harnessing innovative techniques that could provide such information more accurately and at different scales, with minimal costs and time, could enhance biodiversity monitoring and management across different habitats (Benton et al., 2003).

Recent advances in satellite remote sensing imagery with growing resolution and quality have enhanced the capacity to monitor biological diversity and global environmental changes (Pettorelli et al., 2014; Xue & Su, 2017). The multispectral indices extracted from such imagery provide key site-level measures of primary productivity and seasonal variations (e.g., Ghorbani et al., 2020; Harris & Dash, 2011; Peng et al., 2008). This understanding is useful to predict species diversity and distribution across a wide range of habitats (Alabi et al., 2022; Benedetti et al., 2023; Gaitán et al., 2013; Ghorbani et al., 2020). Among multispectral indices, the Normalized Difference Vegetation Index (NDVI) is still the most frequently used index to obtain vegetation information as a proxy for primary productivity (He et al., 2015; Xu et al., 2022). NDVI exploits the red and near-infrared bands of the electromagnetic spectrum, ensuring that the extracted spectral variability is mainly due to vegetation characteristics (Viña et al., 2011). It is, therefore, hardly surprising that most studies find a positive association between NDVI and species diversity (see (Madonsela et al., 2017). However, NDVI shows scaling problems, saturates in areas of high biomass (Gitelson, 2004; Huete et al., 2002; Main et al., 2011), and is affected by soil brightness that lowers its sensitivity to vegetation (Huete & Jackson, 1988). These factors justify the need to incorporate other spectral indicators that have a more comprehensive range for modeling species attributes (Alabi et al., 2022; Benedetti et al., 2023; Gaitán et al., 2013; Ghorbani et al., 2020). This is crucial, particularly in heterogeneous habitats that offer diverse niches/resources such as urban areas (Cramer & Willig, 2005; Hamm & Drossel, 2017; Pianka, 1966). For example, studies testing the relationships between field-based environmental measures and urban biodiversity show that impervious surfaces and soil can exert differing effects on the various components of animal diversity (e.g., Ibáñez-Álamo et al., 2020; Morelli et al., 2021). This indicates that NDVI alone may not be adequate for the estimation of different biodiversity components (i.e., taxonomic, functional and phylogenetic). This information suggests the need to incorporate additional spectral indicators with the potential to overcome the limitations of NDVI (Benedetti et al., 2023). This approach has been deployed in various plant-based studies. For instance, multispectral indices have been used to investigate primary productivity (Ghorbani et al., 2020), ecosystem structure and functioning (Gaitán et al., 2013), and grain yield (Alabi et al., 2022). However, the use of multispectral indices to predict animal biodiversity metrics is still scanty (e.g., Bae et al., 2018; Benedetti et al., 2023).

Thus, this study investigates the relationships between remotely sensed spectral indices and bird taxonomic, functional and phylogenetic diversity using data collected from eight paired locations in Nigeria (each including urban and non-urban study sites) and from two vegetation zones (i.e., rainforest vs savannah). This biodiversity-rich

Afrotropical country is among the most impacted by expanding urbanization at the global level (Awoyemi & Ibáñez-Álamo, 2023; Ezealor, 2001; Seto et al., 2012), suggesting the need for an efficient monitoring system to support conservation decisions. Twenty-nine spectral indices (Figure S1) with the potential to capture the positive and negative site features (field-based environmental measures) affecting different components of avian diversity across urban and non-urban habitats (e.g., Chamberlain et al., 2017; Ibáñez-Álamo et al., 2020; Morelli et al., 2021) were extracted for this study (see Alabi et al., 2022; Benedetti et al., 2023; Ghorbani et al., 2020). This was followed by multistage statistical analyses aimed at investigating the efficient spectral indices that could aid biodiversity monitoring and management given the economic, security and manpower restrictions of the area (Awoyemi & Ibáñez-Álamo, 2023; Garzon-Lopez et al., 2024; Schmeller et al., 2017). The reasons for incorporating multiple spectral indices are threefold. (1) To unravel their suitability for modeling biodiversity metrics across different habitats. This is particularly important given that previous studies have shown strong variations in the effect of field-based environmental measures on bird taxonomic, functional and phylogenetic diversity across urban and non-urban habitats (e.g., Chamberlain et al., 2017; Hagen et al., 2017; Ibáñez-Álamo et al., 2020). (2) To identify alternative spectral indices that could complement NDVI by overcoming its limitations, particularly in urban habitats, where soil and impervious surfaces are pronounced (e.g., (Murgui & Hedblom, 2017). (3) To provide baseline data that could be useful to remotely monitor avian diversity in the Afrotropics. This study focused on birds because they are relatively well-studied across urban and non-urban habitats (Gil & Brumm, 2013; Murgui & Hedblom, 2017). Birds also have a well-validated phylogeny (e.g., Jetz et al., 2012), and experience community changes across seasons and vegetation zones (e.g., Brown et al., 1982; Ezealor, 2001; Hagen et al., 2017; Ibáñez-Álamo et al., 2020; Morelli et al., 2021). Thus, it can provide an important step toward a better and more efficient monitoring system for avian diversity in Afrotropical environments.

Materials and methods

Study area

Data were collected in eight paired urban and non-urban sites equally distributed across the rainforest (Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos) vegetation zones in Nigeria (Fig. 1). The rainforest zone is characterized by dense evergreen forests of tall trees with thick undergrowth, and receives a mean annual rainfall of c. 2000 mm/annum (e.g., Ezealor, 2001) Ezealor, 2001) occurring mainly from April to September level. The savannah is, however, dominated by grasses interspersed by small-medium sized trees and receives an annual rainfall of 600-1200 mm/annum (e.g., Ezealor, 2001), occurring mainly between July and September.

To be considered an urban center, each of the studied cities had a contiguous patch of built-up land greater than 1 km2 and dominated by human-constructed features like buildings (>10 buildings/ha), high human density (>1600 inhabitants/km2), roads, and vehicles (Marzluff et al., 2001; Niemelä, 1999; Nilon et al., 2003; Schneider et al., 2010). In contrast, the adjacent non-urban habitats had extensive wilderness/vegetation cover interspersed with agricultural matrix and sparsely settled villages (MacGregor-Fors, 2011; Marzluff et al., 2001). Following Liker et al. (2008), each urban site was at least 20 km from its paired non-urban site to grant the independence of the bird communities.

Site selection and bird enumeration

Each study site (i.e., urban or non-urban site per city) was stratified into five areas positioned at the center and its four cardinal points (i.e., west, east, south and, north) to guarantee a widespread distribution of data that could be considered representative of the study area (Awoyemi et al. 2024; Ciski et al., 2019). Five random points were then selected from each area. The selection of the areas and points were done using the "create random points tool" in ArcGIS. Each point was marked with a GPS to ensure data collection was from the same location. Each point was separated from any other by at least 200 m to reduce the potential effects of pseudo-replication (Benedetti et al., 2023). During the dry season (November 2020-January 2021), data were collected from 50 points (i.e., 25 urban vs 25 non-urban) in each of the eight paired locations (Møller et al., 2012), totaling 400-point count stations across the two vegetation zones (i.e., 200 rainforest vs 200 savannah).

All birds seen and heard for 5 mins within the 50-m radius of each point were counted (Awoyemi et al., 2024; Sanllorente et al., 2023). These duration and range are ideal for enumerating the optimum number of birds during point count while minimizing potential effects of pseudo-replication (Bibby et al. 2000). The birds were counted in the mornings, up to 4 h after local sunrise (Manu et al. 2007), but only under favorable weather conditions estimated with a mobile electronic device that measured weather variables (e.g., temperature and relative humidity). To reduce detection issues related to identification, the birds were counted only by AGA, an expert ornithologist with > 10 years of experience surveying birds in the study area.

Avian diversity and community metrics

All statistical analyses were performed using the R statistical Package (R Core Team, 2024). In each sampling point (n = 400), three biodiversity metrics were calculated, including taxonomic, functional and phylogenetic diversity. The taxonomic diversity was quantified as the total number of bird species recorded (bird species richness: BSR) (Magurran, 2004). The Rao's Quadratic Entropy (Rao's Q) was used to estimate functional diversity as the abundance-weighted variance of the dissimilarities between all species pairs (de Bello et al., 2010). The Rao's Q was calculated using the avian niche traits related to their feeding and breeding ecology extracted from Pearman et al. (2014). The trait information of each recorded species was obtained from general bird compilations, including the Birds of Africa (Brown et al., 1982; Fry et al., 1988; Fry & Keith, 2000; Fry & Keith Stuart, 2004; Keith et al., 2014; Urban et al., 1986; Urban and Fry, 1997), Birds of the World (Pearson, 2020) and Handbook of Avian Body Mass (Dunning, 2007).

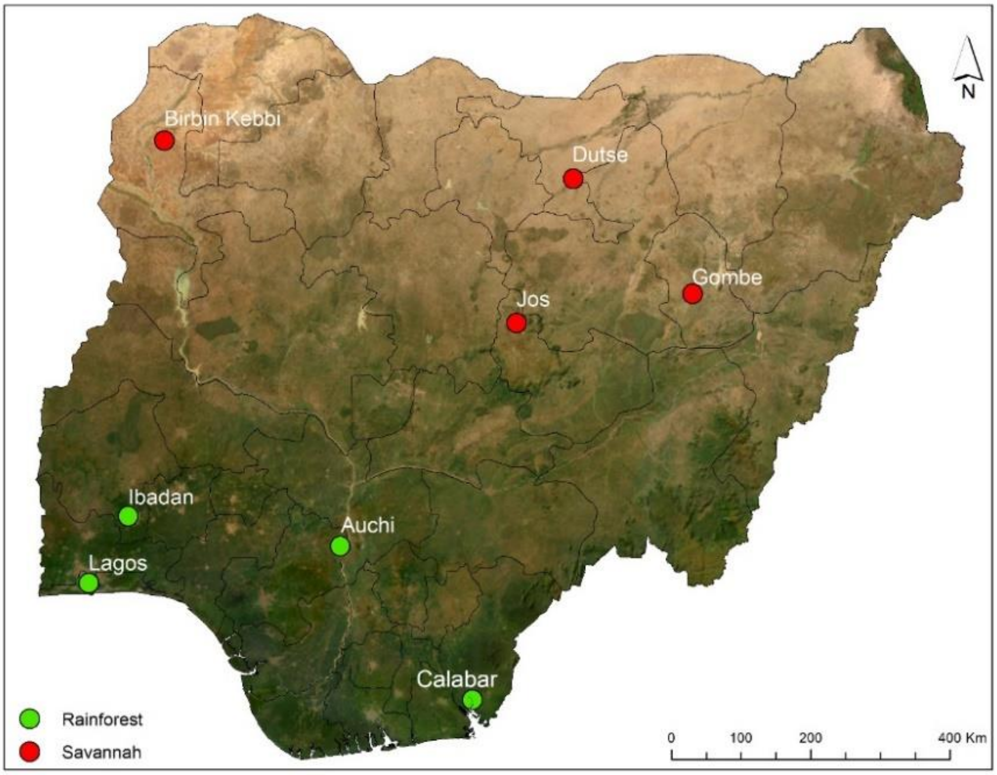


Figure 1: Distribution of study sites across the savannah and rainforest vegetation zones in Nigeria. At each city, data were collected in paired urban and non-urban sites.

A total of 73 traits were compiled (see Awoyemi, Barshep, et al., 2024)) for analyzing the Rao's Q of each point using the 'dbFD' function of the 'FD' package (Laliberté et al., 2015). Thirdly, phylogenetic diversity metrics (Faith, 1992; Helmus et al., 2007), including phylogenetic diversity richness (Faith's phylogenetic diversity; PD), and phylogenetic diversity divergence (phylogenetic species variability, PSV) were calculated given the need to incorporate complementary phylogenetic information of any community assemblage (Tucker et al., 2017). The PD and PSV were calculated by building 100 phylogenetic trees of the species in each point count station based on genetic data from all bird species (Jetz et al., 2012) available at 'BirdTree' (www.birdtree.org). We then obtained average values of PD and PSV using functions 'pd' and 'psv' of the 'picante' and 'ape' packages (Kembel et al., 2010; Paradis et al., 2004).

Extraction of multispectral indices

Cloudless Sentinel 2 Level 1C Images, covering the period of bird censuses (i.e., November 2020-January 2021), were downloaded from the USGS Earth Explorer (https://earthexplorer.usgs.gov/). The Sentinel 2 Level 1C is more applicable to this study given its relatively high resolution and the small coverage of data collection points (50-m radius) compared to large-scale studies (Petrosillo et al., 2022; Wang & Atkinson, 2018). These were first preprocessed using the Semi-automatic Classification Plugin within the QGIS to convert raw pixel values to reflectance values and to perform atmospheric correction using the Dark Object Subtraction Correction Technique. The Sentinel allowed us to obtain reflectance images at the 10-m spatial resolution used to derive spectral indices with 'spectralindices' function of the RStoolbox (Alabi et al., 2022; Avtar & Watanabe, 2020; Leutner et al., 2019). The mean and standard deviation of all available 10-m images/cells/pixels within the 50-m radius of each point count station were taken to estimate the spectral indices (See Figure S1 for a complete list and acronyms) following previous studies using a similar approach (Benedetti et al., 2023; Morelli et al., 2021). The 50-m radius buffer synchronizes with the exact area of bird censuses, which is commonly used in studies on urban avian diversity (e.g., Ibáñez-Álamo et al., 2020; Sanllorente et al., 2023).

Statistical analyses

Multistage statistical analyses were performed to select and model the most suitable remotely sensed spectral predictors of bird taxonomic, functional and phylogenetic diversity. For modeling, all the continuous variables (spectral indices) were scaled and centered with the 'scale' function of the 'optimx' package to ensure they are within the same range and improve the performance of the algorithm and models (Morelli et al., 2021; Nash, 2017). However, the graphs were plotted using the unscaled variables to infer the significant relationships between the dependent and independent variables similar to other previous studies (e.g., Sanllorente et al., 2023; Schielzeth, 2010). In addition, a Mantel test was performed to check for spatial autocorrelation across the point count stations based on a matrix of the geographic distance of the points and a matrix of differences in BSR, Rao's Q, PD and PSV using the Monte Carlo permutations with 9999 randomizations (Legendre & Fortin, 2010; Mantel, 1967). This test revealed no statistically significant spatial autocorrelation issues (all p values < 0.05), thus, allowing us to consider each point count station as independent observations in subsequent analyses (Dormann et al., 2007; Karlin et al., 1984).

Table 1: Topmost ranked spectral indices (mean and SD) with the best predictive power of bird taxonomic (BSR), functional (Rao's Q), phylogenetic diversity richness (PD) and phylogenetic divergence (PSV) across habitats (urban and non-urban) and vegetation zones (rainforest and savannah) in Nigeria. The full ranking of all the spectral indices is presented in Figure S1.

	Mean (50-m radius)						Standard Deviation (50-m radius)			
	BSR	Rao's Q	PD	PSV			BSR	Rao's Q	PD	PSV
MCARI	**1st**		**1st**			**MCARI**				
SR						**SR**	**1st**			
NDWI2		**1st**				**NDWI2**				
NBRI						**NBRI**		**1st**		
SATVI				**1st**		**SATVI**			**1st**	
CLG						**CLG**				**1st**

Thereafter, the spectral indices (mean and SD separately at 50-m radius) were ranked based on their potential to predict each avian diversity metric by carrying out a feature importance analysis using the "Boruta" package (Kursa & Rudnicki, 2010). The Boruta package is an advanced technique built upon the random forest regression model that removes statistically irrelevant variables and is one of the most accurate and robust feature selection methods (Degenhardt et al., 2019; Sanchez-Pinto et al., 2018; Speiser et al., 2019). This machine-learning algorithm constructs various independent decision trees for model fitting, and selects the model with the maximum votes for a specific class or value (Breiman, 2001). From each node, inputted variables are selected randomly, after which the subsets are used to calculate the best model output (Alabi et al., 2022; Herrero-Huerta et al., 2020).

The result of the random forest regression showing the ranking of the 29 spectral indices is presented in Figure S1. Regarding SD analysis, MTCI was rejected as a potential predictor of Rao's Q and PSV, MCARI and REIP were rejected because they were unable to potentially predict PSV. Although this reveals that the remaining spectral indices could be potentially useful in modeling the biodiversity metrics, they differ in their predictive power (Figure S1), and are highly correlated (i.e., VIF > 5) based on the multicollinearity test performed with the 'vif.mer ()' function of the 'performance' package (Bernat-Ponce et al., 2021; Lüdeck et al., 2021). Because of this multicollinearity issue, and to avoid overparameterization of models and enhance the interpretation of results (Baranyi et al., 1996; Marhuenda et al., 2014; Ortega-Álvarez et al., 2022; Seibert et al., 2019), only the topmost ranked spectral indices were incorporated in subsequent analyses based on their predictive power (Table 1).

Subsequently, Generalized Linear Mixed Models (GLMMs) were employed. BSR was included as the response variable modeled assuming Poisson distribution (using 'glmer' function from lme4 package), while the remaining response variables (i.e., Rao's Q, PD, and PSV) were modeled assuming Gaussian distribution based on the 'lmer' function of lme4 package (Bates et al., 2015). In addition, because BSR strongly correlates with PD (Tucker et al., 2017), BSR was included as a control independent variable while modeling this phylogenetic diversity metric following previous procedures (e.g. Morelli et al., 2021; Tucker et al., 2017)). City (n = 8) was included as a random factor to account for possible consistent differences among paired locations. Habitat (urban vs non-urban) and vegetation zone (rainforest vs savannah) were included as fixed factors, while the topmost spectral indices corresponding to each biodiversity metric (see Table 1) were modeled as predictors. However, the vegetation zone strongly correlated with the topmost ranked spectral indices in almost all cases (i.e., VIF > 10), and was therefore removed from the analysis based on the same reasons stated above. The two-way interaction between habitat and the corresponding spectral index was also incorporated in the models. Meanwhile, the Akaike Information Criterion value (Burnham & Anderson, 2002) and generalized R2 with the "rsq" package were calculated as a measure of model fit (Kong et al., 2022; Overs et al., 2023; Zhang, 2022).The Statistical significance was set at p value < 0.05. Finally, the magnitude of effect sizes (<0.2 = negligible, < 0.5 = small, < 0.8 = medium, otherwise = large) of all the variables retained in the final models (Cohen, 1992) were calculated. This incorporation of the magnitude of effect size statistics has been recommended in biological sciences as it enhances the assessment of the relationships within data than the sole use of p-values (e.g., Nakagawa & Cuthill, 2007). This approach has been applied in many biological and social sciences research (e.g., (Díaz et al., 2013; Jungmann & Witthöft, 2020; Strelan et al., 2020).

To determine the strength of the GLMMs, a 10-fold cross-validation was also performed with the "caret" package (Kuhn et al., 2023). This involved dividing the entire dataset into training and testing subsets using 70/30 proportions known to give the best result based on an evaluation of different machine learning techniques (Alabi et al., 2022; Nguyen et al., 2021). The Mean Absolute Error, Mean Squared Error, Root Mean Squared Error, Normalized Root Mean Squared Error, and R-squared (as squared Pearson's r) were computed (Table S1) to assess the quantitative performance of the GLMMs (Kuhn et al., 2023). The whole methodological procedure is summarized in Figure 2.

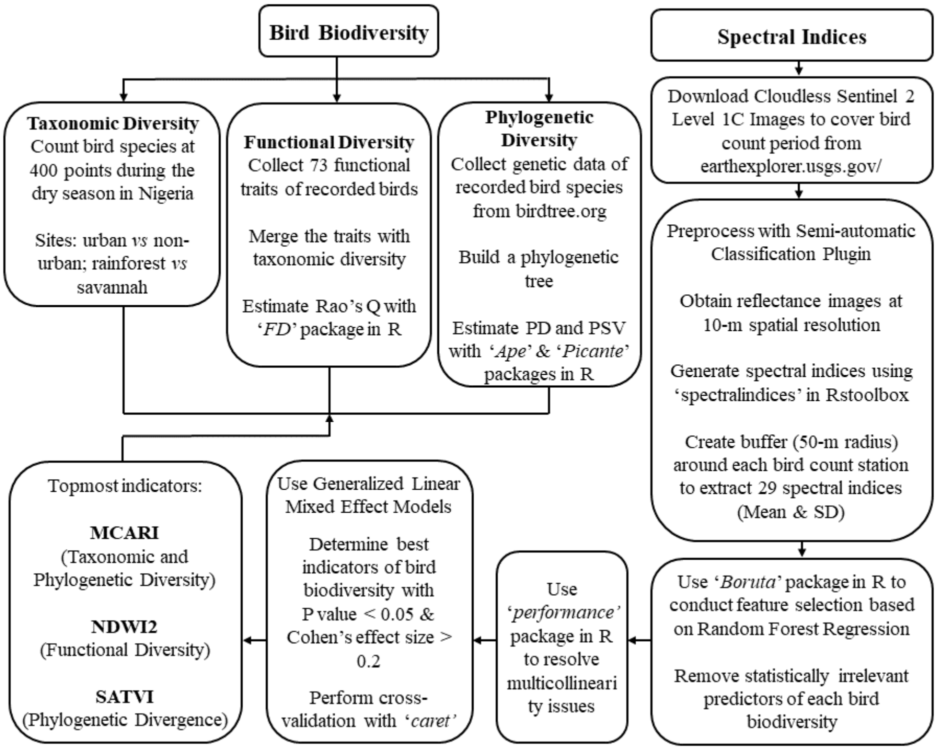


Figure 2: Flow diagram summarizing the study methodology.

Results

In this study, a total of 6,477 birds of 207 species were recorded from the 400-point count stations equally distributed across the study sites, habitats and vegetation zones in Nigeria. In general, more birds were recorded in the non-urban (50.3±17.4 SD) than the urban habitat (21.9±4.8 SD). The differences in the bird species richness recorded across the studied habitats and cities are presented in Table 2.

Table 2: Total bird species richness recorded across habitats (urban *vs* non-urban) in Nigeria, November 2020—January 2021. The size of each city was obtained from Google Earth (accessed October 2020).

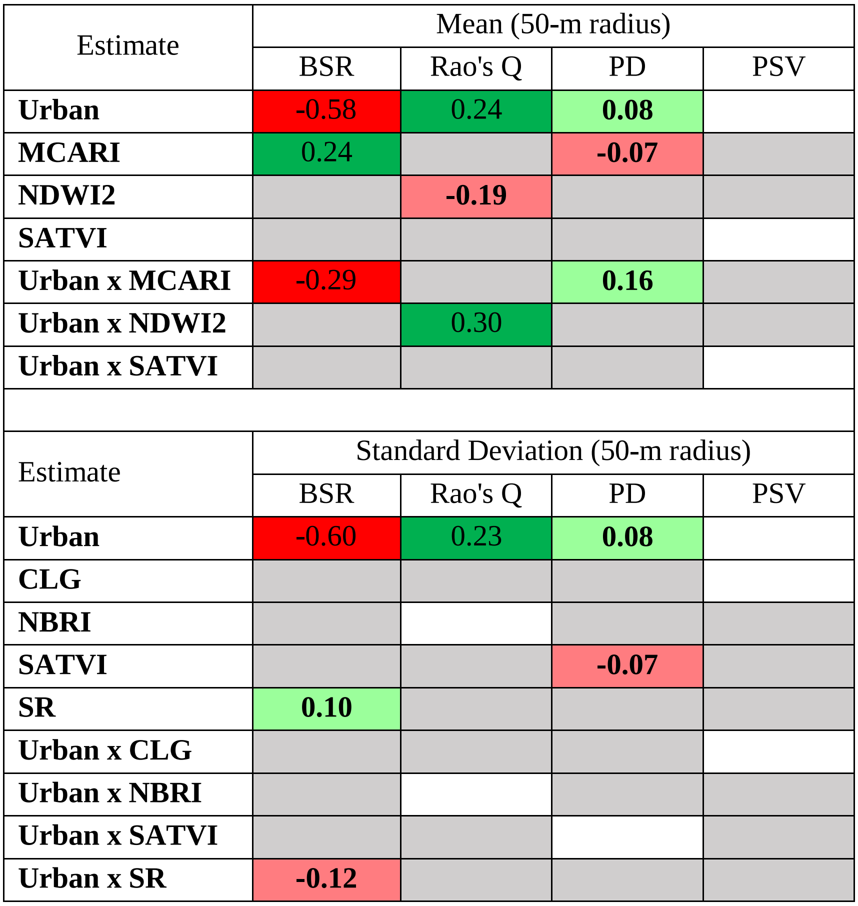
City	City size (km^2)	Bird Count (Urban)	Bird Count (Non-urban)
Auchi	35	20	66
Calabar	406	17	45
Ibadan	3,080	24	80
Lagos	1171	16	56
Birnin Kebbi	35	20	32
Dutse	45	24	48
Gombe	90	23	26
Jos	260	31	49
Mean	**640.25**	**21.875**	**50.25**
Standard Deviation	**1,057.17**	**4.76**	**17.41**
Grand total	**640.3±1,057.2**	**21.9±4.8**	**50.3±17.4**

Ranking of multispectral predictors of avian diversity metrics

The random forest regression reveals the topmost ranked spectral indicators of each avian diversity component (Table 1; Fig. S1). This procedure also discarded several indicators for the mean and SD approach. The results for the mean dataset indicate that MTCI cannot be used to predict phylogenetic divergence. Regarding SD values, MTCI, MCARI, and REIP were rejected as potential predictors of PSV. In addition, MTCI and MCARI were also rejected and selected tentatively as predictors of Rao’s Q, respectively. The ranking of spectral indicators shows MCARI as the most highly ranked index capable of potentially predicting both BSR and PD, simultaneously. The analyses also show the potential of SATVI by ranking it first to simultaneously predict PSV (mean) and PD (SD). In most cases (i.e., mean and SD across all diversity metrics), the commonly modeled NDVI ranks very low (occupying the 25th percentile) based on its predictive power (Fig. S1).

Relationships between avian diversity metrics and the mean of spectral indices across habitats

A significantly higher BSR was found in the non-urban (Estimate ± SE = 1.83 ± 0.05, Z = 36.32, $p < 0.001$; Fig. 3; Table S2) than the urban habitat (Estimate ± SE = -0.58 ±



Estimate	Mean (50-m radius)			
	BSR	Rao's Q	PD	PSV
Urban	-0.58	0.24	**0.08**	
MCARI	0.24		**-0.07**	
NDWI2		**-0.19**		
SATVI				
Urban x MCARI	-0.29		**0.16**	
Urban x NDWI2		0.30		
Urban x SATVI				

Estimate	Standard Deviation (50-m radius)			
	BSR	Rao's Q	PD	PSV
Urban	-0.60	0.23	**0.08**	
CLG				
NBRI				
SATVI			**-0.07**	
SR	**0.10**			
Urban x CLG				
Urban x NBRI				
Urban x SATVI				
Urban x SR	**-0.12**			

Figure 3: Schematic presentation of main associations between values of taxonomic diversity estimated from bird species richness (BSR), functional diversity estimated from Rao's Quadratic Entropy (Rao's Q) and phylogenetic diversity estimated from Faith's phylogenetic diversity (PD) and phylogenetic species variability (PSV), calculated for avian communities across urban and non-urban habitats in Nigeria, and spectral indices. Positive associations are indicated in green color (light green for effect sizes < 0.2), negative ones are highlighted in red (light red for effect sizes < 0.2), grey color indicates indices not incorporated in the model regarding each response variable, while white color denotes tested variables not statistically significant. The magnitude of effect sizes (<0.2 = negligible, < 0.5 = small, < 0.8 = medium, otherwise = large; Cohen, 1992) of all the significant variables are inserted in each cell. These results are simplified to reflect only significant variables from the final models shown in detail in Table S2.

0.05, Z = -11.99, p < 0.001, effect size = -0.58; Table S2). This result contrasts with those obtained for the remaining metrics as the urban habitat holds significantly higher levels of Rao's Q (Estimate ± SE = 8.18 ± 3.25, t = 2.52, p = 0.01, effect size = 0.24; Fig. 3; Table S2) and PD (Estimate ± SE = 14.44 ± 5.90, t = 2.45, p = 0.02, effect size = 0.08; Fig. 3; Table S2) than the non-urban habitat (Fig. 3; Table S2). Although not statistically significant, PSV values were also higher in the urban habitat (Estimate ± SE = 9.42E-04± 1.44E-03, t = 0.66, p = 0.51; Fig. 3; Table S2) compared to the more natural habitat (Fig. 3; Table S2). In all cases, variations in the values of BSR, Rao's Q, PD and PSV here were similar to those obtained by a previous study using the same dataset focused on investigating the influence of urbanization on avian diversity components in the Afrotropics (Awoyemi et al., 2024).

Regarding spectral indices, the main focus of this study, the a significant interaction effect of MCARI with habitat was found on BSR (Estimate ± SE = -0.29 ± 0.08, Z = -3.64, p < 0.001, effect size = -0.29; Table S2), showing an increase in the BSR value as MCARI increases in the non-urban habitat compared with the adjacent urban habitat (Fig. 4a). Further, the significant interaction effect of MCARI with habitat on PD (Estimate ± SE = 28.71 ± 7.39, t = 3.88, p < 0.001, effect size = 0.16; Table S2) showed an opposite pattern to that obtained for BSR: in this case, PD values increases in the urban habitat as MCARI increases in comparison with the adjacent urban habitat (Fig. 4b). Furthermore, NDWI2 mediated the effect of urbanization on Rao's Q as this significant interaction effect (Estimate ± SE = 10.18 ± 3.68, t = 2.76, p = 0.006, effect size = 0.30; Table S2) revealed an increasing Rao's Q values as NDWI2 increases in the urban habitat compared with the non-urban habitat (Fig. 4c). Meanwhile, the interaction effect of habitat and SATVI on PSV showed a marginal statistical significance (Estimate ± SE = 2.81E-03 ± 1.52E-03, t = 1.85, p = 0.07; Table S2). Overall, these results (Table S2) compare with those validated through machine learning approach as revealed by the R-squared values (Table S1).

Relationships between avian diversity metrics and the standard deviation of spectral indices across habitats

The analyses using the SD approach represent the variation in the investigated spectral indices during the entire period of data collection (November 2020-January 2021). Regarding this measure, the findings for the predictor habitat (urban vs non-urban) are very similar to those obtained in the analyses using mean values for the spectral indices. BSR was significantly higher in the non-urban (Estimate ± SE = 1.82 ± 0.10, Z = 18.16, p < 0.001; Fig. 3; Table S2) than the urban habitat (Estimate ± SE = -0.60 ± 0.05, Z = -12.22, p < 0.001, effect size = -0.6; Table S2). Although showing a similar pattern, the higher value of PSV recorded in the non-urban (Estimate ± SE = 3.19E-02 ± 1.26E-03,

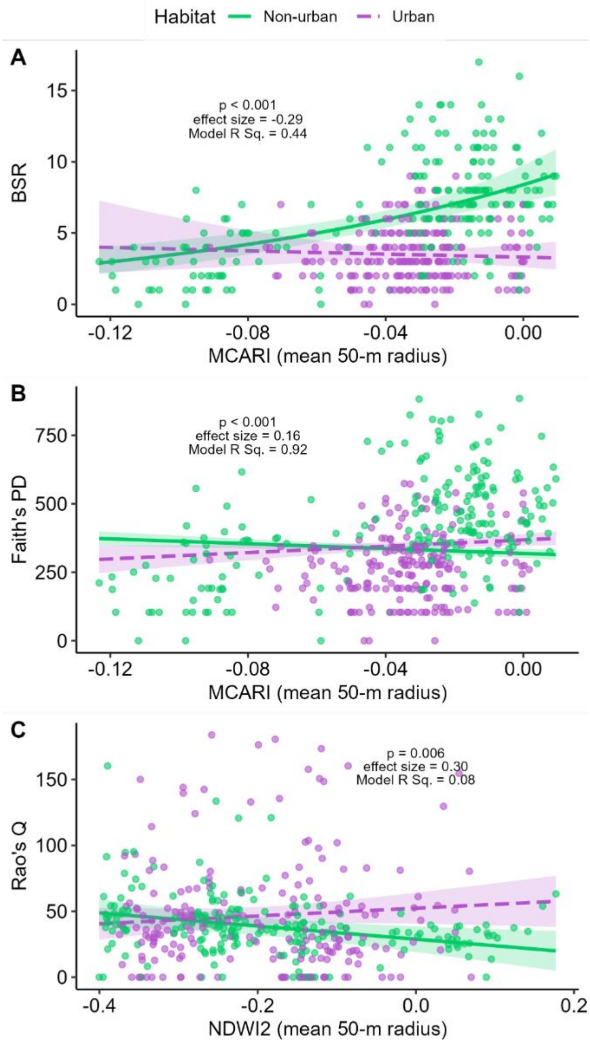


Figure 4: (A) Association of the Modified Chlorophyll Absorption Ratio Index (MCARI) and taxonomic diversity (BSR) by habitat (urban vs non-urban), (B) association of MCARI and phylogenetic diversity (Faith's PD) by habitat (urban vs non-urban), and (C) association of the Normalized Difference Water Index II (NDWI2) and functional diversity (Rao's Q) by habitat (urban vs non-urban). Please, note that the plots are based on unscaled independent variables (i.e., spectral indices) and might not completely match the predicted effect based on the models (e.g. MCARI x habitat for Faith's PD). The p-value, effect size and R2 of the significant effects are inserted in the corresponding panel above (see Table S2 for the full model output).

t = 25.31, p < 0.001; Fig. 3; Table S2) than the urban habitat was not statistically significant (Estimate ± SE = -4.53E-04 ± 1.19E-03, t = -0.38, p = 0.70; Table S2). In contrast, urban habitat supported significantly higher levels of Rao's Q (Estimate ± SE = 7.64 ± 3.29, t = 2.32, p = 0.02, effect size = 0.23; Fig. 3; Table S2) and PD values (Estimate ± SE = 14.17 ± 6.42, t = 2.21, p = 0.03, effect size = 0.08; Fig. 3; Table S2) than the nearby non-urban habitat: Rao's Q non-urban habitat (Estimate ± SE = 38.36 ± 3.21, t = 11.94, p < 0.001, effect size = -0.12; Fig. 3; Table S2); PD non-urban habitat (Estimate ± SE = 332.90 ± 6.30, t = 52.86, p < 0.001, effect size = -0.05; Fig. 3; Table S2).

In general, no significant interaction effects between the SD of spectral indices and habitat were found on any of the diversity metrics considered (Table S2). However, results show that SR significantly increased BSR values (Estimate ± SE = 0.10 ± 0.03, Z = 3.64, p < 0.001, effect size = 0.10; Fig. 3; Table S2), while SATVI significantly decreased PD (Estimate ± SE = -12.44 ± 5.89, t = -2.11, p = 0.04, effect size = -0.07; Fig. 3; Table S2). Finally, neither NBRI nor CLG had any statistically significant effect on Rao's Q (Estimate ± SE = 1.51 ± 2.34, t = 0.64, p = 0.52, effect size = 0.04; Fig. 3; Table S2) and PSV (Estimate ± SE = -1.13E-05 ± 8.40E-04, t = -0.01, p = 0.989; Fig. 3; Table S2), respectively, even if they were the topmost ranked spectral indices selected by the Boruta model.

Discussion

This study revealed suitable remotely sensed spectral indicators of bird taxonomic, functional and phylogenetic diversity across Afrotropical environments. It complements the growing body of literature demonstrating the relevance of these indices for monitoring biodiversity over the use of traditional field-based environmental measures that are potentially less accurate, laborious, expensive and prone to investigators' errors (Ghosh et al., 1995; Gorrod & Keith, 2009; Morrison, 2016). By performing multistage statistical analyses, this study sheds light on the effectiveness of using remotely sensed spectral indices for monitoring biodiversity over space and time. Furthermore, the association between some of these spectral indices and different avian diversity components can change between urban and non-urban habitats, providing useful directions for researchers and conservationists. This study does not aim to discuss differences in avian diversity between urban and non-urban habitats in the region as it has been done in a previous study using the same dataset (Awoyemi et al., 2024). In contrast, it discussed the effectiveness of using the spectral indices as proxies for monitoring changes in multifaceted avian diversity across Afrotropical urban and non-urban habitats.

Predictive power of spectral indices across multifaceted avian diversity

To our knowledge, this study is the first to simultaneously investigate the predictive associations between multispectral indices (29) and avian taxonomic, functional and phylogenetic diversity across Afrotropical urban and non-urban environments (see Awoyemi & Ibáñez-Álamo, 2023). In this respect, the result of this study revealed that spectral indices do not only differ in their capacity to potentially predict avian diversity, but are also strongly influenced by the specific biodiversity component investigated, supporting the need to simultaneously use diverse spectral indices. Considering the mean, for example, while MCARI was the topmost ranked index capable of potentially predicting BSR and PD, NDWI2 and SATVI had the most capability of predicting Rao’s Q and PSV, respectively. It is on this backdrop that we argue against the “universal” use of a single index like the NDVI as a proxy for investigating multiple facets of biodiversity (e.g., Bae et al., 2018; Leveau et al., 2020). The NDVI ranks below average in most cases here (Fig. S1), a pattern found by other plant-based studies (e.g., Alabi et al., 2022a; Alabi et al., 2022b). While this study did not invalidate the use of NDVI, it showed that other spectral indices outperform it. Interestingly, MCARI, NDWI2 and SATVI have been reported that they overcome some of the limitations attributed to NDVI (Gitelson, 2004; A. Huete et al., 2002; Huete & Jackson, 1988; Main et al., 2011; McFeeters, 1996; Wu et al., 2008), and are rated first in this study. In addition, MCARI ranks as the topmost predictor of both BSR and PD, supporting the consistency of the overall results as these two measures of biodiversity are known to be strongly correlated (e.g., Morelli et al., 2021; Sanllorente et al., 2023). Given that Rao’s Q is not correlated with BSR (Botta-Dukát, 2005), it is not surprising that a different spectral index (NDWI2) rather than MCARI ranks as the strongest predictor of functional diversity. This finding also highlights the significance of “non-vegetation” variables on biodiversity (NDWI2 is associated with water; McFeeters, 1996), and strengthening the initial argument revolving around the need to test the efficiency of multispectral indices while investigating biodiversity metrics (Bae et al., 2018; Benedetti et al., 2023). MTCI was the most commonly rejected predictor of avian diversity in this study, which recommends against its use in this context. This index also measures chlorophyll concentration, and has been employed for related measures such as leaf defoliation (e.g., Hawryło et al., 2018). Its rejection here could be attributed to the better performance of MCARI (related index) at predicting avian diversity in the Afrotropical region. This study thus provides a clear direction for future studies aiming to investigate the relationships between spectral indices and multiple facets of biodiversity in Afrotropical environments. Additionally, it opens up this remote sensing research line so that future studies can test the validity and applicability of the ranking result across other taxa, regions and habitats.

Relationships between spectral indices and multifaceted avian diversity across habitats

The GLMM results suggest that using the mean of spectral indices as proxies for biodiversity performs relatively better than the SD. This conclusion is based on the higher number of significant associations using the mean in comparison with the SD (6 vs 3). In fact, all the three significant interaction for SD data indicated negligible effect sizes (0.07—0.12), rather supporting the use of mean data. This result compares with those from other studies (e.g., (Benedetti et al., 2023; Hobi et al., 2021), and suggests that the mean of spectral indices better reflects the different avian diversity components than their variations estimated through the SD. Alternatively, environmental variations during the 3-month period of data collection may not be enough to trigger statistically significant associations with the investigated biodiversity metrics. Future studies could consider longer periods (within or between years) to explore the influence of environmental variations further.

Unlike other studies from temperate regions mainly using NDVI and EVI to evaluate avian diversity (e.g., Bae et al., 2018; Benedetti et al., 2023; He et al., 2015; Xu et al., 2022), this study proposes the use of MCARI, NDWI2 or SATVI to simultaneously model multiple avian diversity components across urban and non-urban habitats. Regarding the mean, MCARI was positively associated with higher avian taxonomic diversity in the non-urban habitat. This index measures leaf chlorophyll content, a good indicator of photosynthetic ability required for various plant metabolic activities, particularly growth and food production (Daughtry et al., 2000; Wu et al., 2008). Increasing photosynthetic ability is closely associated with luxuriant vegetation growth and yield (Long et al., 2006; Makino, 2011), which are key to the persistence of birds due to the provision of food and nesting habitats (Ferger et al., 2014; Moorcroft et al., 2002; Narango et al., 2017). This may partly explain why MCARI was positively associated with bird taxonomic diversity in the non-urban habitat. In contrast, increasing MCARI was negatively correlated with bird taxonomic diversity in the urban habitat. Although initially surprising, this result suggests that a combination of different factors (e.g., habitat richness, vegetation structure…) rather than photosynthetic ability of vegetation alone determines bird taxonomic diversity in the urban habitat (e.g., Beninde et al., 2015). This position is consistent with the intermediate disturbance hypothesis, showing that bird taxonomic diversity peaks in urban areas with intermediate levels of disturbance (Callaghan et al., 2019; Tratalos et al., 2007). As noted during our survey, a high MCARI value in the urban habitat could be disproportionately influenced by certain gardens or parks dominated by few or exotic plant species which cannot hold high bird taxonomic diversity. Supporting this view, studies conducted in Canberra (Australia) and multiple Spanish cities showed that the replacement of native vegetation with exotics significantly reduced bird taxonomic diversity in urban areas (Ikin et al., 2013; Sánchez-Sotomayor et al., 2022). Since bird taxonomic diversity in urban areas is, in general, positively associated with higher and native plant species (e.g., Narango et al., 2017), this result suggests that maintaining a mosaic of habitats (including vegetation dominated by native species) within urban areas could be more important for birds than only the amount of vegetation vis-à-vis MCARI in the area.

Although with a small effect size (0.16), the significant interaction between MCARI and habitat on phylogenetic diversity contrasted with for the result on taxonomic diversity. It showed that while taxonomic diversity reduces with higher MCARI value in the urban habitat, phylogenetic diversity increases. This result suggests that evolutionarily unique groups of distantly related birds are attracted to urban areas with high MCARI values. In this sense, avian assemblages showing a preference for various vegetation compositions associated with MCARI, such as flowers (sunbirds), fruits (hornbills), tree canopy (vultures) or grasses (firefinches) recorded during the study, could have enriched phylogenetic diversity in the urban habitat. This would have added to the phylogenetic diversity values already contributed by birds (e.g., swifts, sparrows or crows) that are more associated with urban features (e.g., built surfaces and telecommunication platforms) than vegetation (MCARI) in comparison with the non-urban habitat. In general, this study showed that Afrotropical urban areas with high productivity levels indicated by high MCARI values are rich in bird phylogenetic diversity. This is probably because urban areas with high MCARI values support evolutionarily unique groups of birds even while the species richness is low relative to the non-urban habitat.

The NDWI2 delineates water resources while eliminating soil and terrestrial vegetation features (McFeeters, 1996), which is useful for assessing bird habitat suitability (e.g., Teng et al., 2021). Interestingly, this study showed that the functional diversity of birds significantly increases as NDWI2 increases in the urban habitat in comparison with the non-urban habitat. This interaction has the highest effect size (0.30) among all the indices investigated in this study, clearly showcasing the significance of water resources to birds in the Afrotropical urban habitat. This study was conducted during the dry season, when water and food resources are scarce in the area (Siegfried, 1972; Sinclair, 1978). Thus, the feeding and breeding opportunities provided by water during these harsh conditions could attract birds with diverse traits, invariably promoting the functional diversity obtained in this study. In addition, this higher functional diversity may not have been contributed by waterbirds alone. For instance, the observation of luxuriantly growing bushes and grasses near urban puddles during the fieldwork could provide feeding and breeding opportunities for other functionally different groups of birds like nectarivores and granivores. Corroborating this finding, a study conducted across Europe showed that the proportion of water coverage in the urban habitat is significantly associated with higher values of avian functional diversity in both the breeding and wintering seasons (Ibáñez-Álamo et al., 2020). During our survey, we observed that the coverage of water permeates extensive building density, and contributes to the mosaic of habitats available for different groups of birds in the urban habitat, further supporting the finding. Regarding the contracting result showing that increasing NDWI2 reduces functional diversity in the non-urban habitat, it could be speculated that the effect of water coverage on functional diversity is mediated by landscape organization shaping bird traits in these two habitats (e.g., (Ibáñez-Álamo et al., 2024). Although with a marginal statistical significance ($p = 0.07$), increasing SATVI tends to increase the degree of phylogenetic relatedness of birds in the urban habitat. With this, urban areas with a high vegetation cover indicated by higher SATVI seem to hold more closely related bird species.

Conclusions

This study provides an evidence base supporting the use of remotely sensed spectral indicators as proxies for monitoring avian diversity in Afrotropical environments, which is crucial given the manpower and socioeconomic restrictions of the region (Awoyemi & Ibáñez-Álamo, 2023). We tested the relevance of this methodological approach using a relatively large dataset from Nigeria (8 paired urban and non-urban sites across rainforest and savannah), one of the most rapidly urbanizing countries at the global level, and a typical representative of the Afrotropical region (Awoyemi & Ibáñez-Álamo, 2023; OECD/SWAC, 2020; Seto et al., 2012).

Bird taxonomic, functional and phylogenetic diversity are not similarly affected by urbanization in the Afrotropics (e.g., Awoyemi, Barshep, et al., 2024) and other regions (e.g., Hagen et al., 2017; Ibáñez-Álamo et al., 2020; Morelli et al., 2021). Thus, one remotely sensed spectral indicator may not be appropriate to monitor all components of avian diversity in tandem, in which case this study recommends the use of several indicators, including MCARI, NDWI2 and SATVI. This study also showed that using the mean of spectral indices outperforms SD while investigating multiple avian diversity metrics. By being the topmost ranked indicator simultaneously predicting taxonomic and phylogenetic diversity, this study identifies MCARI as the best indicator of avian diversity in Afrotropical environments, and recommends its use as such. MCARI estimates the photosynthetic ability of vegetation, a measure of primary productivity, while accounting for shadow, soil reflectance and nonphotosynthetic materials (Daughtry et al., 2000; Wu et al., 2008). Thus, it can overcome some of the limitations of the NDVI, a more commonly used index in this respect that ranks very low among the spectral indices investigated here. This study also showed that high MCARI values in the urban habitat are associated with low bird taxonomic diversity but high phylogenetic diversity. Furthermore, NDWI2, the topmost predictor of functional diversity in the region, exhibits a positive significant effect in the urban habitat. From an applied perspective, these combined indicators could be useful to remotely monitor the different bird diversity metrics in certain Afrotropical urban and non-urban areas (e.g., expansive, inaccessible or insecure sites), which could even be more cost-effective. This insight could be useful for certain governmental and non-governmental agencies responsible for monitoring biodiversity in the region, such as the BirdLife International, represented in the study area by the Nigerian Conservation Foundation. To encourage biodiversity-friendly cities in the Afrotropics, this study showed that maintaining a mosaic of habitats high in photosynthetic ability (MCARI) and water (NDWI2) could boost bird phylogenetic and functional diversity in urban areas, thereby providing a clear applied recommendation for city planners and other urban stakeholders in the area. We recommend future studies to test the validity of our findings across other taxa, regions, and habitats.

Supporting Materials

Supplementary data to this article can be found online:
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Chapter 4

Urban-associated changes in avian-mediated regulating ecosystem services in the Afrotropics

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Abstract

The world is urbanizing at an unprecedented rate with vast implications for biodiversity and natural assets. Many studies have explored the effects of urbanization on ecosystem services, though few of them focused on those provided by wildlife (e.g., animal-mediated regulating ecosystem services –RES-). The Afrotropics is highly biodiverse, but is extremely urbanizing, and understudied regarding RES. Thus, this study investigated urbanization's impacts on avian-mediated RES (i.e., pest control, seed dispersal, pollination, and scavenging). Birds were sampled during the dry and wet seasons in multiple urban and non-urban habitats spread across the rainforest and savannah vegetation zones in Nigeria, a typical Afrotropical country. Additional diet information was extracted from Savitraits as a proxy for ecosystem service provisioning by the sampled bird species. Negative binomial regressions revealed pest control and seed dispersal as the avian-mediated RES most reduced by urbanization. This effect was consistent between seasons and vegetation zones, suggesting a general pattern in the region. Urbanization also significantly reduced pollination but only during the wet season. In contrast, scavenging was significantly higher in the urban than non-urban habitat during the wet season (rainforest alone). Meanwhile, urban attributes like vehicles and pedestrians dramatically reduced pollination and seed dispersal, respectively, while canopy cover enhanced pollination and seed dispersal (wet season only). The socio-ecological and economic implications of decreasing avian-mediated RES due to urbanization are discussed. We recommend that Afrotropical urban development embrace nature-based solutions that bolster ecosystem resilience and services for mutual benefits.

Introduction

The rapid expansion of urban areas, exacerbated by the exponential growth of the human population, exerts negative impacts on nature worldwide (Grimmond, 2007; Seto et al., 2012; United Nations, 2016). Currently, more than half of the global human population (3.8 billion) live in cities, with developing countries, such as those in the Afrotropical region, experiencing a higher human population density than their temperate counterparts (United Nations 2019). In fact, urban land cover in developing countries is predicted to increase from 300,000 km2 in 2000 to 770,000 km2 in 2030 (Angel et al., 2011). By converting natural areas into built environments, urbanization deeply erodes biodiversity (Gil & Brumm, 2013; Piano et al., 2020; United Nations, 2016). This impact on living organisms has important consequences for both the environment and human beings alike (Liang et al., 2019; Moore et al., 2003). One of such negative effects corresponds with the alteration of ecosystem services provided by organisms (e.g., wildlife, vegetation); known as the tangible (e.g., food, water) and intangible (e.g., climate regulation, pest control) benefits people derive from nature (Pinho et al. 2017).

Several studies have demonstrated how urban habitat attributes, such as impervious surfaces (e.g. Yang et al., 2022) and human population density (e.g. Fei et al., 2015), alter the provisioning of ecosystem services. Meanwhile, the coverage of different forms of vegetation, such as tree canopy, shrub, and plants with berries reduce the erosion of urban ecosystem services (Izquierdo et al. et al. submitted; Reynolds & Howes, 2023). Yet, most studies investigating urbanization’s impacts on ecosystem services are restricted to Global North countries relative to those in the Global South (Deeksha & Shukla, 2022; Haque & Sharifi, 2024; Luederitz et al., 2015; Tavares et al., 2019), despite the later holding the majority of the global human population

(United Nations 2019). This mismatch could have far-reaching conservation and management implications. For instance, the Global South is the most impacted by urban development while simultaneously holding the greater proportion of the Earth's biodiversity (Gatti et al., 2015; Seto et al., 2012). Therefore, there is an urgent need to investigate urban-associated effects on ecosystem services in the Global South.

According to the Millennium Ecosystem Assessment (2003), ecosystem services are typically categorized into provisioning, supporting, cultural, and regulating services, all of which directly or indirectly enhance human wellbeing (Spake et al., 2017). In the context of urbanization, regulating ecosystem services (RES) are particularly affected given the impacts of urban expansion on natural processes (Rodríguez et al., 2006). However, our understanding of RES is far from good, especially in certain areas of the planet concentrating high biodiversity and urbanization rates like Africa (Awoyemi & Ibáñez-Álamo, 2023; Mengist et al., 2020; Wangai et al., 2016). Current knowledge on this topic from Africa is restricted to South Africa, focusing on pollination and the regulation of water flow and runoff (du Toit et al., 2018; Reynolds & Howes, 2023). This geographic restriction reflects the general pattern of urban ecology knowledge and advocates for intensifying studies not only on this continent but also on less investigated regions within it like the Afrotropics (Awoyemi & Ibáñez-Álamo, 2023).

In addition to this important geographical bias, we need additional information on specific aspects of RES such as those mediated by wildlife (Mortelliti, 2023; Russo et al., 2022; Sengupta et al., 2022). Wildlife is extremely affected by urbanization (Marzluff, 2001; McKinney, 2008). However, we still do not fully understand how RES mediated by this altered urban wildlife change (du Toit et al., 2018). Several vertebrate studies indicate that urbanization generally favors scavenging (Chamberlain et al., 2017) compared to other RES types such as seed dispersal, pollination, or pest control (Fattorini, 2011; Schneiberg et al., 2020; Wenzel et al., 2020). Moreover, other studies have linked these contrasting relationships with functional traits shaping how species exploit their habitats (e.g., de Bello et al., 2010; Hanisch et al., 2020). For instance, specialist and forest-related species mainly provide seed dispersal, pollination, and pest control services (Bregman et al., 2014; Harrison & Winfree, 2015). In contrast, scavenging is mainly associated with generalist species that have a higher level of urban tolerance (Gomo et al., 2020; Mateo-Tomás et al., 2015; Schwartz et al., 2018) and the ability to exploit novel food resources (Luna et al., 2021). In the case of birds, for example, specialist and forest-related species are more affected by urbanization than generalists (Danmallam et al., 2024; Lee et al., 2021). Additional studies on insect-mediated RES have been published but they focused on pollination, while other services are much less investigated (Brock et al., 2021; Noriega et al., 2018). Despite the interesting and novel information provided by these few studies on the topic, they are mainly restricted to Global North countries. Thus, to comprehend the impacts of urbanization on ecosystem services, we urgently need additional studies from other Global South areas like the Afrotropics, and on other less studied RES types such as pest control, seed dispersal, and scavenging (Awoyemi & Ibáñez-Álamo, 2023; du Toit et al., 2018).

This study aims to fill this important knowledge gap by assessing urbanization's impacts on avian-mediated RES across understudied Afrotropical environments. The study was performed in Nigeria, the most populous country in Africa currently experiencing an urbanization rate > 4 % (World Bank, 2021). This intense urban expansion severely affects biodiversity; with the taxonomic diversity of certain taxa (e.g., birds) reducing by more than half compared to the adjacent non-urban areas (Awoyemi et al., 2024). Birds are particularly important due to their significant contribution to wildlife-mediated RES (i.e., pest control, seed dispersal, pollination and scavenging) (Izquierdo et al. submitted; Murphy et al., 2023; Reynolds & Howes, 2023) and are also important bioindicators used to monitor environmental changes occasioned by urbanization, season and vegetation in the study area and beyond (Awoyemi et al., 2024; Kumdet et al., 2021; Morelli, Reif, et al., 2021).

The objectives of this study are: (1.) To investigate differences in bird-mediated RES (i.e., pest control, seed dispersal, pollination, and scavenging) across habitats (urban vs non-urban), vegetation zones (rainforest vs savannah), and seasons (dry vs wet) in Nigeria. Based on previous findings (Fattorini, 2011; Schneiberg et al., 2020; Wenzel et al., 2020), it could be expected that the urban habitat will provide lower levels of pest control, seed dispersal, and pollination RES than the adjacent non-urban habitat, which will contrast with the result on scavenging (Chamberlain et al., 2017). In addition, the impacts of urbanization on bird diversity are more severe in the rainforest than in the savannah and during the dry than the wet season in Nigeria (Awoyemi et al. 2024). Thus, urbanization-mediated effects on RES types are expected to be lower in the savannah than in the rainforest and during the dry than the wet season. (2.) To explore the effects of local habitat attributes (i.e., numbers of vehicles and pedestrians, and coverage of canopy, bush and water) on each of the four studied RES. Previous research led us to predict that while human activity (e.g., the numbers of vehicles and pedestrians) will significantly reduce all the avian-mediated RES, vegetation and water cover will enhance them (Awoyemi et al., 2024; Izquierdo et al., submitted; Reynolds & Howes, 2023). This second objective will be useful for city planners and policy makers as they can provide specific actions to prevent the loss of wildlife-mediated ecosystem services in urban areas. By shedding light on how urbanization could limit the provisioning of ecosystem services, key stakeholders (urban dwellers and planners, conservationists, and policy-makers) are more likely to adopt and support restorative activities to achieve the UN Sustainable Development Goals, particularly Goals 3, 11 and 15 (United Nations, 2015).

Methods

Study areas

The study was carried out in Nigeria, located within the Afrotropical belt. We collected data from paired urban and non-urban habitats of eight Nigerian cities, evenly distributed across the rainforest (Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos) (Fig. 1), which represent the two primary vegetation zones in the area (Ezealor, 2001). Urban habitats were defined as contiguous areas of built-up land exceeding 1 km2, characterized by high human density (>1600 inhabitants/km2), and dominated by human-constructed features such as buildings (>10 buildings/ha), roads, and vehicles (Marzluff et al., 2001; Niemelä, 1999; Nilon et al., 2003; Schneider et al., 2010). Each urban area was paired with a non-urban area, located at least 20 km away (mean ± SD = 29.4 ± 6.3 km; Liker et al., 2008). Non-urban habitats consisted of extensive wilderness and vegetation cover, interspersed with sparse agricultural landscapes (MacGregor-Fors, 2011; Marzluff et al., 2001). This methodological approach, which involves delineating urban and non-urban habitats, is rarely employed in African studies investigating the impacts of urbanization on ecosystem services (du Toit et al., 2018), despite its relevance to this topic (Awoyemi Ibáñez-Álamo, 2023).

Estimation of site characteristics and bird censuses

We employed the point count method, as described by Bibby et al. (2000), to quantify bird diversity and abundance. First, we stratified each habitat type (i.e., urban or non-urban) into five 1 × 1 km areas, separated by a minimum distance of 500 m, using the ArcGIS software. Each area was positioned at the center of an urban or non-urban habitat, and its four cardinal points (north, south, east, and west), following the methodology outlined by Ciski et al. (2019). Second, we utilized the "Create Random Points" tool in ArcGIS to randomly select five points within each 1 × 1 km area selected. To ensure precise data collection, each point was marked with a GPS device in the field. We then collected data from 50 points (25 urban and 25 non-urban) in each of the eight paired sites, totaling 400 points across the rainforest (200 points) and savannah (200 points) regions. To maintain data independence, each point was separated by at least 200 m (e.g. Adegbola et al., 2024; Morelli et al., 2017). Data collection occurred during the morning, up to 4 hours after local sunrise. At each point, we conducted 5-minute point counts, recording the number of individuals of each bird species, pedestrians, and vehicles seen or heard within a 50-m radius (Awoyemi et al., 2024). Additionally, we estimated field-based environmental measures, including tree canopy, bush cover, grass cover, and built surface, to the nearest 10% (Morelli, Benedetti, et al., 2021; Sanllorente et al., 2023). An expert ornithologist with over 10 years of experience working with birds in the region (AGA) performed the bird counts and environmental measures. To capture seasonal variations, we repeated the sampling procedure during the wet season (August-September 2021). However, due to security concerns in northern Nigeria at the time, the second round of point counts was limited to the rainforest sites (200 point-count stations).

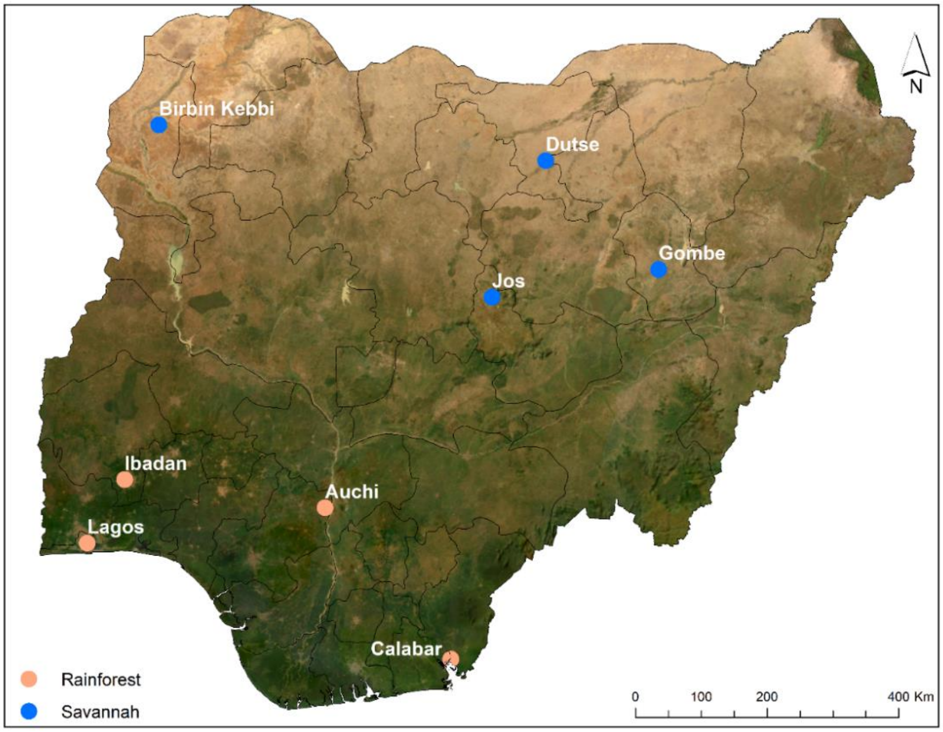

Figure 1: Distribution of study sites across the savannah and rainforest vegetation zones in Nigeria. At each city, data were collected in paired urban and non-urban sites.

Estimation of ecosystem services

We estimated avian-mediated ecosystem service values (RES) per species using diet as a proxy for foraging behavior (Wenny et al., 2011; Whelan et al., 2008). This methodological approach has been applied to investigate RES contributions by various taxa, including birds (Horgan et al., 2017; Ndang’Ang’A et al., 2013), bats (Russo et al., 2018; Yu & Muchhala, 2024), insects (MacQueen et al., 2022; Rodríguez-Gasol et al., 2020) and mammals (Inagaki et al., 2022; Vale et al., 2023). We used the percentage of invertebrates, fruits, nectar, and scavenging as a measure of pest control, seed dispersal, pollination, and scavenging RES, respectively (Barros et al., 2019). We used Savitraits 1.0 to obtain these data. This is a comprehensive compilation of species-specific dietary preferences and their intra-annual variation for over 10,000 extant bird species worldwide (Murphy et al., 2023), including all species encountered during our surveys. This dataset is recent, comprehensive, and provides monthly variations in diets (cf. Tobias et al., 2022; Wilman et al., 2014), and has been utilized in similar urban and non-urban studies (Izquierdo et al. submitted; Ma et al., 2024). Using this dataset, we calculated bird-mediated RES values across the dry (November 2020 – January 2021) and wet seasons (August – September 2021). At each point count, we multiplied the value of each RES per species by the abundance of each bird species. Finally, we calculated the total value of each RES per point by summing the contributions of all species recorded at that point.

Statistical analyses

Separate analyses were performed for the dry (rainforest and savannah) and wet seasons (only rainforest) using the R Statistical Package (version 4.4.1) (R Core Team, 2024). This procedure was due to our inability to collect wet season data in the savannah sites due to security issues.

Before conducting statistical analyses, we employed box plots to visualize the distribution of each ecosystem service (i.e., seed dispersal, scavenging, pollination, and pest control) (Murrell, 2022). This visualization enabled us to identify outliers, defined as data points falling outside the whiskers (1.5 times the interquartile range), which were subsequently removed from the database to ensure data quality (Juggins & Telford, 2012; Sunderland et al., 2019). To guarantee the independence of our point count stations, we followed established protocols (e.g., Izquierdo et al. submitted; Sanllorente et al., 2023) by performing a Mantel test to detect potential spatial autocorrelation issues (Legendre & Fortin, 2010; Mantel, 1967). This analysis involved 9999 Monte Carlo permutations, using two matrices: one representing geographic distances among point counts and another for the differences in avian-mediated ecosystem services (RES). The results revealed no significant spatial autocorrelation issues for any response variables across both dry and wet seasons (all p-values > 0.6). Consequently, we treated each point count station as a statistically independent observation, consistent with previous studies (e.g., Dormann et al., 2007; Sanllorente et al., 2023). Third, we standardized all independent numerical variables using the "scale" function, which centered and scaled the data. This preprocessing step ensured that all variables were on the same scale, improving the performance and stability of the algorithm and models (Morelli, Benedetti, et al., 2021; Nash, 2017; Revelle, 2022). Fourth, we assessed multicollinearity and model convergence issues using the variance inflation factor (VIF) calculated with the "check_collinearity" function of the “performance” package (Fox et al., 2024; Lüdeck et al., 2021). To address these issues, we iteratively removed the most highly correlated independent variables until convergence warnings ceased, ensuring a VIF < 5 for all remaining variables (Dormann et al., 2013; Jou et al., 2014). Notably, interactions between the habitat and other independent variables, as well as the coverage of built surfaces and grasses, exhibited high VIF values (> 5) and were subsequently excluded from further analyses. We then conducted subsequent analyses using negative binomial Generalized Linear Mixed Models (GLMM) using the "glmmTMB" package (version 1.1.9; Brooks et al., 2024) to address overdispersion issues (version 1.1.9; Brooks et al., 2024). In these analyses, RES values per point count served as dependent variables, while habitat (urban vs. non-urban), vegetation zone (rainforest vs. savannah), and local habitat attributes (i.e., coverage of bush, canopy, and water, and the numbers of pedestrians and vehicles) were modeled as predictors. City was included as a random factor to account for potential consistent differences among the 8 cities in the dry season and 4 cities in the wet season. Separate models were run for each RES type (pest control, seed dispersal, pollination, and scavenging) and season (dry and wet). To identify the most informative predictors for each RES type, we employed a model selection and averaging approach using the "MuMIn" package, based on ΔAIC < 2 (Symonds & Moussalli, 2011; Zuur et al., 2009).

Results

During the dry season, our results showed significantly lower levels of bird-mediated pest control (Estimate ± SE = -1.102 ± 0.11, Z = 9.65, p < 0.001; Fig. 2; Table S1) and seed dispersal (Estimate ± SE = -1.024 ± 0.16, Z = 6.41, p < 0.001; Fig. 2; Table S1) in the urban than the non-urban habitat. In contrast, scavenging and pollination did not differ between the urban and the non-urban habitat (app p value > 0.05; Table S1). However, scavenging (Estimate ± SE = -1.635 ± 0.31, Z = 5.31, p < 0.001, Fig. 2) and pest control provided by birds (Estimate ± SE = -0.644 ± 0.28, Z = 2.28, p = 0.02, Fig. 2) were significantly lower in the savannah compared to the rainforest. Also during the dry season, canopy cover was the only significant local habitat attribute enhancing bird-mediated seed dispersal (Estimate ± SE = 0.307 ± 0.08, Z = 3.64, p < 0.001, Fig. 2) and pollination (Estimate ± SE = 0.385 ± 0.14, Z = 2.81, p = 0.005, Fig. 2). Meanwhile, water cover significantly reduced pollination during the dry season (Estimate ± SE = -0.356 ± 0.13, Z = 2.71, p = 0.007, Fig. 2).

Our wet season results (only rainforest) show that pest control (Estimate ± SE = -0.906 ± 0.15, Z = 5.83, $p < 0.001$; Fig. 2; Table S1), seed dispersal (Estimate ± SE = -0.846 ± 0.2, Z = 4.17, $p < 0.001$; Fig. 2; Table S1) and pollination provided by birds (Estimate ± SE = -0.612 ± 0.23, Z = 2.61, $p < 0.009$; Fig. 2; Table S1) were significantly lower in the urban than the non-urban habitat. However, we found significantly higher levels of bird-mediated scavenging in the urban than the non-urban habitat (Estimate ± SE = 1.343 ± 0.50, Z = 2.69, p = 0.007; Fig. 2; Table S1). Among the local habitat attributes investigated during the wet season, only pedestrians and vehicles exert significant effects, drastically reducing seed dispersal (Estimate ± SE = -0.224 ± 0.11, Z = 2.12, p = 0.03; Fig. 2; Table S1) and pollination (Estimate ± SE = -0.256 ± 0.12, Z = 2.16, p = 0.03; Fig. 2; Table S1), respectively. Overall, the significant effects of local habitat attributes reported here are generalizable across habitats (i.e., urban vs. non-urban), as the interactive effects of habitats with other independent variables were removed from our models due to multicollinearity issues (VIF > 5).

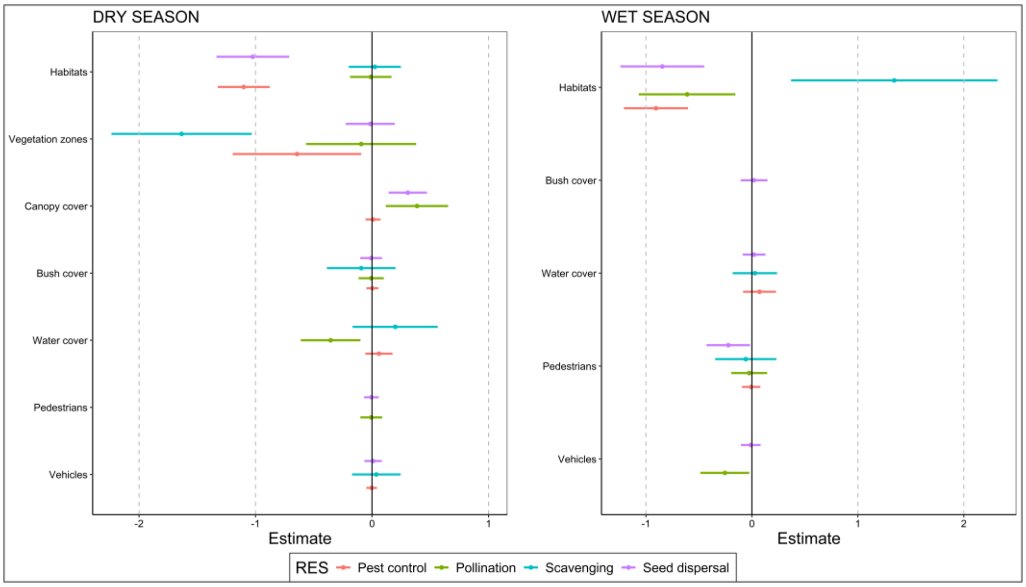

Figure 2: Estimate ± standard errors of regression coefficients for the four averaged models (one each for bird-mediated seed dispersal, pest control, pollination and scavenging) during the dry (left) and wet (right) seasons in Nigeria. Significant variables are those whose standard errors do not overlap with zero. For the variable "Habitat" negative values implies the urban habitat, while positive values indicate the non-urban habitat. For the variable "Vegetation zone", negative values implies savannah while positive values indicate rainforest.

Discussions

Our study identified pest control and seed dispersal as the avian-mediated regulating ecosystem services (RES) most affected by urbanization across Afrotropical environments. Out of the four RES types considered in our study (i.e., pest control, seed dispersal, pollination, and scavenging), only pest control and seed dispersal were significantly lower in the urban than in the non-urban habitat across the dry and wet seasons. These results imply a general and consistent impact of urbanization on avian-mediated pest control and seed dispersal RES in the Afrotropics. Further changes in avian-mediated pollination and scavenging RES were modulated by season (significant only during the wet season). In this context, pollination was significantly lower in the urban than the non-urban habitat. This contrasted with the result on scavenging, which was significantly higher in the urban than in the non-urban habitat.

Differences in avian-mediated regulating ecosystem services across Afrotropical environments

The obtained pest control result is based on the drastic reduction in insectivorous birds controlling pests in the Afrotropical urban habitat. This result is in line with those of a global meta-analysis on pest control that also found that urban development significantly reduced natural insect predators (Korányi et al. 2022). On the one hand, the reduction of natural predators in urban habitats (e.g., birds in this study) could lead to an increase in certain insect pests of high socio-ecological and economic costs. Although Afrotropical examples are scarce, there are studies from other regions of the world that support this potential outcome. For example, Hudgins et al. (2022) estimated that uncontrolled invasive insects in urban areas (e.g., emerald ash borer *Agrilus planipennis*) could kill 1.4 million street trees in the USA between 2020 and 2050, costing an average of US$ 30 million, annually. In addition, a recent comprehensive review demonstrated the public health implications of using pesticides for pest control in urban habitats (Md Meftaul et al., 2020), rather advocating for nature-based solutions (see White et al., 2021). These scenarios underscore the relevance of the natural pest control RES freely available in the studied non-urban habitat, highlighting the need to minimize urban impacts on Afrotropical avifauna. Alternatively, the observed reduction of pest control services could be linked to the lower diversity of some insect groups in Afrotropical urban areas. Insects are a major group of avian diet that is also negatively affected by urban development (Fenoglio et al., 2020; Murphy et al., 2023; Planillo et al., 2021). Thus, cascading negative effects of urbanization on biodiversity could be speculated here given that its effect on these organisms (e.g., insects as a prey) does not only reduce the other (e.g., birds as a predator) but also the associated ecosystem services. However, irrespective of the causes (i.e., direct urbanization effects on birds and/or indirect effects mediated by insects), the reduction in bird-mediated pest control RES in the Afrotropics due to urbanization is a clear finding based on our data. Meanwhile, the significantly lower pest control RES in the savannah than in the rainforest reinforces the need to consider the vegetation zone in this kind of studies. Here, we could associate this result with a higher concentration of insectivorous birds controlling insect pests in rainforests than in savannahs, which is consistent with previous studies. According to a global literature review, birds in forests account for > 70% of the global annual prey consumption of insectivorous birds (≥ 300 million tons year^{-1}) compared to insectivorous birds from other biomes such as savannas or grasslands (Nyffeler et al., 2018).

Similarly, our results revealed a significant decline in bird-mediated seed dispersal RES in urban compared to non-urban Afrotropical areas across both dry and wet seasons. This suggests that urbanization negatively impacts avian seed dispersers in the Afrotropics, a finding supported by the fact that specialist and forest-related bird species, which are primary seed dispersers (Bregman et al., 2014; Elgood et al. 1994; Harrison & Winfree, 2015), tend to avoid urban areas (Danmallam et al., 2024; Lee et al., 2021). The avoidance of urban habitats by frugivorous birds (e.g., those belonging to the Bucerotidae and Capitonidae families in our study) can disrupt plant dispersal processes (Gelmi-Candusso & Hämäläinen, 2019). This can potentially lead to the local extinction of plant species that rely on animal-mediated dispersal (zoochory) and the associated loss of ecosystem services (Heinen et al., 2023; Pérez-Méndez et al., 2016; Wotton & Kelly, 2012). Furthermore, urban areas are characterized by extensive impervious surfaces reducing available land areas that could aid plant diversity (Yan et al., 2019; Zhao et al., 2023), seed dispersal networks (Cruz et al., 2013), and potentially their associated ecosystem services.

The significant reduction in avian-mediated pollination RES during the wet season provides further evidence of a trophic cascade triggered by urbanization. This suggests that avian pollinators are probably more common in non-urban areas during the wet season in the study area, highlighting the seasonal uniqueness of the Afrotropical region. The higher abundance of nectar resources in Afrotropical non-urban habitats (e.g., Pauw & Louw, 2012) likely contributes to this pattern during the wet season. In contrast, during the dry season, supplemental irrigation in urban gardens, parks, and lawns can enhance flowering, promoting bird-mediated pollination in urban habitats (e.g., Chamberlain et al., 2020; Reyes-Paecke et al., 2019). This human activity may mitigate the expected significant differences in bird-mediated pollination RES between Afrotropical urban and non-urban habitats during the dry season, providing an opportunity for pollinator conservation in this human-perturbed environment (e.g., Llodrà-Llabrés & Cariñanos, 2022). Given the critical role of pollination in food security, the decline of avian pollinators can have substantial consequences for seed and/or food production also in urban habitats like vegetable gardens (Anderson et al., 2011).

In contrast, the result of bird-mediated scavenging meets our expectations only during the wet season (rainforest). Scavenging RES was significantly higher in the urban than in the non-urban habitat during the wet season. One possible explanation for this result is that urbanization leads to the segregation of scavenger communities. For instance, both avian (e.g., white-backed vulture *Gyps africanus*) and mammalian scavengers (e.g., spotted hyena *Crocuta crocuta*) coexisted with humans in Africa until the perturbation of this relationship by urban explosion linked to the industrial revolution (Moleón et al., 2014). It thus appears that birds, relative to other taxa like mammals, perform a higher scavenging RES in the Afrotropical urban than non-urban habitats. This scenario is likely given that no wild mammalian scavengers were encountered in the urban habitat during our survey (unpubl. data). In contrast, a higher abundance of some avian scavengers (e.g., yellow-billed kite *Milvus aegyptius*) was observed in the urban than in the non-urban habitat, which could explain the obtained results in this respect. The fact that the abundance of the few successful scavenging birds is always higher in this human-disturbed habitat than in the adjacent non-urban habitat (e.g., Chamberlain et al., 2017) supports our reasoning. In addition, the significantly lower scavenging RES in savannahs compared to rainforests during the dry season may be attributed to the higher abundance of scavenging birds in the latter. Alternatively, the concentration of scavenging activity in rainforests during the dry season may also contribute to this pattern. For example, the yellow-billed kite, a common scavenging bird observed during our survey, is an intra-African migrant that breeds in rainforests during the dry season (Awoyemi et al., 2024; Brown et al., 1982; Ezealor, 2001).

Effects of local habitat attributes on avian-mediated regulating ecosystem services

Expectedly, during the wet season, the number of vehicles and pedestrians significantly reduced bird-mediated pollination and seed dispersal, respectively. Similar to impervious surfaces, the presence of vehicles and pedestrians are a typical urbanization footprint affecting bird diversity and the associated ecosystem services (Marzluff et al., 2001; Murgui & Hedblom, 2017). In this study, a higher number of vehicles and pedestrians in the urban compared to non-urban habitats could limit the extent of greenspaces supporting flowering/fruiting plants upon which pollinators and seed dispersers depend. Supporting this position, Pauw & Louw (2012) demonstrated how larger avian pollinators (e.g., sugarbirds) avoided the city of Cape Town (South Africa) due to its lower nectar availability compared to the adjacent non-urban areas, while Schneiberg et al. (2020) showed how urbanization alters the networks existing between plants and frugivorous birds. In addition, bird sensitivity to road traffic and collisions are other mechanisms by which the presence of vehicles could limit the provisioning of pollination RES in urban areas (Kiros et al., 2016). The Orange-breasted Sunbird *Anthobaphes violacea* is a typical African avian pollinator sensitive to road traffic (Geerts & Pauw, 2009). In Africa, bird-vehicle collisions are also more common during the breeding season (Mansouri et al., 2022), which could partly explain our result during the wet season, the peak of breeding in the area (Elgood et al., 1994). Meanwhile, the significant decline of pollination RES due to the coverage of water during the dry season did not meet our expectations. However, similar to the above urban attributes, the coverage of water (unlike the irrigation of lawns and gardens), could also limit the extent of available land upon which flowering plants could grow.

Independently of urbanization or vegetation zone, canopy cover generally enhanced seed dispersal and pollination provided by birds, but only during the dry season. Precipitation and vegetation are reduced in the study area during the dry season (Ezealor, 2001), making the remaining green areas crucial for birds (Awoyemi et al., 2024), potentially affecting the nectar-and-fruit eater birds that mediated pollination and seed dispersal in the study area. This is consistent with previous studies showing that increasing vegetation in either urban or non-urban habitats positively correlates with higher levels of pollination and seed dispersal RES (Mexia et al., 2018; Reynolds & Howes, 2023; Sutter et al., 2018; Vega & Küffer, 2021). This result highlights the significance of and the need to conserve vegetation across different landscapes. This is particularly important in cities of this continent, where the urban-induced disappearance of vegetation drastically reduced Afrotropical birds (Awoyemi et al., 2024; Chamberlain et al., 2017; Seto et al., 2012). Bird-mediated pollination and seed dispersal are two biological activities crucial for food production and ecosystem connectivity/resilience (Giannini et al., 2015; Mueller et al., 2014) and, thus, our results reinforce the concept of the strong interdependence of the socio-ecological system in Africa as it has been shown in other regions (Klein et al., 2007; Papanikolaou et al., 2017; Potts et al., 2010).

Conclusions and recommendations

This study supports the link between urban-induced changes in biodiversity and the loss of associated ecosystem services. Overall, pest control and seed dispersal were the avian-mediated RES most affected by urbanization in the Afrotropics, independently of season or vegetation zone. This finding is crucial to understand resultant effects of the rapid urbanization experienced by this region on ecosystem services

(Awoyemi & Ibáñez-Álamo, 2023; du Toit et al., 2018). In contrast, we found a significantly higher scavenging RES in the urban than non-urban habitats, similar to what previous studies had reported (e.g., Chamberlain et al., 2017). Thus, our findings are in line with other research indicating that urbanization can severely impact wildlife-mediated RES (e.g., Fattorini, 2011; Schneiberg et al., 2020; Wenzel et al., 2020), with important consequences not only for the ecosystem but also for human well-being.

In general, our results indicated that birds contribute more to scavenging in urban habitats and rainforests compared to non-urban habitats and savannahs. Future studies should investigate scavenging mediated by other wildlife, such as mammals, to provide a more comprehensive understanding of the impacts of urbanization on this essential ecosystem service provided by animals.

In addition, this study identified the increasing availability of vehicles and pedestrians as key local attributes significantly reducing pollination and seed dispersal RES mediated by birds in Nigeria, respectively. Thus, it is recommended that onward urban designs in the area should integrate nature-based solutions (e.g., pathways for urban nature walks, hiking, biking…) that minimize the presence of cars within cities or restrict the presence of citizens to specific areas. Interestingly, this study uncovered how canopy cover (vegetation) could help in this endeavor by enhancing seed dispersal and pollination RES provided by birds. We hope the findings and recommendations of this study will promote the achievement of sustainable urbanization in the Afrotropics so that people can live in harmony with and benefit from nature.

Supplementary Material

Table S1: Results of negative binomial GLMMs for the four averaged models investigating relationships between avian mediated regulating ecosystem services (i.e., seed dispersal, pest control, pollination and scavenging), and habitats (urban vs. non-urban), vegetation zones (rainforest vs. savannah), seasons (urban vs. non-urban), greenness, and number of pedestrians, modelled as predictors in eight (8) Nigerian cities. See the online version of the potentially published paper.

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Chapter 5

Human-nature interactions in the Afrotropics: Experiential and cognitive connections among urban residents in southern Nigeria

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Abstract

Many people are losing direct contact with nature, a phenomenon termed as the extinction of experience. Urban dwellers are particularly affected by this process that influences public health and habitat conservation. We explored the extinction of experience among the urban populace in Nigeria, a clear Global South representative with rapidly increasing human population. We interviewed 600 adults from several cities and performed statistical tests. Results show that most respondents have no contact nor connection with nature, revealing an important distancing from the natural world. The reasons respondents gave for not experiencing nature more often are mainly related to material terms (e.g., lack of time, money and nearby natural areas). We found that respondents with higher nature contact are also more connected to nature, which is promoted by the perception of neighborhood safety. Respondents living in Lagos, and those with lower levels of income and education show greater dissociation from nature. The relationships between real and perceived neighborhood naturalness and bird species are decoupled, but the perception of naturalness and bird species richness correlates. Our study provides novel information on the loss of human-nature interactions and its determinants in the Afrotropics. We recommend different actions necessary to ameliorate this problem.

Introduction

In recent decades, an increasing number of people are losing direct contact with nature, a phenomenon termed as the “extinction of experience” (Pyle, 1993). This process of continued isolation and alienation of humans from nature is commonly reported across the world (Miller, 2005), and constitutes a challenge for public health and for curbing environmental degradation (Soga & Gaston, 2016). On the one hand, the extinction of experience undermines the multiple benefits that interactions with nature have for people's physical and mental health (reviewed by Keniger et al., 2013). On the other hand, it also has a negative indirect effect on the environment through changes in people's behaviors and attitudes, as contact with nature can facilitate the appreciation of the natural world (Soga et al., 2016), and encourage pro-environmental behaviors and practices (Alcock et al., 2020; Prévot et al., 2018).

According to Soga and Gaston (2016), the extinction of experience is primarily a result of the loss of opportunities to experience nature and the loss of positive orientation towards it. Both loss of opportunity and orientation can be exacerbated as societies grow and develop economically. Specifically, the decline in opportunities is often associated with environmental degradation, increasing urbanization of the human population, over-scheduling, and technological advancements that put television, videogames and internet as the main leisure activities (Hartig et al., 2014; Hartig & Kahn, 2016; Soga and Gaston, 2016). While recreational activities, such as hiking, camping, insect catching, fishing and birdwatching, attract people to nature (Gao et al., 2019; Kurnia et al., 2021; Szczytko et al., 2020), natural areas that support these activities are quickly disappearing due to anthropogenic activities (e.g., Newbold et al., 2015; OECD/SWAC, 2020). The fragmentation of natural areas and the rural-to-urban migration of humans (United Nations, 2019b) create large isolation distances that disconnect people from nature (Miller, 2005). In fact, long distances and transportation costs affect visitation rates to natural areas across age groups, gender, and educational levels (Okello et al., 2012; S. Zhang & Zhou, 2018).

While these opportunity-related factors may be important in explaining the loss of interactions with nature, loss of orientation, understood as the feeling of connection or affinity with nature, may be an even more relevant factor (Cox et al., 2018; Lin et al., 2014). Interpretations and measures of the concept of nature connectedness are diverse in the literature, ranging from affective and cognitive aspects to facets of engagement and identity (Tam, 2013). Regardless of the indicator used, the literature suggests that nature connection is strongly associated with nature contact (Cheng & Monroe, 2012; Colléony et al., 2017; Nisbet et al., 2009; Tam, 2013), making it a key element in understanding physical detachment from the natural world. Some authors (e.g., Pyle 2003), associate the feeling of disconnection from the natural world with the change of values in our societies and the predominance of materialism and consumerism. More recently, Riechers et al. (2020) suggested that landscape simplification induced by economic growth and dietary changes could have a negative impact on various relational values and impair human-nature connectedness.

The interplay of human-nature interactions, opportunities to experience nature, and orientation towards it is neither linear nor unidirectional, marring an understanding of the causes and consequences of the loss of nature experiences (Soga & Gaston, 2016). A clear example of this is the relationship between nature contact (i.e., interactions with nature) and connectedness (i.e., feelings or affection for nature), two concepts that appear to be interdependent. Although connectedness is sometimes considered as a predictor of nature contact (e.g., Cheng & Monroe, 2012; Colléony et al., 2017), there are also several studies showing that a greater nature contact enhances connectedness (e.g., Braun & Dierkes, 2017; Lumber et al., 2017; Mayer et al., 2009). In addition, the intensity of nature contact during childhood has been reported as a strong predictor of later visits to natural areas during adulthood (Colléony et al., 2017), as well as nature connectedness and involvement in environmental actions as an adult (van Heel et al., 2023). In fact, Hosaka et al. (2018) noted, based on a study conducted in Japan, that these early nature experiences may be more important than socio-demographic factors for explaining participation in nature-based activities.

The characteristics of the environment also have an impact in the extinction of experience. For instance, the extent of urban vegetation is known to be positively associated with fascinating animal groups like birds, butterflies, and beetles (see Arjona et al., 2023; Beninde et al., 2015; Ibáñez-Álamo et al., 2020), invariably influencing nature awareness and connectedness (Lim et al., 2022; White et al., 2023). Another important factor affecting visitation rate and duration of stay in natural areas is the perception of safety in many protected and unprotected wilderness areas (e.g., Lapham et al., 2016; Mata et al., 2022), consequently shaping nature connectedness (Adams & Savahl, 2015; Sedawi et al., 2020).

Although there is a large body of literature investigating the various components and mechanisms driving the extinction of experience, such investigations are strongly biased towards countries in the Global North (Barragan-Jason et al., 2022; Bashan et al., 2021; Pett et al., 2016), leaving important knowledge gaps in our understanding of human-nature interactions in regions of the Global South. The Global South consists of underdeveloped and developing countries, many of which are in the southern hemisphere, including Africa, Latin America, Asia, and Oceania (Dados & Connell, 2012; Shackleton et al., 2021). It presents biophysical and socioeconomic contextual characteristics that differentiate it from the Global North (Shackleton et al., 2021), which could influence nature connectedness in the area. For instance, most countries in the Global South experience higher urbanization rates, and socioeconomic crises (e.g., unemployment, poverty, health, and safety) than those from the Global North (World Cities Report, 2020), which could reduce investments (e.g., time and money) in nature visitation. Furthermore, people's responses and preferences for nature vary across cultures and countries (Colléony et al., 2019). These factors justify the importance of performing studies on the extinction of experience in the Global South. However, few studies have been conducted there in this respect, and they are focused mainly on touristic aspects like analyzing visits to natural areas such as national parks or protected areas (Kruger et al., 2017; Martinez-Harms et al., 2018; Wambani et al., 2021), and the consequences (mainly in terms of knowledge impacts) of distancing from nature (e.g., Binoy et al., 2021; Muslim et al., 2018; Silva et al., 2022). Among specific regions of the Global South, Africa has received the least scientific attention in terms of human-nature connectedness research (Barragan-Jason et al., 2022) that is directly related to the extinction of experience concept. In fact, a recent systematic review of African urban ecology revealed that human dimension studies in the continent during the last century mainly focused on ecosystem services approaches rather than other topics such as the extinction of experience (Awoyemi & Ibáñez-Álamo, 2023), suggesting that additional studies are needed from this discipline. This is particularly important given the declining state of the continent’s huge biodiversity, and that outdoor activities have positive effects on human wellbeing (Lumber et al., 2017).

In the present study, we set out to determine the applicability of the extinction of experience in the Global South, specifically in an African context, by analyzing data collected from 600 respondents from four cities in southern Nigeria (Auchi, Calabar, Ibadan, and Lagos), one of the most densely populated, yet under-studied regions in Africa (e.g., Awoyemi & Ibáñez-Álamo, 2023; Seto et al., 2012). Our study's motivation was to determine the drivers of disconnection between the urban population and nature, given that previous studies have already shown that rural people in the area are more connected to nature than urban dwellers (e.g., Pam et al., 2021a, 2021b). While those studies were conducted in the rural-urban gradient in central Nigeria, the rural areas of the southern part of Nigeria are relatively insecure due to ongoing social unrest and kidnapping activities in the area (see Ojukwu, 2011; Otu et al., 2018), further explaining why we focused on urban centers. Therefore, we set the following objectives for our study: (1) To explore the extinction of experience in Nigeria, identifying patterns of contact with nature across socio-demographic groups; (2) To find out the self-reported reasons why people do not interact more frequently with nature; and (3) To investigate the cognitive dimension of human-nature connection, exploring possible associations with the identified tendencies of contact with nature. As a cognitive measure of nature connectedness, we used the Inclusion of Nature in Self scale proposed by Schultz (2002), which captures "the extent to which an individual includes nature within his/her cognitive representation of self" (p. 67). We also considered awareness of the environment by comparing perceptions with objective indicators of vegetation and birds. To achieve the proposed objectives, we adopted a two-stage empirical strategy: a first stage of descriptive and latent class analysis (to investigate the first two stated objectives); and a second stage of regression analyses (to address the third objective).

In this way, this study aims to make several contributions to the scientific literature. On the one hand, it examines human-nature relationships in a largely unexplored context. On the other hand, to our knowledge, this is the first study that attempts to identify and characterize segments of the population according to their patterns of contact with nature. An additional strength of the present research is the simultaneous investigation of experiential and cognitive dimensions of connection with nature. Through the results of this research, we intend to contribute to the proper channeling of resources aimed at improving experiences of nature in Afrotropical environments. Identifying factors underlying low levels of nature contact can inspire the design of interventions that favor intentional contact with nature and, ultimately, counteract the negative implications of the extinction of experience.

Methods

Study area and design

The study was carried out in four Nigerian cities, including Auchi, Calabar, Ibadan and Lagos (Fig. 1). In terms of landmass, Nigeria is the 14th largest country in Africa, covering about 923,768 km^2, and supporting several parks, natural areas, biodiversity hotspots and scenic sites (Ezealor, 2001). However, by mid-2023, Nigeria has an estimated human population of 223.8 million, translating to *c*.242 $humans/km^2$

(United Nations Population Fund, 2023), and suggesting an increasing need for awareness creation about nature conservation, particularly in highly urbanized areas.

Table 1. Human Population (2016), Gross Domestic Products (GDP Per Capita; 2007) and land area (2006) of the state the studied cities are located (https://nigeria.opendataforafrica.org/).

City	State	Land area (km^2)	Population	*Density (persons/km^2)	GDP Per Capita $ (2007)
Lagos	Lagos	3,671	12,550,598	9,270	4,333
Ibadan	Oyo	26,500	7,840,864	6,116	2,666
Auchi	Edo	19,187	4,235,595	3,308	3,623
Calabar	Cross River	21,787	3,866,269	9,059	3,150

Note: *The density of the cities is based on data from Africapolis (http://africapolis.org), allowing us to gauge the qualification of each city as an urban center (i.e., >1600 inhabitants/km^2 according to Marzluff, 2001). Other indicators in the table are only available at the state (regional) level.

Nigeria has two vegetation zones: rainforest and savannah (Ezealor, 2001). The studied cities fall within the rainforest zone characterized by dense evergreen forests of tall trees with thick undergrowth (Ola-Adams & Iyamabo, 1977). Additional information on population density and Gross Domestic Product of the study area is provided in Table 1.

Before choosing the studied cities, we first ensured that each of them qualified to be considered an urban center by having a contiguous patch of built-up land > 1 km^2, and dominated by human-constructed features like buildings (>10 buildings/ha), high human density (>1600 inhabitants/km^2), roads, and vehicles (Marzluff, 2001; Niemelä, 1999; C. H. Nilon et al., 2003; Schneider et al., 2010). In addition, two of our studied cities (Lagos and Ibadan) are among the most densely populated in the entire African continent (World Cities Report, 2020). Thus, our selection of cities followed the criterion used by Taylor et al. (2018), who performed a similar survey in the two most-populous cities in each of Australia and New Zealand. Second, we ensured the widespread geographic distribution of our studied cities to cover the diverse cultural or ethnic groups (e.g., Yoruba, Igbo, Ibibio, etc.) in southern Nigeria (Oladipo et al., 2007). Third, our studied cities share similar biotic and abiotic conditions (Ezealor, 2001). By meeting these criteria, our sample could be considered a fair representation of urban southern Nigeria (*cf.* Table S1).

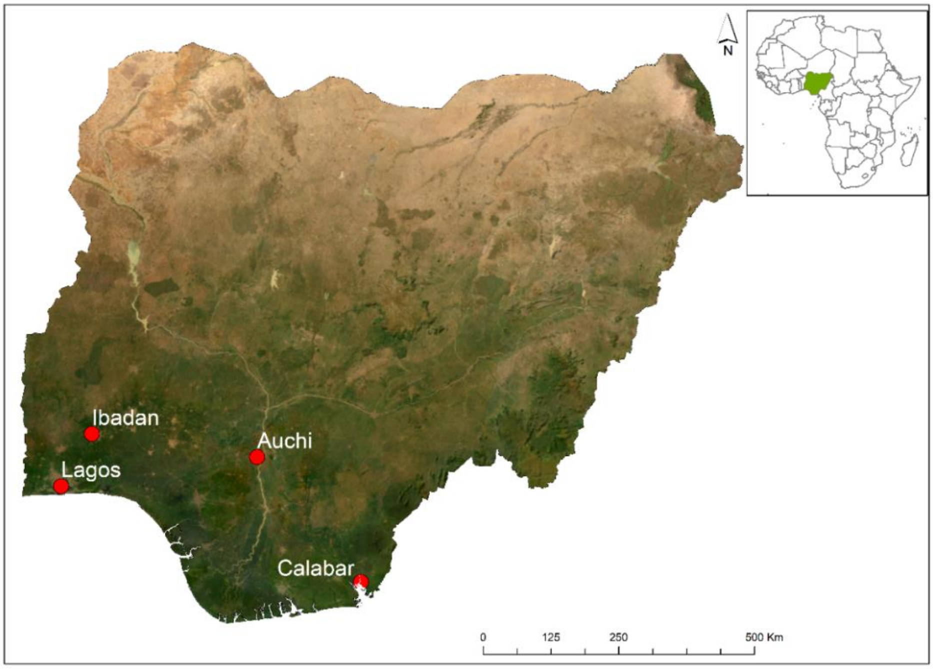


Figure 1. Location of the study cities within Nigeria (highlighted box) and the African continent.

We used the "create random points tool" in ArcGIS (https://pro.arcgis.com/en/pro-app/latest/tool-reference/data-management/create-random-points.htm) to stratify each city into five compartments stationed at the city center and its four cardinal points (i.e., west, east, south and north of the city center) similar to Ciski et al. (2019). Each compartment measured 1 X 1 km, and separated from any other by at least 500 m, allowing us to capture information from respondents living in neighborhoods with different urbanization levels, vegetation cover and other socioeconomic characteristics following previous studies using a similar approach (e.g., Cox et al., 2018; Galbraith et al., 2015). Within each compartment, we also used the "create random points tool" in ArcGIS to randomly select five points (at least 200 m apart among them) as focal areas to perform the face-to-face interviews (see below), thus, securing a wide representation of inhabitants from each compartment. All points were marked with a Global Positioning System device (Garmin etrex 20 X) to identify the exact geographic coordinates. Furthermore, the selection of these compartments and focal points was also needed to match the socioeconomic information obtained from the interviews with the remotely sensed vegetation data (i.e., Normalized Difference Vegetation Index) and bird data (i.e., bird species richness) that require a similar methodological approximation to grant its independence from point to point (e.g., Kubiszewski et al., 2019). This standardization of compartments and points across the studied cities matches the methodology followed by other studies (e.g., Cox & Gaston, 2015; Ibáñez-Álamo et al., 2020).

We purposively used questionnaires to interview six respondents from each point, totaling 150 people from each city and 600 respondents across the four cities. The total sample of 600 people consisted of an equal number of men and women as gender quotas were established to ensure equal representation. The surveys were conducted face-to-face (led by A.G. Awoyemi) between August and November 2021. At each point, six potential respondents (3 women and 3 men) were approached and asked if they lived within the 200-m radius of each point before interviewing them on a voluntary basis as no payments were made (otherwise they were not interviewed). This was relevant as it reflects respondents' experience and contact with nature on a daily basis (Taylor et al., 2018). Participants that agreed to answer the survey questions were then introduced to the purpose and objectives of the research, guaranteed anonymity and confidentiality of their responses, and were informed of their right to withdraw from the survey at any time. In addition, they were given the option to leave blank any questions they preferred not to answer. Each participant was interviewed independently of any other to ensure the uniqueness of the responses received. We conducted the interviews at different hours (mornings and evenings) of the day (week days and weekends) across the studied cities similar to other previous studies (e.g., Cox & Gaston, 2015). This procedure allowed us to cover a broad segment of the society with different socio-demographic and economic characteristics (Table S1).

Structured questionnaire and variables

Current experience of nature

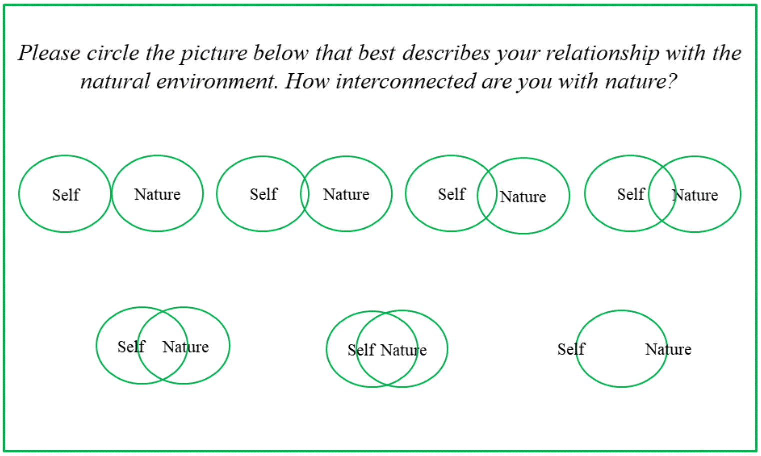
To assess experiences of nature, we relied on direct and intentional contact with nature. We opted for a broad definition of nature, including neighborhood greenspaces, parks and managed settings, because they can play a crucial role in reversing the extinction of experience, especially in urban centers. Previous evidence indicates that the benefits of interacting with nature are not limited to wilderness environments, but also to a broader definition of nature (Gaston & Soga, 2020).

We asked about the frequency of contact with nature adapting the measures used by Soga et al. (2016). Thus, respondents were asked the following questions: (1) "How frequently do you visit natural places (e.g., neighborhood green areas, parks with lots of trees, beach, mountain, orchards, forest reserves, woodlot)?" (*visits*); (2) "How frequently do you touch plants or flowers in natural places?" (*plants*); (3) "How frequently do you observe or touch animals (e.g., birds, insects) in natural places?" (*animals*), which could facilitate nature connection, particularly during childhood

(Franco et al., 2017; Kahn, 1997; Lumber et al., 2017). In addition to the frequency of visits, we considered the frequency of interactions with animals and plants to capture interactions that involve a more conscious and meaningful engagement with nature. Participants responded to those questions using a 6-point Likert scale (with 1 = never, 2 = once yearly, 3 = once every season, 4 = every month, 5 = every week, and 6 = every day). Those respondents who did not report the maximum frequency for all nature interaction questions were asked why they did not experience nature more often. They could choose several of the following options to answer this question: 1 = “I don’t have time”, 2 = “I don’t have money to visit them”, 3 = “Lack of natural areas nearby (it is too far)”, 4 = “I have a disability / Health problem”, 5 = “I am not interested / I don’t like nature”, 6 = “Other reason”. We also considered the duration of visits to natural places (*duration*). Respondents answered the question “How long do you normally stay in natural places?” on a 5-point Likert scale (1 = some minutes, 2 = some hours, 3 = half a day, 4 = whole a day, and 5 = several days).

Previous experiences and setting

Respondents also answered the three previous questions on the frequency of contact with nature (*visits, plants* and *animals*) during their childhood, classified here as when they were 6—12 years old. We created an aggregated indicator of the frequency of interactions with nature during childhood as the sum of the scores of the three questions (*childhood frequency of nature contact*). We also asked if they had ever lived outside their current city (yes or no) as a factor that could influence opportunities to interact with nature (*lived outside current city*).



Please circle the picture below that best describes your relationship with the natural environment. How interconnected are you with nature?

Figure 2. Schematic representation of the level of nature connectedness adopted from Schultz (2002).

Nature connectedness

We evaluated affinity with nature (*nature connectedness*) using the Inclusion of Nature in Self Scale (Schultz, 2002), which is an adaptation of the Inclusion of Other in Self Scale by Aron et al. (1992). Based on self-concept, this scale captures the cognitive dimension of connectedness with nature through a graphic question. Seven pairs of circles are shown overlapping to different degrees, one labeled “Self” and the other “Nature”, and respondents were asked to choose the pair that best reflects their interconnectedness with the natural world (Fig. 2). Each pair of circles is assigned a score from 1 (separate circles) to 7 (completely overlapped circles).

Perception of nature

We assessed the opportunity to experience nature by asking about the participants' perception of the level of nature in their neighborhood (*perception of neighborhood naturalness*). Here, we described neighborhood naturalness to respondents as the coverage of vegetation (%) within the 200-m radius of each sampling point (i.e., where respondents live) following previous studies (e.g., Cox et al., 2018; Ugolini et al., 2020, 2021). We then asked them to rate (on a 5-point Likert scale) how natural the location they live in is (i.e., the 200-m radius), whereby 1 = very artificial (≤20% vegetation cover), 2 = artificial (≤40% vegetation cover), 3 = intermediate (≤60% vegetation cover), 4 = natural (≤80% vegetation cover), 5 = very natural (100% vegetation cover). We also asked for the types (based on taxonomic families) of birds (e.g., sparrows, pigeons, kites, crows; *perception of bird types*) they usually found there (1 = very few (<3), 2 = few (3-4), 3 = intermediate (5-7), 4 = many (8-18), 5 = very many (>18)) by showing them different images using the guide to the Birds of Western Africa (Borrow & Demey, 2014). We defined the number of bird types for each category based on the information on bird censuses (5 mins/point) carried out in the same sampled cities and points in November 2020-January 2021 as part of another study on the association of urbanization with avian diversity.

Measured indicators of nature (vegetation and birds)

The Normalized Difference Vegetation Index (NDVI) estimates the presence and photosynthetic vigor of vegetation, and is commonly used to investigate the relationships between nature and human well-being in urban areas (Pereira et al., 2012; Taylor et al., 2018). To estimate the NDVI, we downloaded Cloudless Sentinel 2 Level 1C Images to cover the survey period (November 2021), from the USGS Earth Explorer (https://earthexplorer.usgs.gov/). We then used the “spectralindices” function to estimate the mean NDVI using the R Statistical Software (Alabi et al., 2022; Leutner et al., 2019; Suab & Avtar, 2020).

Some months before the interviews (November 2020-January 2021), a single observer (A.G. Awoyemi, an expert ornithologist with > 10 years of experience censusing birds in Nigeria) recorded the number of individuals of each bird species seen and/or heard within a 50-m radius (Ivande & Cresswell, 2016) of each point where respondents were interviewed (bird species richness). The bird censuses were done following general recommendations for quantifying birds (Bibby et al. 2000) and thus carried out only under good weather conditions and during the morning (up to 4 h after local sunrise; Manu et al., 2006).

Safety perception

We asked respondents to score how safe they felt in their neighborhood (*safety*), translating to a 200-m radius of each sampling point, where they could have direct and daily interaction with nature (Cox et al., 2018; Taylor et al., 2018). This was also scored on the following 5-point Likert scale, including not at all (1), a little (2), moderately (3), quite a bit (4) or extremely (5).

Socioeconomic characteristics

We obtained socio-demographic information from respondents, including age (continuous), gender (male or female) and marital status (single, married, divorced or widow); children (continuous). We also asked for their level of education (no formal education, primary, secondary, technical/polytechnic or university), employment status (self-employed, employed by someone or not employed); and level of monthly income, scaled based on the approved Nigerian minimum wage of 30,000 Naira (National Minimum Wage Act, 2019), and converted to USD ($) on 30 November 2021 (<$73, $73-$145, $145-$218, $218-$290, >$290).

Methods of data analysis

This study was conducted following a two-stage empirical strategy. Statistical analyses were conducted using the R Statistical Software (R Core Team, 2022).

Latent class analysis

To identify latent and unobserved groups, and to determine how the resulting subgroups differ in their pattern of human-nature interactions in the study area, we performed a Latent Class Analysis (LCA), which offers a probability-based classification

(Scheier & Komarc, 2020; Song et al., 2021; Walsh et al., 2023). To achieve that, we used the "MixAll" package, which consists of algorithms and methods for model-based clustering and classification (Iovleff & Bathia, 2022). The MixAll package was relevant to our LCA because it supports different types of data (e.g., continuous, categorical/qualitative, count), missing values, and models (e.g., Gaussian, Gamma, Poisson), and is commonly deployed in clustering analysis (e.g., Ma et al., 2021; Nagode & Klemenc, 2021).

A total of 11 indicator variables (described above), including those related to socio-demography (*gender, age, education, marital status, children, employ* and *income*) and intentional contact with nature (*visits, plants, animals* and *duration*) were incorporated into the LCA to identify the groups. In MixAll, the number of classes must be ≥ 2 (Iovleff & Bathia, 2022). Thus, we ran models up to five classes following Song et al. (2021), and selected the best model (see Table 2) as the one with the lowest Bayesian Information Criterion (BIC) value (Burnham & Anderson, 2002; Nylund et al., 2007; Schwarz, 1978; Song et al., 2021). It is worthy of note that the incorporation of additional classes (i.e., > 5) increased BIC values, supporting our selection of five classes. The LCA generated an additional categorical variable, termed "Class" with two levels, including Class 1 (low nature contact) and Class 2 (high nature contact), which was included in further analyses. Thus, we first explored the distribution of the respondents across the identified latent classes, and how such variations influenced their self-reported reasons for not visiting nature more often.

Table 2: Goodness of fit of Latent Class Analysis of human-nature interaction in southern Nigeria (n = 600).

Class	Log Likelihood	Bayesian Information Criterion	NFP
2-class	**-8968.52**	**19197.23**	**197**
3-class	-8742.85	19379.18	296
4-class	-8521.19	19569.16	395
5-class	-8368.98	19898.05	494

Note: NFP = Number of Free Parameters of the Mixture Model. The best model (2-class) is highlighted in bold.

Regression analysis

At the second stage, we performed regression analyses to determine differences in: (1) nature connectedness due to latent class membership (Class 1 vs Class 2) and the remaining variables not used to define the classes, including safety, childhood frequency of nature contact and living outside the current city, (2) NDVI due to subjective perception of neighborhood naturalness and latent class membership, and (3) bird species richness due to subjective perception of types of birds and latent class membership. We decided to use bird species richness since it positively correlated with the number of families of the sampled birds (*r* (598) = 0.98, $p < 0.001$).

We checked the assumptions of normal distribution of our response variables (Shapiro & Wilk, 1965) and use log-transformed data when it was possible to obtain a reasonably normal distribution (i.e. NDVI). When the normal distribution was not obtained even after transforming data, we fitted our models using Poisson distribution (i.e., bird species richness). However, for the nature connectedness response variable, which is ordinal with natural and ordered categories, we performed an Ordered Probit Analysis using the "ordinal" package and probit link (Christensen 2023; Ferreira & Moro 2013). To check for potential interactions between the latent classes and our predictors on these response variables, we included an interaction of the latent class membership with all the independent variables included in the models.

We then used a stepwise backward selection method to simplify the models (Crawley, 2013; Marhuenda et al., 2014). Thus, starting with interaction terms, variables with the highest p-values were first removed, and the procedure repeated until the best model (containing significant effects) was selected as the one with the lowest Akaike Information Criterion value (Burnham & Anderson, 2002). We set statistical significance at p-value < 0.05.

Results

Description of the sample

The study sample was balanced in terms of gender and the number of respondents from each city. Participants ranged in age from 14 to 72 years old (Mean ± SD = 34.89 ± 11.69 years). Approximately, 40% of the participants had a secondary school education, 30% technical school, and 20% university education. In terms of marital status, most of the participants were married (59.7%). In relation to income, 49% of the respondents who indicated their monthly income chose the lower range (<$73). This low-income level is very similar to that found by the Nigeria Poverty Map, which reveals that about 4 of 10 Nigerians (40%) are poor according to the 2018/19 national monetary poverty line (National Bureau of Statistics, 2023). In fact, when other factors, such as deprivations in cleaner cooking energy, sanitation, healthcare, food insecurity, housing, and education, were incorporated (termed multi-dimensional poverty), the poverty level increases to 63%. Given that the data also show that poverty level in northern Nigeria (65%) is higher than in the south (35%; our study area), and is also higher in rural (72%) than in the urban areas (42%) (National Bureau of Statistics, 2023), our data could be considered a fair representation of urban areas in southern Nigeria (*cf.* Table S1). The descriptive statistics of socioeconomic characteristics and other variables are given in Table 3.

Table 3. Descriptive statistics of the main variables of the questionnaire: current nature experience, previous experiences and setting, nature connectedness, perception of nature, safety perception and socioeconomic characteristics.

Variables	Obs	Mean / %	Std. dev.	Min	Max
Current experience of nature					
Duration	500	2.24	0.841	1	5
Visits	598	2.115	1.544	1	6
Plants	598	2.296	1.762	1	6
Animals	597	2.323	1.810	1	6
Previous experiences and setting					
Childhood frequency of nature contact	596	10.675	5.997	3	18
Living outside current city	599	0.841		0	1
Nature connectedness					
Nature connectedness (INS)	597	3.173	2.132	1	7
Perception of nature					
Perception of neighborhood naturalness	597	2.931	0.938	1	5
Perception of bird types	596	2.678	1.055	1	5
Safety perception					
Safety	596	3.5	1.134	1	5
Socioeconomic characteristics					
Age	572	34.886	11.686	14	72
Gender (female)	600	0.503		0	1
Marital status					
Single	598	0.383		0	1
Married	598	0.597		0	1
Divorced	598	0.012		0	1
Widow	598	0.008		0	1

Table 3 cont'd

Variables	Obs	Mean / %	Std. dev.	Min	Max
Children	600	1.965	1.886	0	10
Education					
no formal education	583	0.012		0	1

Primary	583	0.098	0	1
Secondary	583	0.401	0	1
technical/polytechnic	583	0.290	0	1
University	583	0.199	0	1
Employment status				
self-employed	592	0.578	0	1
employed by someone	592	0.329	0	1
not employed	592	0.093	0	1
Income				
<$73	418	0.490	0	1
$73-$145	418	0.258	0	1
$145-$218	418	0.086	0	1
$218-$290	418	0.089	0	1
>$290	418	0.077	0	1

Latent class membership: patterns of nature experience

Through the LCA, we identify unobserved groups or classes of cases that explain associations between the indicator variables (contact with nature and socio-demographic characteristics). Overall, the LCA disaggregated the sampled respondents into two classes: Class 1 (low nature contact, n = 323) and Class 2 (high nature contact, n = 277) as shown in Figures 3 and 4.

Regarding human-nature interaction, a large proportion of the respondents in Class 1 reported to never visit natural areas (Fig. 3a) nor observe animals (Fig. 3b) or plants (Fig. 3c), and spend little time in natural areas (Fig. 3d) in comparison with Class 2. The differences between the two groups were more pronounced in terms of frequency of contact, while they were less evident in terms of the time spent in nature. For both groups, spending a few hours in nature was most common, although people in Class 2 are more likely to spend longer periods than those in Class 1.

In terms of socio-demographic variables, there were similar levels of interactions with nature by females and males (Fig. 4a), though a higher level of nature contact was observed among younger respondents (Fig. 4b), and those with slightly lower number of children (Fig. 4c). While Class 1 with low nature contact was dominated by married respondents, Class 2 has a more balanced proportion of married and single respondents (Fig. 4d). We found lower levels of nature contact among respondents with lower educational levels (e.g., secondary/high school) than those with higher qualifications, such as university and technical degrees (Fig. 4e). Regarding the studied cities, respondents living in Lagos showed lower levels of nature contact (Class 1) relative to others, such as Ibadan, where respondents interacted with nature more often (Class 2; Fig. 4f). Occupational status also seems to exert some influences on nature interaction behavior as we found that the group with lower contact with nature was mainly comprised of self-employed people (Fig. 3g). Finally, results of income are noteworthy, with respondents earning less than $73 showing lesser likelihood of nature contact (Class 1).

As for the declared reasons for infrequent interactions, the lack of time, money, and nearby natural areas was commonly reported across the two class memberships (Fig. 5). All stated reasons were relatively higher in Class 1 (low nature contact) than Class 2 (high nature contact).

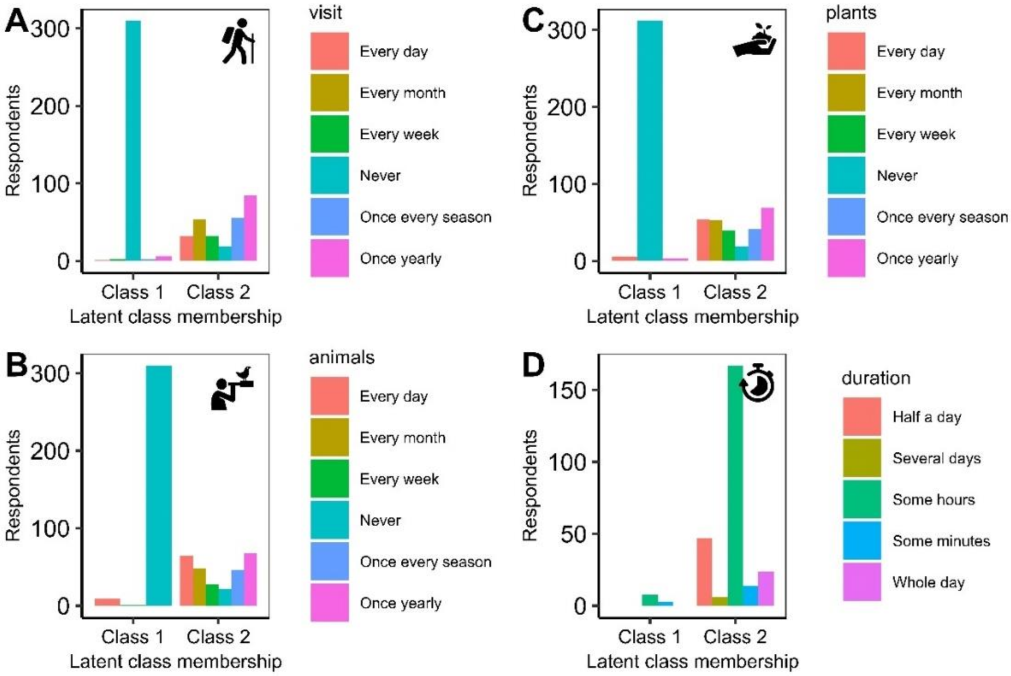


Figure 3. Latent class membership of nature contact among sampled urban populations in Nigeria.

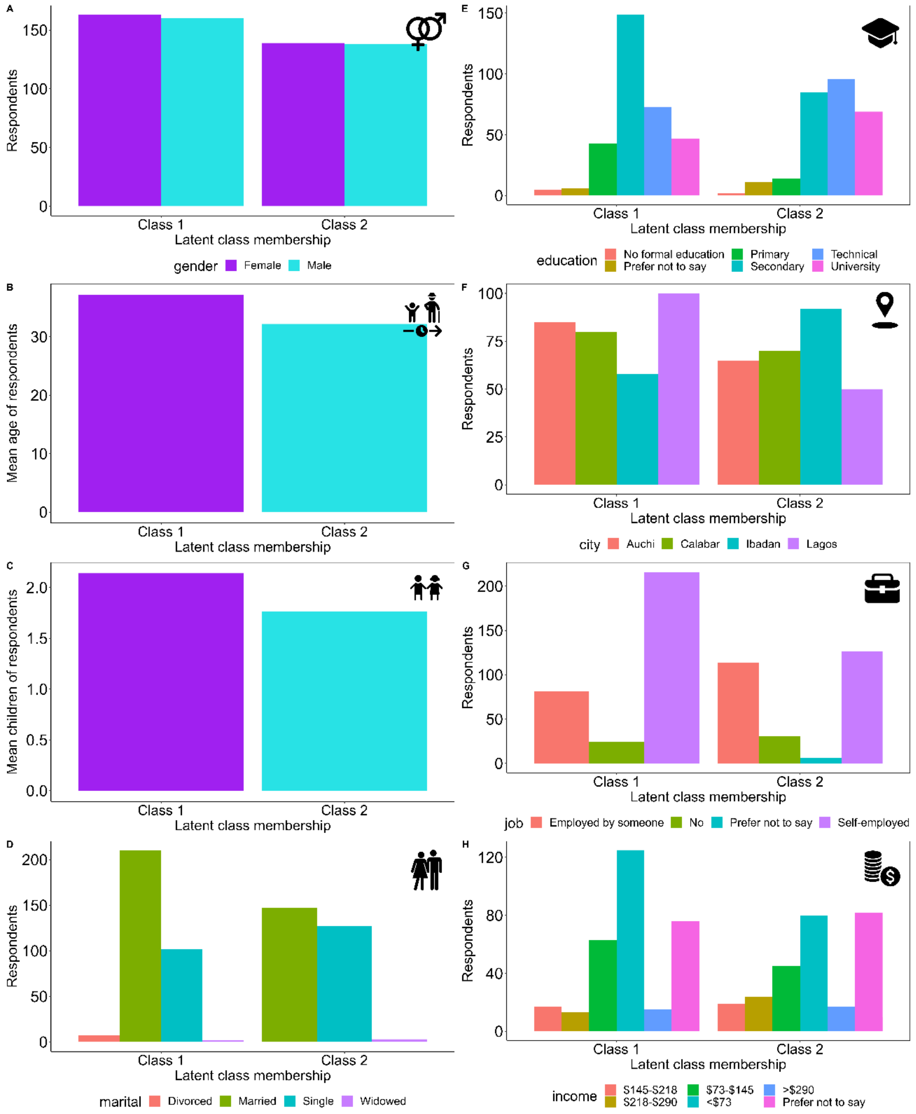


Figure 4. Latent class membership of socio-demographic variables of sampled urban populations in Nigeria.

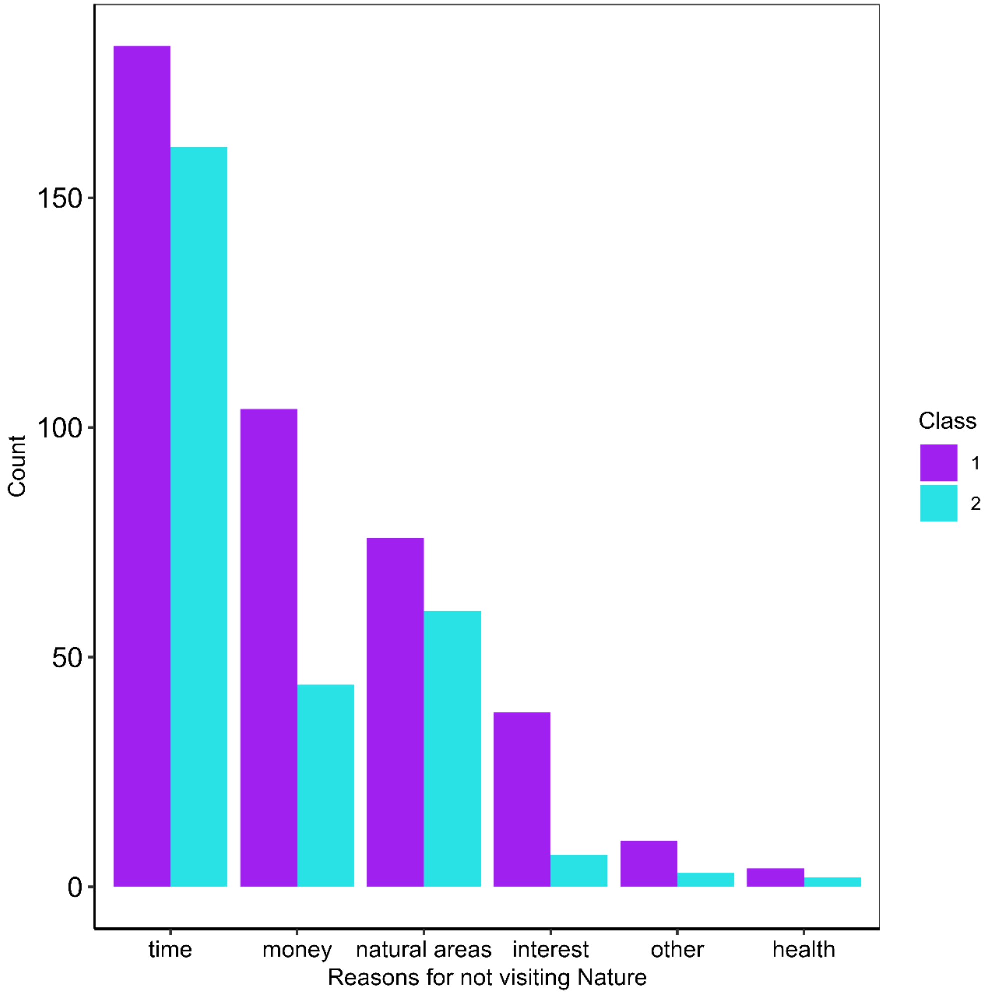


Figure 5. Differences among latent classes of declared reasons for infrequent interactions with nature among sampled urban populations in Nigeria.

Cognitive connection to nature

The results of our regression analyses showed interesting trends that consolidate the results obtained in the LCA. As anticipated, the Class 2, with higher nature contact based on the LCA, also demonstrated a significantly higher nature connectedness than Class 1 (Table 4; Fig. 6). Furthermore, while nature connectedness (independently of class membership) increased as the perception of neighborhood safety improves, we found no significant correlation between nature connectedness and whether respondents ever lived outside their current city or not (Table 4). The only significant interaction effect shows a negative correlation between nature visitation during childhood and Class 2 (Table 4; Fig. 7).

Table 4: Results of an Ordered Probit Model exploring the predictors of nature connectedness in Nigeria. It includes the best model (AIC = 1981.97), and the statistically non-significant and rejected interaction effects.

	Estimate (SE)	**p-value**
Class 2	1.438 (.19)	< 0.001***
Safety	0.065 (.04)	0.106
Childhood frequency of nature contact	0.025 (.01)	0.016*
Lived outside current city	0.111 (.12)	0.369
Class 2 * Childhood frequency of nature contact	-0.035 (.02)	0.022*
Rejected variable		
Class 2 * Safety	-0.004 (.08)	0.963
Class 2 * Lived outside current city	0.119 (.246)	0.628

Note: Significant effects are indicated by * at p values < 0.05, and *** at p value < 0.005. Threshold Coefficients of the final model show estimate (se): 1|2 = 0.556 (.22); 2|3 = 1.026 (.22); 3|4 = 1.417 (.22); 4|5 = 1.887 (.22); 5|6 = 2.027 (.22); 6|7 = 2.320 (.23).

We found a negative significant correlation between respondents' perception of neighborhood naturalness and the real (measured) naturalness estimated through NDVI irrespective of class membership (t = -2.600, p = 0.010; Fig. 8a; Table S2). In addition, we found no significant association between the respondents' perception of types of birds (independently of class membership) and the real (measured) bird species richness (t = -1.080, p = 0.280; Table S3). Exploring this dissociation further revealed that perception of neighborhood naturalness and types of birds significantly (positively) correlated (*r* (593) = 0.33, p < 0.001; Fig. 8b). Finally, the bird species detected in our censuses showed 35 different bird species of 22 families (Table S4). Of this total bird species, 23, 19, 16 and 16, were recorded in Ibadan, Auchi, Calabar and Lagos, respectively.

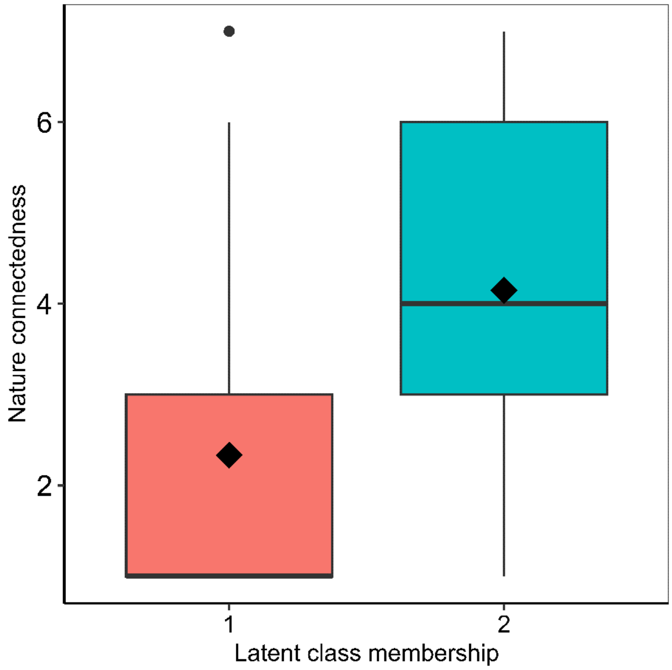


Figure 6. Differences in nature connectedness between Class 1 (low nature contact) and Class 2 (high nature contact) of respondents sampled in Nigeria. The boxplots show the mean (black rhombus), median (bar across rectangles), upper and lower quartiles and extreme values.

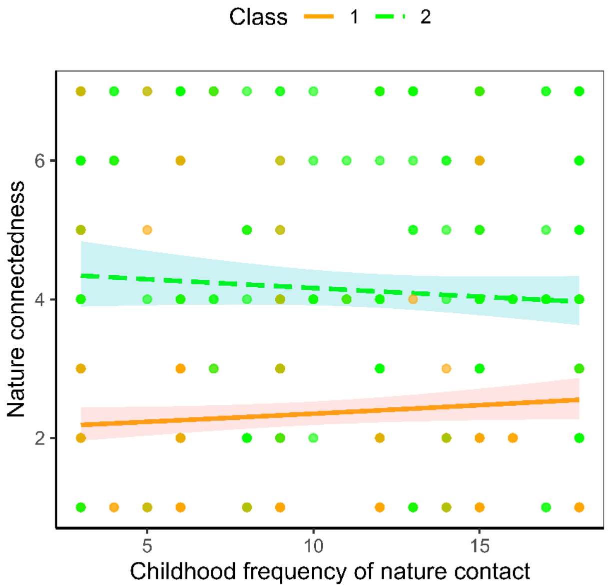


Figure 7. Interaction between nature connectedness and visitation to natural areas during childhood between Class 1 (low nature contact) and Class 2 (high nature contact).

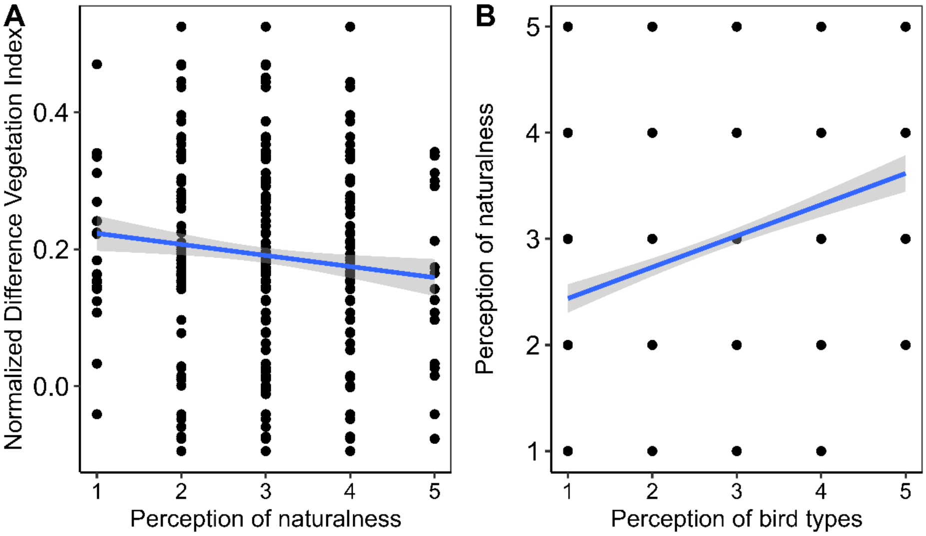


Figure 8. (a) Association between perception and real (measured) neighborhood naturalness in Nigeria, (b) Correlation between perception of neighborhood naturalness and perceived number of bird types in Nigeria.

Discussion

Many cities in the Global South are growing rapidly, leading to the loss of biodiversity (Seto et al., 2012; United Nations, 2019a). This urbanization process also has the potential to disconnect people from nature as supported by our findings. Our study analyzed the human-nature connection from a broad perspective, considering both the experiential and cognitive dimensions, as well as their interrelationships and shows a high level of extinction of experience in Nigeria. Thus, it fills an important knowledge gap by broadening our understanding of this crucial process from a Global South perspective (Barragan-Jason et al., 2022; Pett et al., 2016).

Relationships between experiential connection to nature and socioeconomic and demographic variables

Our study reveals a relatively large proportion of people with no nature experiences, corroborating the weakening of the relationship with nature reported by previous studies (Binoy et al., 2021; Cox et al., 2017; Imai et al., 2019; Soga et al., 2018). Despite this consistency of results, the proportion of people who never interacted with nature in this study (55%) was substantially higher than those reported from the Global North, where such proportion was ≤10%, whether considering only urban greenspaces (Ishibashi et al., 2020; Soga et al., 2015) or a wide variety of natural places (Colléony et al., 2017). The obtained low levels of contact with nature were particularly striking, especially given the temporal context of this study. We conducted our surveys in 2021 after the lock-down measures taken to curb the Covid-19 pandemic, when Lee et al. (2022) predicted a surge in nature experiences in Africa. Studies from other geographic areas have reported changes in preferences for contact with nature after the coronavirus crisis, favoring a higher frequency of visits to natural areas (Berdejo-Espinola et al., 2022; Lenaerts et al., 2021; Stankowska & Stankowska-Mazur, 2022).

However, distancing from nature did not occur homogeneously among the study participants. The performance of the LCA allowed us to disaggregate the respondents into two homogenous groups differing in their behavioral tendencies. Despite its potential benefits, this methodological approach is seldom used to investigate human-nature interactions so far (Batool et al., 2022; Huynh et al., 2022; Jorgensen & Meis-Harris, 2022). Based on the segmentation of the intensity of nature contact by the LCA, the socioeconomic and demographic variables investigated in this study reveal important patterns that could be useful to improve our understanding of human-nature interactions from an African perspective. Our result showing a lower level of nature contact among older respondents suggests the potential influence of ageing that could limit the ability of older people from visiting nature more often, a pattern revealed by previous studies (e.g., Freeman et al., 2019). In contrast, the higher nature contact among younger respondents could also be associated with the recent increasing environmental consciousness across the world (e.g., Urbański & ul Haque, 2020). However, if that applies to the study area, we would have expected that respondents with a higher number of children (synchronizing with recent decades) to experience nature more often, which was not the case here. This contrasting result suggests the influence of other potential factors. For instance, a higher number of children could imply higher family responsibilities for our study participants, and consequently reducing investments (e.g., time) on nature contact. Supporting this position regarding higher responsibilities, we also show that low nature contact was more prominent among married participants in comparison with those identified as being single. Nevertheless, environmental education shows promise in mitigating the low level of nature contact in Nigeria as our result already shows that nature contact is higher among more educated respondents.

Meanwhile, Lagos holds the largest proportion of respondents with low nature contact, which is hardly surprising. On the one hand, Lagos is one of the most rapidly developing cities in the world (World Cities Report 2020), which could have negative impacts on the associated biodiversity. This is supported by our study given that we recorded the lowest bird species richness in this city relative to others. Birds are an important animal group that promotes the interconnectedness of people with nature across different cities (e.g., Cox & Gaston, 2015). This could in part explain why Ibadan respondents experience nature more often relative to those sampled in each of the remaining studied cities. In addition to the highest bird species richness, the Ibadan Bird Club was established in 2014, growing in membership and meeting at monthly intervals, to promote birdwatching around the city of Ibadan, consequently reconnecting people with nature in the area (Awoyemi & Bown, 2019). On the other hand, Lagos is the center of economic activities in Nigeria (National Bureau of Statistics, 2023), which could partially restrict nature contact too. For instance, our result showing low nature contact among respondents that were self-employed than those employed by someone or had no job, suggests that people in the study area could prefer to invest more time in their businesses to boost their income and profit. This makes sense given that the majority of respondents earn less than $73 monthly, particularly those in the class with low nature contact. Our results are unique in this respect by allowing us to quantify the influence of socioeconomic and demographic variables on an additional facet of living standard (i.e., human-nature interaction), which is now recognized globally as an antidote against mental health issues (Keniger et al., 2013; Tillmann et al., 2018).

Factors influencing cognitive connection to nature

Our study supports the growing body of literature (e.g., Lumber et al., 2017; Tam, 2013) showing the positive associations between nature contact (i.e., experiential connection) and connectedness (i.e., cognitive connection). Here, the investigated nature connectedness based on the Inclusion of Nature in Self Scale (Schultz, 2001, 2002) reveals interesting findings. Overall, the perceived relationship between self and nature was very weak, with a third of the respondents perceiving themselves as completely separate from nature. This could be due to the low level of direct interaction with nature, as the different dimensions of nature connection may interact and influence each other (Ives et al., 2018). The results of the Ordered Probit Analysis support this idea, as Class 2 (high nature contact) shows a significantly higher connectedness too.

As expected, the perception of safety by respondents positively correlates with nature connectedness irrespective of class membership, reinforcing previous findings (e.g., Sedawi et al. 2020). This result is crucial for potential decision-making and actions. For instance, the non-urban sites (e.g., wilderness, national parks and forest reserves) where people could also connect with nature are riskier in Nigeria (Ojukwu, 2011; Otu et al., 2018), suggesting that the perception of safety risks in the cities could further aggravate the low level of nature connectedness detected in our study. On this note, we call for the need to make urban greenspaces safer in Nigeria, and potentially in other areas of the Global South, where this peculiar situation exists.

Regarding the variables relating to participants' past, nature connectedness did not significantly correlate with whether respondents had lived outside their current city, but significantly declined with increasing number of visits to natural areas during childhood (for the Class 2 with high nature contact). These results contradict the notion that earlier (childhood) experiences in nature are very important for developing a strong bond with nature during adulthood (Passmore et al., 2021; van Heel et al., 2023). Nevertheless, our results are encouraging as they suggest that strong nature connectedness could still be developed later in life regardless of the individual's background.

Perhaps, surprising were our results showing a dissociation between real (measured) and perceived neighborhood naturalness and bird species richness independently of class membership. Here, NDVI significantly (negatively) correlates with the perception of neighborhood naturalness by the respondents on the one hand. This result suggests that the study participants were probably not aware of, not interested in or even underestimate the amount of greenness in their neighborhood, which is plausible given the low nature contact and connectedness detected in this study. This is particularly concerning given that our research focused on the immediate vicinity, where respondents could interact with nature on a daily basis. It is also possible that the respondents were rather more interested in certain plant parts like flowers or fruits (see Shwartz et al. 2014) than the amount of green vegetation in their neighborhood, pinpointing the need to investigate further the items that attract people to nature in the area. On the other hand, we found no significant association between the real (measured) and perceived bird species richness of the neighborhood. Poor identification skills could make it difficult for the study participants to differentiate the different kinds of birds found in their neighborhood, potentially leading to an important underestimation. Our result showing a positive significant correlation between the perception of neighborhood naturalness and bird species richness supports this position, and in general could indicate the need for additional educational activities involving birds (like those performed in the area by the Ibadan Bird Club or the A.P. Leventis Ornithological Research Institute; https://www.aplori.org/) in order to improve the value of nearby urban nature.

In general, studies have shown a weak relationship between real and perceived biodiversity while recommending different ameliorative strategies (e.g., Belaire et al., 2015; Dallimer et al., 2012; Shwartz et al., 2014). In the UK for example, the deployment of bird feeders shows promise in mitigating the gap between perceived and actual bird species richness (Cox & Gaston, 2015). However, we did not record any act of feeding wild birds during our survey, an uncommon practice in Nigeria. Since respondents with higher levels of education experienced nature more often according to our results, environmental education could be more applicable in bridging the gap in biodiversity knowledge in the Nigerian context.

Reasons for infrequent nature visitation

The main reason participants gave for not interacting with nature more often was the lack of time. This finding is in line with that found by Boyd et al. (2018) that revealed "too busy at work" or "too busy at home" as the two main reasons for not visiting natural environments. As these authors pointed out, more research is needed to understand how people prioritize and allocate their time across different activities.

The lack of money was the second most important reason for not visiting natural areas more often given by respondents in Class 1 (low nature contact). Given the various economic crises experienced by Nigeria, particularly during the Covid-19 Pandemic (Ozili, 2021; Stanley et al., 2020), respondents might have to prioritize the items on which they expend their limited income, which was <$73 for almost half of the respondents (49%). This total monthly income will, for example, only cover a 2-day return travel for a person to visit the Okomu National Park from Lagos, suggesting why respondents in our study may not have enough money to visit natural areas amidst other demanding living expenses like feeding, housing, healthcare, and education. It is thus hardly surprising that people with higher incomes tend to visit greenspaces more frequently (Jones et al., 2009), spend more time in them (Soga & Akasaka, 2019) and participate more in nature-based activities (Hosaka et al., 2018). On the one hand, higher incomes could enhance mobility due to the availability of private vehicles and capacity to travel farther to explore more natural areas (Martinez-Harms et al., 2018). On the other hand, wealthier neighborhoods tend to have higher quality greenspaces that are relatively easier to explore (Cox et al., 2017; Hoffimann et al., 2017), a pattern known as the luxury effect that is present in various urban ecosystems and cities around the world including Africa (Chamberlain et al., 2019; Leong et al., 2018).

Another main reason why respondents did not increase their nature experience was the lack of nearby natural areas. This reason was particularly noticeable among members of Class 2 (high nature contact), suggesting the existence of people who would like to interact more with nature but lack the opportunities to do so. This result could be explained from two dimensions. First, it could be due to the respondents' lack of knowledge/awareness of the urban nature associated with their immediate environment as we had found a no significant or even negative associations between the real and subjective perception of nature and birds. Second, it could have arisen from the lower levels of biodiversity associated with urban centers in our studied cities. For instance, the cities included in our investigation are located in southern Nigeria, a region in Africa that has experienced an exponential loss of forest cover stemmed from different factors (FAO, 2011; Popoola, 2016), particularly urbanization (Awoyemi & Ibáñez-Álamo, 2023; Seto et al., 2012). This urban expansion seems to be an important predictor of people's affection for nature in the area (Bashan et al., 2021). For instance, Lagos is the most densely populated of the sampled cities (2,607 people/km^2), but also holds the highest number of respondents who never visited natural areas as well as the lowest bird species richness. Although accounting for a small fraction, our study also reveals the lack of interest and health issues as reasons for not visiting nature more often.

Study limitations and future research directions

Before concluding, some limitations of the study should be highlighted, one of which lies in the cross-sectional nature of our data. Although we could identify relationships between variables, we were only able to interpret them in terms of associations and could not infer cause-effect relationships. Secondly, to assess interactions with nature (e.g., Soga et al., 2016; Yamanoi et al., 2021), we considered activities beyond mere exposure but involving experiencing nature through different senses (Colléony et al., 2020; Moss, 2012). However, some behaviors may constitute a negative form of engagement with nature if they involve unintentional harm to wild species and habitats (e.g., picking flowers or touching animals). Although this is beyond the scope of our paper, it would be valuable for future studies to examine the activities that people undertake in nature, distinguishing their effects on people, flora and fauna.

Another aspect of the present study that should be considered for future investigation is that most participants reported to have lived outside their current city (84%). However, we did not collect further information on where they actually lived in the past, preventing us from knowing whether the participants grew up in an urban or rural area, which may have important implications. Only direct and intentional contact with nature during childhood was considered, ignoring the possible influence of incidental exposure to natural areas during early life. Other potentially relevant information such as the type (wild or managed), quality and distances of natural environments or the motivation to visit them could also be important in this context (Clayton et al., 2017; Colléony et al., 2020a; Soga et al., 2015; Y. Zhang et al., 2017). We therefore encourage future studies to gain a deeper understanding of nature experiences by overcoming the limitations of our study. Despite these limitations, we hope that our study will help to outline a clearer picture of the relationship that residents of urban areas in Nigeria (and potentially inhabitants of other African countries) have with nature.

Conclusions

Expanding our knowledge of human disengagement from nature is necessary if we are to take measures to reverse it. Differences between countries and cultures demand regional studies, so that possible measures can be tailored to the specificities of each context (Bashan et al., 2021; Colléony et al., 2019). The bulk of research on human-nature interactions is based in Global North countries, but the extinction of experience is not a phenomenon unique to these countries. To our knowledge, this is the first study that assessed the extinction of experience by analyzing patterns of interaction with nature and its determinants in the Afrotropics.

Using a reasonably large sample of Nigerian adults, we found evidence of a strong distancing of people from the natural world, indicating an important level of extinction of experience that is even more pronounced than previous studies have found in other areas. A second conclusion of this study is that low nature contact was more prominent in Lagos, and among those respondents with lower educational and income levels. Interestingly, we found a positive significant association between experiential and cognitive nature experiences, and that neighborhood safety is a promoter of nature connectedness. On the one hand, our study reveals a strong dissociation between real (measured) and perceived neighborhood naturalness and bird species richness. On the other hand, the perception of neighborhood naturalness and bird types significantly (positively) correlated. Finally, we identified the lack of time, money and nearby natural areas as the main reasons for not visiting natural areas more often in the area and provided some useful recommendations to try to revert the observed disconnection with nature by Nigerians. We hope that the findings of this study will help in the design of interventions that favor direct and intentional contact with nature for urban residents, so that the benefits associated with this contact can reach broad segments of the population.

Supporting Materials

Supplementary data to this article can be found online:
https://doi.org/10.1016/j.ecolecon.2024.108105

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General discussion

By focusing on understudied Afrotropical areas, this thesis contributes to the understanding of urban ecology from a Global South perspective. It elucidates the interrelationships of socioecological systems in the region (Fig. 1), providing new findings useful to promote sustainable urban development.

Through a systematic literature review, Chapter 1 identified critical knowledge gaps in African urban ecology, and uncovered factors influencing research efforts across Africa (e.g., economic wealth and size and conservation status of ecoregions). This review detected < 1000 urban ecology papers published across the entire African continent in the last century (1920—2020). Thus, it affirms previous findings showing that Africa urban ecology is relatively understudied compared to other regions of the Global North like Europe or North America. Interestingly, the review added an extra layer of information by pinpointing knowledge gaps across specific taxonomic groups, ecoregions and scientific fields, which is crucial for research and conservation purposes.

Regarding the taxonomic result of the review, the kingdom Animalia, particularly those belonging to the class Aves, was the most commonly studied in African urban ecology. This baseline result was crucial in developing the remaining Chapters of the thesis that focused on birds and tried to elucidate the impacts of urbanization on various socioecological systems across Afrotropical environments. In addition, validated designs and hypotheses from the well-studied African urban ornithology could be deployed to investigate more about underrepresented taxa in the region, such as reptiles, amphibians, insects and microbes (see Chapter 1). For instance, Chapters 2 and 3 investigated how urbanization shapes the taxonomic, functional and phylogenetic diversity of Afrotropical birds. Meanwhile, the review (Chapter 1) revealed that no such urban studies existed for other taxa in the entire African continent, and recommended that additional studies be conducted in this respect. Such multi-taxa and comprehensive studies will be useful to inform appropriate policies and conservation measures that could enhance the overall African urban biodiversity.

At the continental level, urban expansion is concentrated in the Afrotropics that simultaneously holds vast but declining biodiversity (OECD/SWAC, 2020; Seto et al., 2012). Despite the need for relevant data that could enhance the conservation of the declining Afrotropical biodiversity, Chapter 1 identified a lack of significant associations between urbanization intensity and urban ecological studies conducted in Africa. Chapter 2 alleviated this knowledge gap by showing how urbanization influences bird taxonomic, functional and phylogenetic diversity across Afrotropical environments. This study revealed that urbanization drastically reduced bird taxonomic diversity, with urban areas supporting less than half the number of bird species recorded in the adjacent non-urban areas. In general, this result is consistent with those few studies from other avian and non-avian studies conducted in the Afrotropics (Alexandrino et al., 2022; Chamberlain et al., 2017) or the most abundant investigations from other regions (Alexandrino et al., 2022; Chamberlain et al., 2017; e.g. McKinney, 2008). However, by adopting a comprehensive study design that incorporated multiple cities (8), seasons (dry vs wet) and vegetation zones (savannah vs rainforest), Chapter 2 granted a nuanced understanding of how urbanization affects Afrotropical bird diversity. For instance, Chapter 1 detected that most African urban ecological studies were conducted in a single city (55%), often lacking temporal replicates. Further, a key finding of Chapter 2 is that the effects of urbanization on Afrotropical birds were more severe in rainforests than in savannahs independently of seasonal variations. Therefore, these two chapters strongly recommend the use of spatial and temporal replication while investigating the impact of urbanization, particularly on the African continent. They also imply that the clearance of Afrotropical forests to pave the way for urban development is accompanied by a massive loss (more than half) of the associated bird species. This scenario underscored the need to promote sustainable urbanization in the Afrotropics in line with SDG Goal 11.

In contrast, Chapter 2 also shows that functional and phylogenetic avian diversity was significantly higher in the urban than the non-urban habitat. Here, a mosaic of microhabitats found in the studied urban sites (e.g., parks, gardens, cemeteries, sanitary landfills, residential areas, impervious surfaces and offices) would offer a higher number of ecological niches in these cities as it has been proposed in previous studies (Lokatis & Jeschke, 2022; Palacio, 2020; Petchey & Gaston, 2002). This situation could have attracted birds with diverse functional traits compared to the mainly forest habitat of the studied non-urban habitat, supporting the obtained result. Similarly, unique urban features (e.g., buildings, vehicles or pedestrians) could provide opportunities for some evolutionarily unique groups of species (e.g., swifts, sparrows, crows) to colonize urban environments relative to the non-urban ones. This evolutionarily differentiated species would have added to the phylogenetic diversity values already contributed by other species recorded across the urban and non-urban habitats, thereby increasing phylogenetic diversity in the urban habitat (Sanllorente et al., 2023; Tucker et al., 2017). These contrasting results (i.e., lower taxonomic but higher functional and phylogenetic bird diversity in urban habitats) could be onerous for urban planners and conservation managers who want to maximize multiple components of urban avian diversity. Interestingly, Chapter 2 also revealed that the incorporation of a mosaic of water bodies, bushes, and trees could boost multiple avian diversity components in Afrotropical urban centers, particularly during the dry season.

The review in Chapter 1 also identified landscape ecology as an underrepresented discipline in African urban ecology (see Fig. 10 of Chapter 1). This scientific field employs remote sensing applications for large-scale monitoring of landscapes and biodiversity, particularly in expansive and inaccessible areas (e.g., Benza et al., 2016; Kowe et al., 2020). Security challenges that prevented the wet season data collection for Chapter 2 offered an excellent opportunity to determine the best remotely sensed spectral indicators of bird taxonomic, functional and phylogenetic diversity (Chapter 3). The Modified Chlorophyll Absorption Ratio Index (MCARI) was the best indicator of taxonomic and phylogenetic diversity, while the Normalized Difference Water Index II (NDWI2) and Soil Adjusted Total Vegetation Index (SATVI) got the most support for functional diversity and phylogenetic divergence, respectively. In most cases, the commonly employed Normalized Difference Vegetation Index (Benedetti et al., 2023; Leveau et al., 2020) ranks very low (occupying the 25th percentile). Conclusively, since bird taxonomic, functional and phylogenetic diversity are not similarly affected by urbanization in the Afrotropics (Chapters 2) and other regions (e.g., Hagen et al., 2017; Ibáñez-Álamo et al., 2020; Morelli et al., 2017), a single remotely sensed spectral indicator may not be appropriate to simultaneously monitor all avian diversity components. Chapter 3 found and recommended the use of several indicators, including MCARI (taxonomic and phylogenetic diversity), NDWI2 (functional diversity) and SATVI (phylogenetic divergence) that rated first in Afrotropical environments. In addition to being more accurate than field-based measures of local influential variables (Ghosh et al., 1995; Gorrod & Keith, 2009; Morrison, 2016), MCARI, NDWI2 and SATVI could be employed to remotely monitor birds in inaccessible, insecure and expansive Afrotropical areas.

The significant attention devoted to human dimension studies in African urban ecology underscores its relevance (Chapter 1, Fig. 10). This thesis contributes to the applied field of human dimension in African urban ecology by investigating the impacts of urbanization on regulating ecosystem services (Chapter 4) and drivers of human-nature interactions, including the increasingly worrying extinction of experience phenomenon (Chapter 5). The analysis of four bird-mediated regulating ecosystem services (fruit dispersal, pest control, pollination, and scavenging) revealed that urbanization significantly (negatively) affected pest control and seed dispersal, regardless of season or vegetation zone. These ecosystem services were estimated using abundance-weighted foraging preferences of recorded birds. Thus, the findings suggest that urban-induced loss of taxonomic bird diversity (Chapter 2) has cascading negative effects on pest control and seed dispersal ecosystem services mediated by birds (Chapter 4), highlighting the crucial importance of this animal group in urban environments (Murphy et al., 2023; Reynolds & Howes, 2023). This filtering out of insectivorous birds from urban habitats has important socioecological and economic implications, including increased costs and public health concerns associated with chemical pest control (Hudgins et al., 2022; Md Meftaul et al., 2020). Furthermore, the reduced seed dispersal in urban habitats may lead to the local extinction of plant species reliant on animal-mediated dispersal (zoochory) and associated ecosystem service losses (Heinen et al., 2023; Pérez-Méndez et al., 2016; Wotton & Kelly, 2012). Notably, the result of this chapter indicates that birds contribute more significantly to scavenging ecosystem services in urban habitats and rainforests than in non-urban habitats and savannahs. This positive finding highlights the importance of conserving urban bird populations that facilitate scavenging ecosystem services beneficial to urban residents and provide novel information on this understudied but highly relevant ecosystem service (Chamberlain et al., 2017; Gomo et al., 2020; Mateo-Tomás et al., 2015; Moleón et al., 2014).

The findings of this thesis demonstrate the cascading effects of biodiversity loss on ecosystem services, highlighting the need for conservation efforts in the region. By illustrating the consequences of biodiversity decline, this research can garner greater support for conservation among stakeholders, including urban dwellers, planners, policymakers, and conservationists. This is particularly crucial in the Afrotropics, where the awareness of urban biodiversity is limited (Fig. 8a, Chapter 5), with 55% of citizens reporting no interaction with urban nature (*cf*. Ishibashi et al., 2020; Soga et al., 2015; Coll´eony et al., 2017). The primary reasons cited for this lack of interaction was limited time, financial resources, and access to nearby natural areas. Addressing these socioeconomic constraints is essential for promoting investments in biodiversity conservation, research, and ecosystem service management (Chapters 1—4). Moreover, fostering human-nature interactions in the Afrotropics (Chapter 5) is critical for mitigating the impacts of rapid urban expansion on bird diversity and ecosystem services. What is not known cannot be protected (Lawton, 1999). This thesis demonstrates that incorporating a mosaic of water bodies, bushes, and trees can help alleviate these challenges by promoting a more diverse bird community in Afrotropical cities. Moreover, from a research perspective, this study highlights the significance of vegetation zones and seasons in shaping Afrotropical bird diversity and their associated ecosystem services, also in the context of urban ecology.

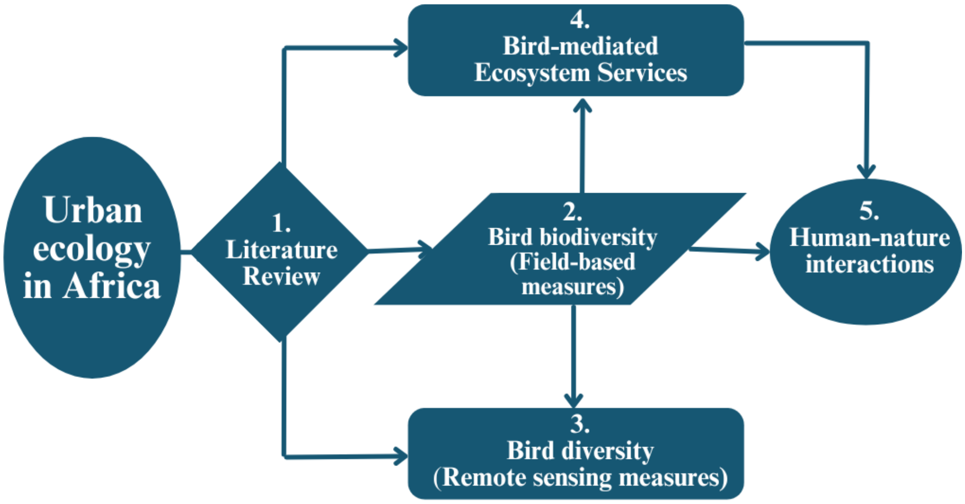

Figure 1: General study framework.

The systematic literature review first detected crucial knowledge gaps in African urban ecology (Chapter 1). Subsequent research (Chapters 2—5) addressed some of the detected knowledge gaps and their interconnectedness by investigating the impacts of urbanization on avian diversity (incorporating field-based and remote sensing estimation of local habitat attributes), ecosystem services and human-nature interactions. Data were collected across habitats (urban vs. non-urban), seasons (dry vs. wet) and vegetation zones (rainforest vs. savannah) in Nigeria, a typical Afrotropical country.

Conclusions

1. Urban ecology is clearly a significantly understudied scientific field in Africa despite the high urbanization rates that this continent suffers. Our lack of knowledge on the topic is particularly gross/flagrant for certain ecoregions (e.g., tropical and subtropical dry broadleaf forests biome), taxonomic groups (e.g., Arthropoda, Bacteria, Chromista and Protozoa) and scientific fields (e.g., wildlife disease and landscape and community ecology).
2. Research in African urban ecology has traditionally prioritized less urbanized areas, with a bias towards wealthier countries and specific ecoregions that are larger and more threatened. To create more integrated and biodiversity-friendly cities in the region, a shift in research focus is necessary, emphasizing a more inclusive and representative approach.
3. Urbanization exerts profound impacts on bird taxonomic diversity in the Afrotropics. Of the total 237 bird species recorded across the urban and non-urban habitats, a striking 65 % of these species were absent from the urban habitat.
4. Not all biodiversity components are similarly affected by urbanization. While taxonomic bird diversity was significantly lower in urban Afrotropical areas compared to non-urban ones, functional and phylogenetic bird diversity followed the opposite pattern. These unexpected findings may be attributed to the presence of diverse urban microhabitats (e.g. parks, gardens, cemeteries, sanitary landfills, residential areas, offices…) facilitating the presence of bird species with a wide range of functional traits and different evolutionary histories.
5. The impacts of urbanization on bird diversity components exhibited seasonal consistency but were more pronounced in rainforests than savannahs. This suggests that cities within the rainforest vegetation zone should employ special conservation plans to minimize this disproportionately greater effect.
6. The integration of a mosaic of water bodies, bushes, and trees boosts avian diversity in Afrotropical urban centers, particularly during the dry season.
7. The novel application of machine learning and remote sensing techniques can be effectively employed to monitor bird diversity components in the Afrotropics. This approach can be a potentially more efficient and cost-

effective method for estimating local habitat variables compared to traditional field estimation techniques.

8. The remotely sensed Modified Chlorophyll Absorption Ratio Index (MCARI) is the most effective indicator of taxonomic and phylogenetic bird diversity in the Afrotropics. Meanwhile, the Normalized Difference Water Index 2 (NDWI2) and Soil Adjusted Total Vegetation Index (SATVI) were the best predictors of functional diversity and phylogenetic divergence, respectively. Notably, the commonly employed Normalized Difference Vegetation Index (NDVI) ranked relatively low (25th percentile) in most cases, which is consistent with its known limitations, including scaling issues, saturation in high-biomass areas, and sensitivity to soil brightness.
9. Urbanization in the Afrotropics deeply affects bird-mediated regulating ecosystem services. This human-induced landscape change had the most pronounced impact on pest control and seed dispersal provided by birds. These services were significantly reduced in urban habitats compared to non-urban habitats in Nigeria, regardless of the season. In contrast, the negative impact of urbanization on pollination was only significant during the wet season.
10. Urban habitat attributes such as vehicles and pedestrians significantly reduced bird-mediated pollination and seed dispersal regulating ecosystem services in the Afrotropics. Interestingly, canopy cover (vegetation) significantly enhanced seed dispersal and pollination ecosystem services provided by birds in the Afrotropics. Urban planners and practitioners should consider these results while developing city action plans in the area.
11. Urbanization can also enhance some bird-mediated regulating ecosystem services like scavenging. This is probably due to the higher concentration of carrion in urban habitats, which will attract scavenging birds. Furthermore, this ecosystem service is generally higher in rainforests than savannahs in the region.
12. Human-nature interactions are remarkably limited in Afrotropical cities. A substantial proportion of citizens in the region (55%) reported no interaction with nature, a figure significantly higher than those reported for the Global North (≤10%).
13. Respondents residing in high-density commercial urban centers, such as Lagos, Nigeria, presented an important disconnection from nature. Additionally, individuals with lower socioeconomic status, characterized by lower income and educational levels, exhibited a greater disconnection from nature.
14. Overall, the disconnection between people and nature in the Afrotropics can be attributed to three primary factors: insufficient time, financial limitations, and a lack of proximity to natural areas. Regional and local authorities should work

on reducing these potential causal factors to revert the extinction of experience phenomenon in the region.

Conclusiones

1. La ecología urbana es claramente un campo científico poco estudiado en África a pesar de las altas tasas de urbanización que sufre este continente. Nuestra falta de conocimiento sobre el tema es particularmente grave/flagrante para ciertas ecorregiones (p. ej., bioma de bosques secos latifoliados tropicales y subtropicales), grupos taxonómicos (p. ej., Arthropoda, Bacteria, Chromista y Protozoa) y campos científicos (p. ej., enfermedades animales, ecología del paisaje y de comunidades).
2. La investigación en ecología urbana africana tradicionalmente ha priorizado áreas menos urbanizadas, con un sesgo hacia países más ricos y ecorregiones específicas, más grandes y amenazadas. Para crear ciudades más integradoras y amigables con la biodiversidad en la región, es necesario un cambio en el enfoque de investigación, priorizando un enfoque más inclusivo y representativo.
3. La urbanización ejerce profundos impactos en la diversidad taxonómica de aves en el Afrotrópico. Del total de 237 especies de aves registradas en hábitats urbanos y no urbanos, un sorprendente 65 % de éstas estaban ausentes en el hábitat urbano.
4. No todos los componentes de la biodiversidad se ven afectados de manera similar por la urbanización. Si bien la diversidad taxonómica de aves en la región tropical africana fue significativamente menor en las áreas urbanas que en las no urbanas, la diversidad funcional y filogenética de aves siguió el patrón contrario. Estos hallazgos inesperados pueden atribuirse a la presencia de diversos microhábitats urbanos (por ejemplo, parques, jardines, cementerios, vertederos sanitarios, zonas residenciales, oficinas…) que facilitan la presencia de especies de aves con un amplio rango de rasgos funcionales y diferentes historias evolutivas.
5. Los impactos de la urbanización sobre los componentes de la diversidad de aves mostraron una consistencia estacional, pero fueron más pronunciados en los bosques tropicales que en la sabana. Esto sugiere que las ciudades ubicadas en la zona de bosques tropicales deberían usar planes de conservación especiales para minimizar este efecto desproporcionadamente mayor.

6. La integración de un mosaico de cuerpos de agua, arbustos y árboles impulsa la diversidad de aves en los centros urbanos del Afrotrópico, particularmente durante la estación seca.
7. La novedosa aplicación de técnicas de aprendizaje automático y teledetección puede emplearse eficazmente para monitorizar los componentes de la diversidad de aves en el África tropical. Este enfoque puede ser un método potencialmente más eficiente y rentable para estimar las variables del hábitat local en comparación con las técnicas tradicionales de estimación de campo.
8. El Índice de Absorción de Clorofila Modificado (MCARI) detectado remotamente es el indicador más eficaz de la diversidad taxonómica y filogenética de las aves en el Afrotrópico. Mientras tanto, el Índice de Diferencia Normalizada de Agua 2 (NDWI2) y el Índice de Vegetación Total Ajustado del Suelo (SATVI) fueron los mejores predictores de la diversidad funcional y la divergencia filogenética, respectivamente. En particular, el Índice de Diferencia Normalizada de Vegetación (NDVI), comúnmente utilizado, obtuvo una clasificación de idoneidad relativamente baja (percentil 25) en la mayoría de los casos, lo que es consistente con sus conocidas limitaciones, incluidos problemas de escala, saturación en áreas de alta biomasa y sensibilidad al brillo del suelo.
9. La urbanización en la zona tropical de África afecta profundamente los servicios ecosistémicos reguladores mediados por las aves. Este importante cambio de paisaje inducido por el hombre tuvo el mayor impacto en el control de plagas y la dispersión de semillas proporcionadas por las aves. Estos servicios se redujeron significativamente en los hábitats urbanos en comparación con los hábitats no urbanos en Nigeria, independientemente de la estación. Por el contrario, el impacto negativo de la urbanización sobre la polinización sólo fue significativo durante la estación húmeda.
10. Las características del hábitat urbano, como los vehículos y los peatones, redujeron significativamente la polinización y dispersión de semillas mediada por aves en el Afrotrópico. Curiosamente, la cobertura arbórea mejoró significativamente los servicios ecosistémicos de dispersión de semillas y polinización proporcionados por las aves en la región. Los urbanistas y otros profesionales urbanos deberían considerar estos resultados al desarrollar planes de desarrollo urbano en el área.
11. La urbanización también puede mejorar algunos servicios ecosistémicos reguladores mediados por las aves, como el consumo de carroña. Probablemente esto se deba a la mayor concentración de carroña en los hábitats urbanos, lo que atraería a las aves carroñeras. Además, este servicio ecosistémico es generalmente mayor en los bosques tropicales que en la sabana.

12. Las interacciones entre humanos y naturaleza están muy limitadas en las ciudades del África tropical. Una importante proporción de ciudadanos de la región (55%) reportó no interactuar con la naturaleza, una cifra significativamente mayor que la reportada para el Norte Global (≤10%).
13. Los encuestados que residen en centros urbanos comerciales de alta densidad, como Lagos (Nigeria), presentaron una importante desconexión de la naturaleza. Además, las personas con un nivel socioeconómico más bajo, caracterizado por menores ingresos y niveles educativos, mostraron una mayor desconexión de la naturaleza.
14. En general, la desconexión entre las personas y la naturaleza en el Afrotrópico puede atribuirse a tres factores principales: tiempo insuficiente, limitaciones financieras y falta de proximidad a las áreas naturales. Las autoridades regionales y locales deberían trabajar para reducir estos posibles factores causales para revertir el fenómeno de extinción de la experiencia en la región.

List of publications

Publications from the thesis

Awoyemi, A. G., & Ibáñez-Álamo, J. D. (2023). Status of urban ecology in Africa: A systematic review. *Landscape and Urban Planning*, 233: 104707, 1–16. https://doi.org/10.1016/j.landurbplan.2023.104707

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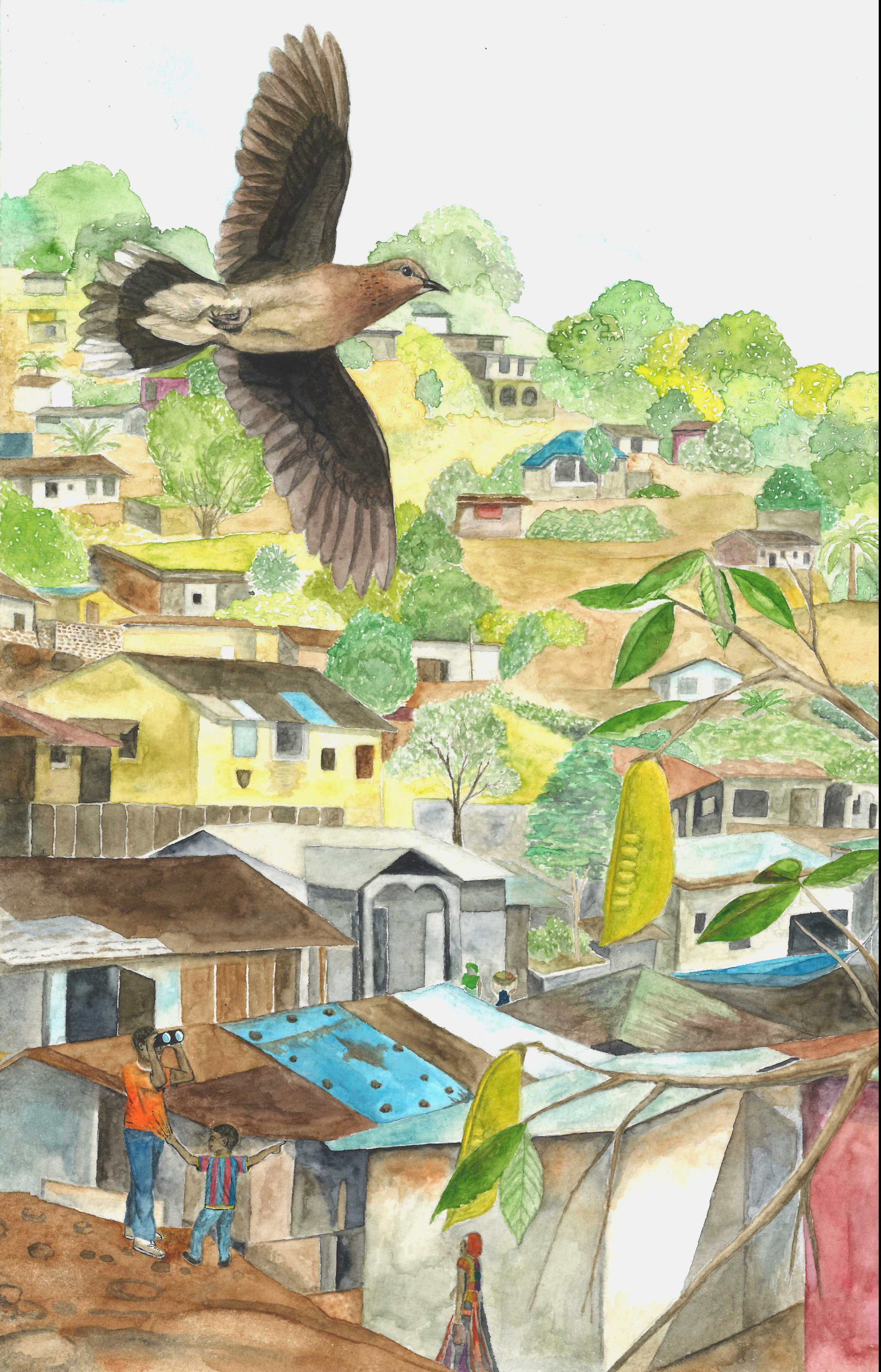

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