MSc by Research in Environmental Studies

Bats and the City: Urban Bat Biodiversity in a Tropical Biome Transition Zone

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2019

School of Environment & Life Sciences

MSc by Research Thesis

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Acknowledgements

I would like to thank my supervisor, Dr Christoph Meyer, for his advice and encouragement whenever this project became tough. I would also like Dr Camila Teixeira for her unending patience for all of my questions. Finally, I would like to thank Natalie Yoh, and my family for their unending support throughout this degree. This would not have been possible without any you.

Statement of Originality

I declare that, with the exception of any statements to the contrary, the contents of this report/dissertation are my own work, that the data presented herein has been obtained by experimentation and that no part of the report has been copied from previous reports/dissertations, books, manuscripts, research papers or the internet.

Signed ……………………………………..

Print name ...Peter Syme.......................

Date.... 31st January 2019 ....

Glossary of Terms and Abbreviations

TD – Taxonomic Diversity – Measurement of the taxon or species diversity of a community (Magurran, 2011). Is this study, taxonomic diversity is quantified as species richness, which acts as a count of the number of unique species within a given sample or community (Gotelli and Colwell, 2011).

FD – Functional Diversity – Measures the extent of differences in traits that influence ecosystem functioning and adaptation between species within a given community (Petchey and Gaston, 2006; Magurran, 2011).

PD – Phylogenetic Diversity – The evolutionary relatedness between species within a given community or sampling unit (Magurran, 2011).

Alpha diversity – The taxonomic, functional or phylogenetic diversity of a single sampling unit or sampling site (Whittaker, 1960). In this study, an individual year or season is considered a single sampling unit.

Beta diversity – The variation in taxonomic, functional, or phylogenetic alpha diversity of two or more sampling units or sites (Whittaker, 1960).

HSM – Habitat Suitability Model – Statistical model that determines the importance of specified environmental predictor variables (e.g. land cover type) in predicting the presence of a given species.

HSI – Habitat Suitability Index – The relative suitability of a specified location for a given species, based on previously calculated habitat suitability model.

Abstract

Urbanisation is an important factor in global land-use change which dramatically alters habitats at great detriment to wildlife. Our understanding of urban biodiversity patterns and their driving factors in tropical cities which interact with high levels of biodiversity is limited, yet it is pivotal to developing efficient and effective conservation guidelines for urban planning. This study uses a long-term data set (>10 years) of species occurrence records, collected as part of a public health monitoring scheme within the city of Belo Horizonte, Brazil to quantify the taxonomic, functional, and phylogenetic diversity of bats in the city for each year and season of the study period. Linear regressions were then carried out to test whether the different facets of diversity show any significant trends over the study period. Moreover, a habitat suitability analysis for the five most common species was conducted using the MaxEnt algorithm, following the framework of Bellamy et al. (2013), and the most important factors affecting the presence of these species were identified. It was found that there was a significant increase in bat taxonomic diversity over time, however, functional and phylogenetic diversity remained unchanged over the period of 2004-2014. Maps of habitat suitability were produced for each focal species. Human population density and distance to natural resources, such as water and forest bodies, were important variables for all species modelled. The information gained from this study can be used to aid the development of effective bat conservation strategies and guidelines within the urban environments of southern Brazil.

Chapter 1 - Introduction

1.1 The Range and Effects of Urbanisation

Urbanisation is one of the main drivers of land-use change and is a significant threat to global biodiversity (Jung & Threlfall, 2016; Russo and Ancillotto, 2015; Voigt and Kingston, 2016; Stone, Harris and Jones, 2015; Border et al., 2017). Since the latter half of the 20th century, the global rate of urbanisation has increased at an unprecedented rate (Concepción et al., 2015; Figure 1). This is partially due to the migration of the majority of the human population to urban areas and the dramatic increase in size of the human population, with over half of the human population now living in urban environments (Goddard, Dougill and Benton, 2010; Figure 1). Although the rate of urbanisation in developed countries (such as those in North America and Western Europe) is now slowing, it is now rapidly increasing in developing countries (Myers et al., 2000; Figure 1). The rate of urbanisation is increasing particularly fast in the Neotropics and Asia (McGranahan and

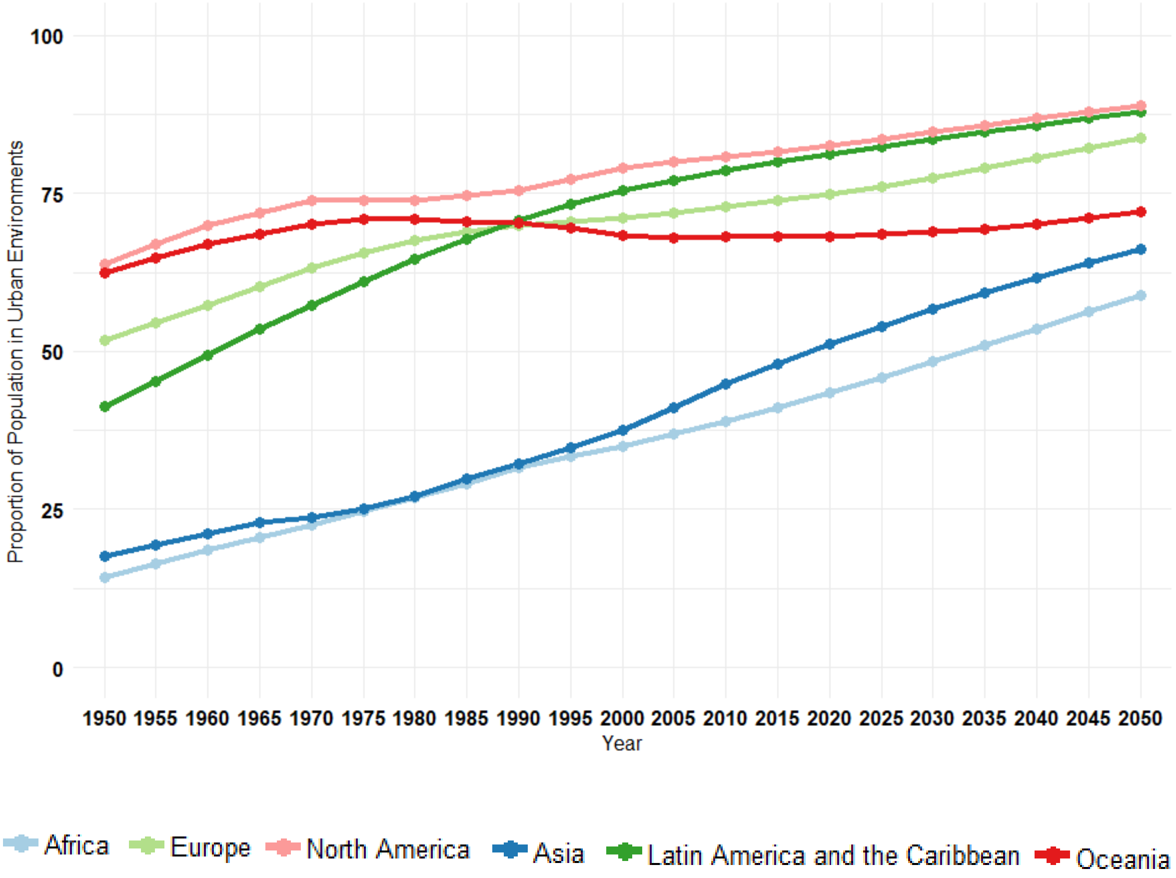

Figure 1. The estimated proportion of the population that lives in urban environments per geographic region over time with predictions until 2050. Data source: United Nations Population Division, World Urbanisation Prospects (2018).

Satterthwaite, 2014; Figure 1). This may be due to rapid economic growth of multiple industries in these regions which has led to higher rate of human migration to cities (McGranahan and Satterthwaite, 2014). These rapidly developing countries harbour many biodiversity hotspots that are highly vulnerable to anthropogenic pressure (Bellard et al., 2014). Despite the slowing rates of urbanisation in some developed countries of the world, the global human population is predicted to increase to 9.7 billion by 2050, and 11.1 billion by 2100 regardless (UNPD, 2017). This continuous population growth will further accelerate the global demand for resources such as food, water, and space. Because of this, the pressures of urbanisation will continue to increase and the negative impacts of urbanisation on global biodiversity and wildlife will become even greater.

Urbanisation has consequences and effects that can range far beyond a city's own boundaries (Jung & Threlfall, 2016). These effects can be local, such as urban expansion causing the loss of various surrounding habitats, or such as increasing the species mortality rate through human-wildlife conflict and direct road mortalities. The effects may also cause regional disruptions, such as fragmentation of natural forest due to increased resource demand, the reduction of native biodiversity, the introduction of domestic and alien taxa, increased pollution, and an increase in dominance of generalist taxa (Concepción et al., 2015; Aruninta, 2012; Sol et al., 2014; Zapata and Robledano, 2014; Gaston, 2010). There are also global consequences of urbanisation through the increased greenhouse gas emissions furthering the effects of climate change, which is also considered one of the main challenges for modern conservation efforts. Urban environments are also highly uniform globally in terms of landscape composition and configuration, microclimate, and levels of perturbation (Clergeau et al., 2006; McKinney, 2006). Because of this uniformity, all of the effects associated with the increasing urban sprawl that is occurring in multiple locations globally are able to compound together, resulting in even larger effect sizes (Pauchard et al., 2006).

However, despite the radical effects and transformations caused by urbanisation, certain species can persist in urban environments with some species even thriving under such conditions (Sorace and Gustin, 2009; Shochat et al., 2006). The persistence of such species in these environments is testament to species adaptability and the niche flexibility that allows them to exploit different resources effectively (Clare et al., 2013). These species are often termed urban-exploiters or urban-tolerant dependant on the degree by which they take advantage of urban environments (Winchell et al., 2017). However, there is currently no set criteria for the definition of urban-exploiter species. This is due to the difficulty of identifying quantitative indicators that reflect species success or failure in urban environments.

Nonetheless, in order for a species to be considered urban-tolerant or an urban-exploiter, they must be able to exploit particular aspects of urban environments and be tolerant of the characteristics associated with them. One of the main pressures of urban environments on nocturnal species is the increased artificial lighting and tolerance to this can heavily influence whether a species is able to persist in these areas (Winchell et al., 2017). Additionally, road density and activity are substantially higher, which thus increases anthropogenic noise and also directly increases mortality rates through traffic collisions (van Langevelde and Jaarsma, 2004). Finally, the increased population density of urban environments, particularly within cities, leads to significantly increased human-wildlife contact and potentially conflict (Tait et al., 2014). However, if a species has adaptations that allow it to be tolerant to these and other main pressures, urban environments have several characteristics which can be highly favourable for wildlife. For example, the concrete used for constructions retains heat over a much longer period than in a natural environment and can act as a heat buffer during the night (Kowarik, 2011). Furthermore, these buildings can also act as potential shelter and roosting resources for certain taxa (Perini, Tavares and Nascimento, 2003; Nunes, Rocha and Cordeiro-Estrela, 2016). These factors can lead to the homogenisation of biodiversity within and around urban environments as specific functional traits and adaptations become highly advantageous (Clergeau et al., 2006; Pauchard et al., 2006). Moreover, species without these traits cannot adapt at a rate comparable to the rate of urbanisation and are placed under serious anthropogenic pressure.

1.2 Urbanisation in the Neotropics

The Neotropics have undergone extensive urbanisation over the past 60 years (UNPD, 2017). A key driver of this urbanisation is the mass migration of human populations from rural to urban environments. For example, in 1950, 36.2% of the population of Brazil existed in urban areas, however, this has increased to 86.6% of the population in 2018 and is predicted to increase to over 90% by 2050 (UNPD, 2017; Figure 1). The Neotropics also contain many biodiversity hotspots (Myers et al., 2000; Figure 2). Many of these hotspots have been significantly reduced from their original sizes and damaged by rampant urbanisation as well as anthropogenic pressures such as deforestation and habitat fragmentation, climate change, and invasive species, though this list is not exhaustive (Bellard et al., 2014). Biodiversity hotspots contain the majority of species worldwide and support a very high amount of endemism. With the ever-increasing damage to these habitats, biodiversity is under more threat than ever before.

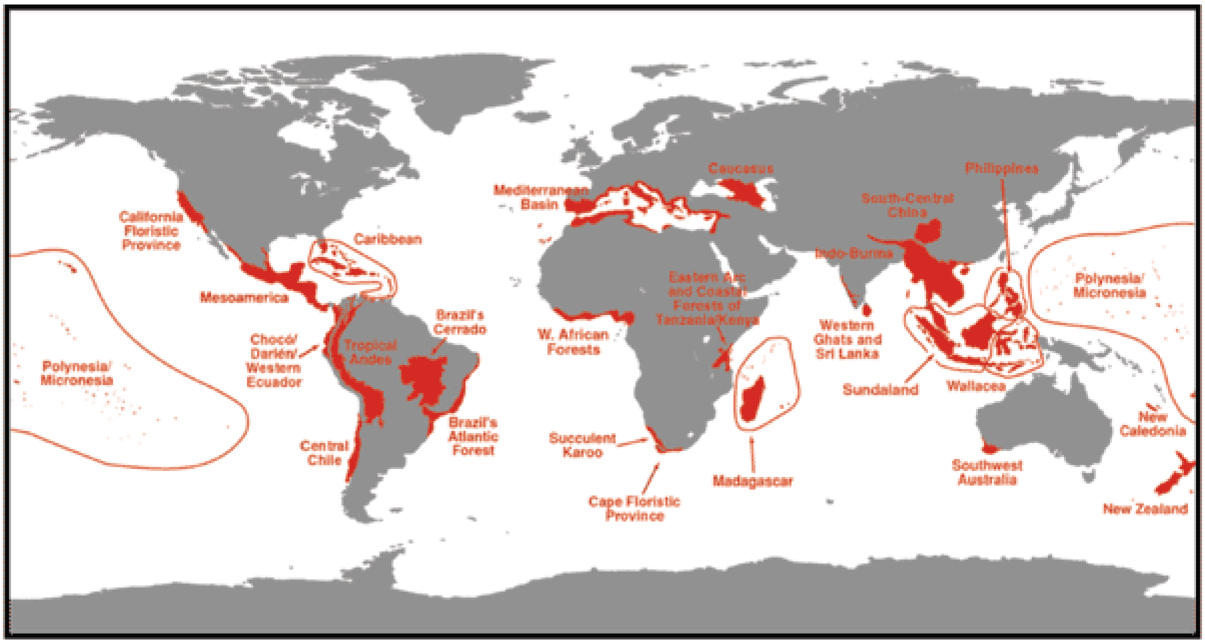

Figure 2. The 25 biodiversity hotspots of the world. In total, the neotropics contain seven biodiversity hotspots. Source: Myers et al. (2000).

An example of the effects of urbanisation alongside other anthropogenic pressures, such as deforestation, habitat fragmentation, and the introduction of invasive species, can be seen with the Atlantic rainforest and Brazilian Cerrado of Southern Brazil. Both biomes have undergone massive amounts of habitat destruction and degradation as a result of urbanisation and these additional pressures. Of the original 1,227,600 km^2 of Atlantic rainforest and 1,783,200 km^2 of Brazilian Cerrado, less than 8% and 20% remains respectively (Myers et al., 2000). Furthermore, both biodiversity hotspots have undergone large amounts of habitat fragmentation, exacerbating the effect of biodiversity loss. Despite all of this, the Neotropics have received comparatively little research attention, in comparison to other regions such as Europe. The threats to global biodiversity caused by urbanisation will increase if this research deficit is not addressed and the effective management of urbanisation is not achieved in the near future.

1.3 Bats and Urban Environments

1.3.1 Bat Diversity and Ecosystem Services

Bats constitute approximately one fifth of all mammalian species, making them the second largest order of mammals after rodents in terms of species richness (Medellín, Equihua and Amin, 2000). Furthermore, bats are an incredibly functionally diverse order (Frick, Kingston & Flanders, 2019). Since their evolution over 50 million years ago (Simmons et al., 2008), bats have evolved to utilise a large range of food groups and now contain species that feed on fruit, insects, nectar, pollen, fish, blood, meat, and leaves (Medellín, Equihua and Amin, 2000). Furthermore, the radiation of diversity that bats have undergone has led to an incredible amount of variation in their forms and ecosystem functioning. Two distinct suborders of bats are currently recognized: The Yinpterochiroptera (Megachiroptera) and Yangochiroptera (Microchiroptera). These suborders are typically known for their differences in size but also differ in their usage of echolocation, whereas Yinpterochiroptera do not typically utilise echolocation and rely more heavily on eyesight (Jones and Teeling, 2006). The huge diversity of bats has allowed them to adapt to an incredibly wide range of niches and habitats. Because of this, bats have become ubiquitous on almost every vegetated region and habitat on the planet (Medellín, Equihua and Amin, 2000).

In addition to their incredible diversity, bats also carry out several highly valuable ecosystem services, such as seed dispersal, pollination, and arthropod suppression (Kunz et al., 2011; Boyles et al., 2011; Cleveland et al., 2006). Seed dispersal by bats substantially aids forest regeneration in deforested areas on a global scale (Medellin and Gaona, 1999; Ingle, 2003; Wunderle, 1997). Although bats are not the only group to perform this ecosystem service, their ability to disperse seeds during flight is highly advantageous for forest regeneration (Kalko, Herre and Handley, 1996). Birds and primates are also known to be key to seed dispersal and forest regeneration, however, due to the behavioural differences of these taxa (i.e. birds typically defecating whilst perching), this ability can be significantly reduced in highly degraded areas (Charles-Dominique and Cockle, 2001).

Arthropod suppression has multiple direct benefit to human populations regarding both public health and economics. Bats consume approximately two-thirds of their body mass in insects every night on average (Coutts, Fenton and Glen, 1973). Although estimations of the economic value of this service are difficult, recent studies suggest it to be substantial, with estimates of up to $53 billion for the USA alone (Boyles et al., 2011; Cleveland et al., 2006; Ghanem and Voigt, 2012; Maas, Clough and Tscharntke, 2013). Furthermore, malaria is the cause of over 400,000 deaths per year worldwide (World Health Organization, 2019) based on 2017 estimates. Mosquitoes are a key host of the malaria parasite and are the primary pathway of human infection of this zoonotic disease (Holt et al., 2002). Bats have been shown to feed on mosquitoes and considerably suppress their population sizes (Rydell, McNeill and Eklöf, 2002a; Ancillotto et al., 2017; Ghanem and Voigt, 2012). Although it is incredibly difficult to estimate the change in malaria prevalence due to bat predation of mosquitoes, it is expected to be considerable, thus preventing many deaths per year whilst also reducing global medical costs.

Whilst it is estimated that approximately one in three mouthfuls of food for human consumption is due to pollination by honey bees (Ragsdale, Hackett and Kaplan, 2007), bats have also shown to be incredibly valuable for pollination of agricultural- and cash-crops (Kunz et al., 2011; Cleveland et al., 2006; Boyles et al., 2011). A key example of this is the lesser long-nosed bat (*Leptonycteris yerbabuenae*). This species is the main pollinator of the agave flower which is crucial in the tequila industry of Mexico which produces millions of litres of alcohol every year (Trejo-Salazar et al., 2016; Hoffmaster, Vonk and Mies, 2016). All of these ecosystem services provide both direct and indirect benefits to human populations and are key support for the conservation of these species (Cleveland et al., 2006; Boyles et al., 2011).

1.3.2 Bat Responses to Urbanisation

There is a consensus that urbanisation has a negative impact on bat biodiversity at a global scale (Gehrt & Chelsvig, 2004; Russo and Ancillotto, 2015). However, recent studies and meta-analyses have shown that bat responses to urbanisation are also known to be highly species-specific and dependant on the functional traits and adaptations of the species affected (Jung and Threlfall, 2018; García-Morales, Badano and Moreno, 2013; Russo and Ancillotto, 2015; Safi and Kerth, 2004; Gehrt & Chelsvig, 2004; Santini et al., 2019). Whilst some bats species have very specific habitat requirements and are highly specialised to particular environments, others are considered more generalist regarding their habitat selection and requirements. Furthermore, Safi and Kerth (2004) highlight that the response of bat populations to urbanisation is not binary and depends heavily on the amount of the niche specialisation the species exhibits and the degree of urbanisation. Typically, it is observed that specialist species show declines in activity within urban environments but the degree to which this occurs has been linked with the degree of specialisation and type of habitat they are specialised for (Safi & Kerth, 2004).

For example, *Pipistrellus kuhlii* is a common insectivorous bat in Europe. This species commonly exploits street lights during foraging activities and has thus become highly prevalent in urban areas (Tomassini et al., 2013; Ancillotto, Tomassini and Russo, 2015). In comparison, the phyllostomid species *Chrotopterus auritus* and *Vampyrum spectrum* are carnivorous bat species present in the Neotropics. Both of these species are highly adapted to undisturbed primary forest and are seldom found in urban environments (Gorresen and Willig, 2004; Fenton et al., 1992). The sensitivity and responses of forest-specialist bat species to habitat disturbance and degradation from urbanisation allows them to be utilised as bioindicators (Russo and Ancillotto, 2015; Jones et al., 2009). This can prove highly useful for monitoring the impact of anthropogenic change on natural environments.

1.4 Multiple Dimensions of Diversity

In recent years, conservation and ecological research has begun to move away from the single-dimensional view of measuring only taxonomic diversity (TD). However, taxonomic diversity is still utilised at present day and is the simplest form to measure biodiversity, and has been the basis of biodiversity monitoring efforts for many decades. Taxonomic diversity measures the taxon or species diversity of a community (Magurran, 2011). The most common quantification of TD is the use of species richness, which acts as a simple count of the number of unique species in a community or habitat (Gotelli and Colwell, 2011). Species evenness can also be used to quantify TD and takes the abundance of species in a community into consideration. Species evenness considers a community where a single or few species dominates is less diverse than a community with roughly even numbers of different species. A number of metrics and indices combine the use of species richness and evenness to quantify TD, the most commonly used being Shannon's H and Simpson's D. Although both indices provide similar information, each index relies on differing assumptions and can prove more useful in different scenarios (Magurran, 2011; Simpson, 1949; Shannon, 1948).

The use of taxonomic diversity has proved crucial in identifying areas of importance for conservation or biodiversity hotspots. However, in recent years, the limitations of using only TD for biodiversity monitoring have been highlighted. A key issue is that TD is easily driven by the desire to produce lists of species rather than to understand the ecological significance of the species present (Fleishman, Noss and Noon, 2006; Dornelas et al., 2014). As such, TD is now increasingly considered an insufficient measure of conservation importance when used by itself, often over-simplifying the current state of biodiversity (Fleishman, Noss and Noon, 2006). Despite this, species richness is still an incredibly useful tool for the monitoring of taxonomic diversity, however it should be utilised with other methods to supplement the information gained.

Phylogenetic diversity (PD) can highlight key information regarding species diversity that is unavailable when considering taxonomic diversity alone (Tucker et al., 2016). This dimension of biodiversity measures the evolutionary relatedness between species within a given community (Magurran, 2011). PD has been quickly adopted in conservation efforts, is often used to identify areas of biological importance and it has been shown that higher levels of PD indicate more stable and productive communities (Rolland et al., 2011; Cadotte, Dinnage and Tilman, 2012).

In more recent years, functional diversity (FD) has received increasing attention as a facet of diversity to provide greater insight into the ecological adaptation of communities to their habitats. Functional diversity refers to the extent of differences between species within a community in traits that influence ecosystem functioning (Petchey and Gaston, 2006; Laureto, Cianciaruso and Samia, 2015; Magurran, 2011), such as wing morphology in bats. Functional diversity measures also have the ability to highlight how species may respond to environmental change and how they may influence ecosystem functioning (Laureto, Cianciaruso and Samia, 2015), thus providing significant information which cannot be captured with other facets of diversity. Ecological studies have recently shifted towards the use of more than one facet of diversity, as no single measure can accurately represent a community (Cisneros et al., 2014). It is clear that all aspects of biodiversity must be investigated thoroughly in order to effectively understand species responses to anthropogenic threats.

1.5 Data Deficiency in Conservation

It is often stated that the monitoring of species and biodiversity is limited by the amount of financial and human resources available (Schmeller et al., 2009; Lindenmayer et al., 2011; Chavan & Penev, 2011). These resources are often scarce and thus large gaps in global biodiversity data are highly prevalent. This is extremely common in developing countries, particularly within Africa and South America, which are less equipped to fund the conservation and management of biodiversity (Frick, Kingston & Flanders, 2019). As well as this, research is often biased towards developed countries, with the highest amount of biodiversity research conducted in Europe, further contributing to the gap in knowledge of many taxa (Trimble & van Aarde, 2012).

The issue of data deficiency and regional research bias in conservation has recently received more attention (Trimble and van Aarde, 2012). From this, the usage of public databases has shown significant potential for reducing the knowledge gap of biodiversity in less represented areas. As well as this, there has been large-scale development of public access diversity and climate databases. For example, the Global Biodiversity Information Facility (GBIF) and WorldClim are large-scale databases that have been utilised in many ecological studies to date (Fick & Hijmans, 2017; GBIF, 2018). Although these developments have substantial potential for reducing the current knowledge gap, they have received criticisms and outlined limitations. A key issue with these systems is highly common spatial and temporal bias, which can potentially distort our view on large-scale diversity patterns and therefore how we attempt to manage and conserve biodiversity (Boakes et al., 2010; Beck, Böller, Erhardt & Schwanghart, 2014). Another key issue that has been highlighted with public access databases and systems is the lack of quality control of data that is included. This is is particularly true for bats as this taxa frequently present difficulties in univocal identification, thus making citizen-science data less reliable and potentially leading to incorrect conclusions being drawn from their use. However, with the rise in usage of species distribution modelling in ecology, multiple techniques have since been used to address these issues. Methods such as spatial filtering, pair-wise distance sampling, and the inclusion of a sampling bias grid have been developed and shown to be highly effective at removing sampling bias and even increasing model performance (Hijmans, 2012; Boria, Olson, Goodman & Anderson, 2014; Syfert, Smith & Coomes, 2013). With these advances and careful consideration regarding the quality of the data used, public access databases and systems can be highly effective in remote biodiversity monitoring and in the reduction of current knowledge gaps.

1.6 Species Distribution Modelling

Species distribution models (SDMs), also known as habitat suitability models (HSMs) or ecological niche models (ENMs), have become highly common in conservation and ecological research. Major developments in the field of species distribution modelling have also taken place over the past 20 years. This has created many different methods which utilise different types of data to calculate SDMs (Elith et al., 2010). However, all methods of species distribution modelling use a similar approach, whereby they estimate the relationship between species occurrences at a site and the environmental characteristics of the sites they are recorded in (Elith et al., 2010; Wisz et al., 2012).

SDMs also show significant potential for identifying the habitat requirements of species on both small and large geographic scales. A large amount of SDM-based research has been conducted for multiple taxa on continental, country, regional, and local geographical scales (Papeş and Gaubert, 2007; Sangermano et al., 2015; McNyset, 2005; Wang and Lin, 2013). As the effects of urbanisation range over multiple geographical scales, the multi-scale capabilities of SDM techniques can be incredibly useful. Furthermore, with the changing environmental conditions caused by urbanisation and other global threats (e.g. climate change, habitat fragmentation), the ability to model potential shifts in species ranges and habitat requirements has become incredibly valuable for the global conservation of many taxa (Wisz et al., 2012). In particular, species distribution modelling shows substantial potential for future planning of “eco-cities” where the understanding of species-specific requirements is necessary (Wang and Lin, 2013; Uy and Nakagoshi, 2008).

Bats exhibit large home ranges and nocturnal behaviour (Razgour, Hanmer and Jones, 2011), which causes them to be highly challenging to monitor. Because of the challenges associated with monitoring bat populations, data is often scarce for this group and only presence-only datasets may be available, especially when using public access databases such as museum records. However, the development of presence-only based SDM algorithms has allowed these datasets to be utilised and has dramatically increased the power of conservationists and ecologists to understand the requirements of these species and conserve them in a changing environment. As well as this, the multi-scale capabilities of these algorithms have highlighted how habitat requirements of species change depending on the scale observed and allow conservationists to adapt strategies based on these differences (Razgour, Hanmer and Jones, 2011; Bellamy, Scott and Altringham, 2013). It is important these techniques and resources are used to their full capabilities to monitor and conserve global bat biodiversity.

1.7 Aims & Objectives

Using a large, long-term public health system database, this thesis aims to assess the temporal and spatial variation in bat biodiversity in the city of Belo Horizonte, Brazil, a potentially incredibly biodiverse city. The specific objectives of this work were:

1. To quantify the variation in time and space of taxonomic, functional, and phylogenetic diversity of bats in the city.

2. To determine the most important environmental factors to consider in future conservation efforts and urban planning via a habitat suitability analysis of the most common species in the study.

1.8 Hypotheses

1. Objective 1 - Bat taxonomic, functional, and phylogenetic alpha diversity will show no significant trends over the years within study period. Beta diversity values will also show relatively little difference between years of the study.

2. Objective 1 - Bat taxonomic, functional, and phylogenetic alpha diversity will show no significant difference between the wet and dry seasons of the study. Beta diversity values will also show almost no difference between the wet and dry seasons of the study.

3. Objective 2 - Environmental factors regarding distance to key habitat and resources, such as woodland and water sources, and human population density will be considered important in multiple species habitat suitability models.

4. Objective 2 - The responses of individual species to the specific environmental predictors used in the habitat suitability analysis will be highly species-specific.

Chapter 2 - Materials and Methods

This chapter describes the research methodology that was used for this thesis. It provides information on the study area, Belo Horizonte, including location, size, environmental conditions, an overview of socioeconomic structure, and describes the ecological importance of this city. The chapter also describes the acquisition of data, the method of data collection, and the data quality control protocol. Finally, the ways in which the data was analysed and the rationale behind analysing the data in this way have been highlighted.

2.1 Study Area

The study area for this research was the city of Belo Horizonte, Minas Gerais, Southern Brazil (19.9167° S, 43.9345° W), which is located in the transition zone between two biodiversity hotspots distinct biomes, the Cerrado and Atlantic rainforest. Belo Horizonte's geographical position gives it the potential for incredibly high levels of biodiversity, making it of significant research and conservation interest. The city covers an area of approximately 330 km^2 with an average elevation of 858m and supports approximately 2.5 million inhabitants as of 2017 (IBGE, 2019; Teixeira et al., 2015a). Belo Horizonte is split into nine administrative regions: Venda Nova, Norte, Nordeste, Pampulha, Noroeste, Leste, Centro-Sul, Oeste, and Barreiro. Each of these regions show differing environmental and socioeconomic characteristics with fragments of natural habitats throughout, with over 150 of these fragments larger than 2 ha in area (Teixeira et al., 2015b).

Belo Horizonte experiences a wet season from October to March, and a dry season from April to September (Goulart, Teixeira and Young, 2010). Other climatic conditions are relatively stable throughout the year, with an annual mean temperature of approximately 21°C (Pessanha et al., 2012).

Figure 3. Location of Belo Horizonte within Brazil. Includes a map of Belo Horizonte as divided into respective administrative regions. Scale of Belo Horizonte map is 1:180,000. Source: Rocha et al., 2014.

2.2 Data Collection

All bat records were obtained as part of a database for the Zoonosis Control Centre within Belo Horizonte. This centre acts as a section of the public health infrastructure of Belo Horizonte. The zoonosis control staff respond to individual callouts when a bat is found in a civilian home or public building. All bats, whether found dead or alive, were captured and collected in the location they were found and were identified to species level where possible by a specialised taxonomist. When species-level identification was not possible, individuals were identified to genus level. Following identification, captured bats were euthanised as part of a rabies control program and recorded in a single, centralised database. This database contained records from 2002 to 2014 and was used as the basis of this study. In total, 2,997 records were collected over the study period, with a mean of 224.1 ± 129.9 records per year.

Prior to any analysis, all data was run through a quality control protocol to ensure a consistent standard of the records available. Records where individuals had not been identified to species level were first removed. Following this, species with fewer than five recordings over the full study period were then removed. As well as this, individual years with less than 100 records were also discarded. This was done to ensure statistical robustness and to account for any changes in funding/availability of the zoonosis control team, which occurred between 2002 and 2003. As well as this, a change in governance occurred between the years of 2010 and 2012. During this time, the Zoonosis Control Centre received substantially less funding for the collection and identification of bats in the city. The records collected during this time were of significantly lower quality and were not representative of the bat populations in Belo Horizonte. Because of this, the years 2010 to 2012 were removed from further analysis. In total, 735 records were removed from the dataset during the quality control protocol, resulting in 2,262 total records for analysis.

2.3 Temporal Diversity Measures

All measures of taxonomic (TD), functional (FD) and phylogenetic (PD) diversity were calculated in Rstudio version 3.4.4 (R Core Team, 2018), using the "BAT" package (Cardoso, Rigal and Carvalho, 2014). In addition to this, the package "picante" was used to extract phylogeny data for the quantification of phylogenetic diversity of bats (Kembel et al., 2010). Bat records were also partitioned into individual years between wet and dry seasons for all years combined across the study period (2004-2014). When calculating both alpha and beta diversity, records were rarefied to 80% of the number of records for the year and season with the fewest occurrence records, and rarefaction was based on 10000 iterations. This was done to account for uneven sampling effort within the study area and thus improve overall accuracy of diversity estimations (Gotelli and Colwell, 2001).

TD was quantified as species richness for each year and each season. Species richness acts as a simple count of the number of unique species present and has been utilised as a common measure of biodiversity for many ecological studies to date (Gotelli and Colwell, 2001).

FD was calculated based on Petchey & Gaston (2002, 2006), who quantifies functional diversity using the hierarchal clustering of species based on the similarity of common functional traits. Using this measure, FD is calculated as the total branch length of the cladogram generated from the clustering method. Functional trait data for all species was collected through a large variety of literature sources. The majority of functional trait data was obtained from Norberg and Rayner's (1987) study on bat wing morphology and from Farneda et al. (2018). A full list of functional trait values for each species and the sources for the functional trait data can be found in appendices I and II. Functional trait data could not be found for the species *Cynomops planirostris*, because of this, *C. paranus* was used as a replacement for the functional analysis as functional trait data was available. *Cynomops paranus* was selected as this is the closest sister taxon for which trait data was available which also occupied a similar niche and geographic range (Cisneros, Fagan and Willig, 2014). The functional traits used to quantify functional diversity were: feeding guild, wing aspect ratio, wing loading, and log (base e) of body mass in grams. These traits have been identified as highly important when considering Neotropical bat assemblages and are reflective of diet, foraging behaviour, and migration/dispersal ability (Farneda et al., 2018; Meyer et al., 2008; Cisneros et al., 2015).

Finally, PD was calculated following Faith (1992), which measures PD as the total branch length of a phylogenetic tree containing only the species included in the study. Shi and Rabosky's (2015) bat phylogeny was used to quantify alpha and beta phylogenetic diversity of bats. The R package "picante" was used to prune this phylogeny to contain only species that were recorded during the study. After the quality control protocol was conducted all species in the dataset were present in the bat phylogeny used. The final pruned phylogeny can be found in appendix III.

2.3.1 Alpha Diversity

Alpha diversity was first calculated for all individual years of the study, followed by the overall wet and dry seasons of the study. As such, alpha diversity is considered the individual TD, FD, and PD of a sampling unit (Cardoso, Rigal and Carvalho, 2014). In this study, an individual year and an individual season is considered a unique sampling unit. The median value was calculated for each facet of alpha diversity. In addition, the minimum, maximum, and lower and upper 95% confidence interval values were also calculated for each diversity facet.

A linear regression was then performed on the quantified alpha TD, FD and PD of bats recorded between all years of the study. The correlation was tested on the median values for TD, FD, and PD against a time-trend series of data points which corresponded with each year of the study (Figure 6). This was only performed for the changes in yearly biodiversity.

2.3.2 Beta Diversity

Beta diversity was calculated for all facets of biodiversity (TD, FD, and PD, Figure 6) and was used to investigate the degree of similarity between years and seasons of the study. The “BAT” package follows the frameworks developed independently by Podani and Schmera (2011), Carvalho et al. (2012), and Cardoso et al. (2014) to calculate beta diversity. This approach partitions beta diversity into richness and replacement components, which combine to inform the total beta diversity of a sample. The richness component of beta diversity shows the amount of the total beta diversity that is explained by the loss and/or gain of species alone. Conversely, the replacement component of beta diversity indicates the proportion of total beta diversity that is explained by the replacement of species alone (turnover).

All measures of beta diversity were calculated utilising Jaccard’s dissimilarity index, which produces a value between zero and one. A value of zero indicates complete similarity between samples, whereas a value of one indicates complete dissimilarity. The sum of the richness and replacement components of beta diversity will also always equate to the total beta diversity observed.

2.4 Habitat Suitability Modelling

2.4.1 Environmental Layer Creation and Standardisation

Five raster maps containing environmental information were obtained for the habitat suitability modelling (HSM) analysis. These maps contained information regarding population density, road density, land cover type, lamp post type, and lamp post power within Belo Horizonte. Selection of HSM variables was based on availability of data and previous research demonstrating the importance of these factors in determining bat activity and distribution (Gehrt and Chelsvig, 2003; Threlfall et al., 2011). The population and road density layers were created using data provided by the Company for Information Technology and Information of the Municipality of Belo Horizonte (Prodabel, 2019). The population density raster was created based on values of inhabitants per square kilometre whilst road density was based on a kernel density estimate of all streets within the city. Following this, both raster maps were defined into five caption classes by the “Natural Break” method. This method groups similar classes according to the largest differences in the entire sample set, so that the boundaries between classes are defined by the maximum distance between the values of the data. The caption classes for these layers were set as: low, low to medium, medium, medium to high, and high.

The lamp post type and power layers were created based on public lighting data made available by CEMIG (Cemig, 2019). This data contained UTM georeferenced points of every street lamp within Belo Horizonte and the lighting characteristics of these lamps. In order to transform this data into a raster-based map, each data point was transformed into a single pixel which contained the characteristics of the individual lamp. The caption classes for lamp post type were defined as: sodium vapour, tubular sodium vapour, mercury vapour, and metallic vapour. Conversely, the caption classes for the lamp post power were defined as: 70 to 80, 100 to 125, 150 to 250, and 350 to 400 watts.

Finally, the land cover type raster layer was created based on a database made available by Magalhães (2010). This dataset classifies the city into urban, open, and forested areas and was the basis for mapping land cover and land use. The caption classes for this layer were defined as: open, urban, and forested.

Two additional environmental variables detailing distance to the nearest water body and nearest body of trees were created using the ArcGIS suite (Esri, 2019). Two shapefiles were obtained which contained the locations and size of every significant water body and cluster of trees within the study area. The shapefile was used with the Euclidean Distance tool within ArcMap to create two distance-based raster maps which were then included in all MaxEnt analyses.

Prior to the MaxEnt analysis, all environmental variable raster files were standardised using R 3.4.4 (R Core Team, 2018). The R package “Raster” was used to match all raster files under the same coordinate reference system (CRS), grid resolution, and geographic extent (Hijmans, 2018). A mask was also created using a shapefile which detailed the outline of Belo Horizonte’s border. This was used to ensure all raster files contained information which solely regarded the study area.

Moreover, the mask was used to exclude any records which were located outside of the city border.

2.4.2 MaxEnt Analysis

The MaxEnt standalone software was used to perform all habitat suitability analyses (Philips et al., 2004, 2006). MaxEnt uses a presence-only approach to modelling habitat suitability whereas other methods require presence-absence data which was not available for this study. The algorithm predicts the geographical distribution of species by overlaying known presence points with layers of environmental data and extracting information from the surroundings of each presence.

The five most common species within the data set were included in the MaxEnt analysis: *Artibeus lituratus* (501 records), *Platyrrhinus lineatus* (107 records), *Molossus molossus* (464 records), *Cynomops planirostris* (208 records), and *Glossophaga soricina* (266 records). Each of these species were recorded on at least 100 separate occasions, allowing enough samples for the five-fold cross validation of models for all species. These species cover a range of niches with dietary specialisations including frugivory (*A. lituratus* & *P. lineatus*), nectarivory (*G. soricina*), and insectivory (*C. planirostris* & *M. molossus*) bats. These species also show a wide range of functional adaptations which play a key role in determining species-specific habitat requirements (Farneda et al., 2018; Tavares, 2013; Norberg and Rayner, 1987).

2.4.2.1 Spatial Autocorrelation and Sampling Bias Correction

The seven environmental variables included in the HSM analysis for all species were: population density, road density, lamp post power, lamp post type, land cover type, distance to the nearest water body, and distance to the nearest forest body. These variables were identified as having biological significance for bats. Prior to analysis, all environmental predictors were checked for multicollinearity with the calculation of Variance Inflation Factors (VIFs) and a Pearson’s correlation test. An R^2 value of 0.7 or greater or a VIF of greater than 10 was considered the threshold value for multicollinearity for this analysis. These threshold values were determined based on previous research in ecological spatial modelling (Feng et al., 2019). No environmental variables tested showed a R^2 value of 0.7 or higher or a VIF higher than 2.0 (Appendix IV and V) and thus no variables were removed from the analysis.

Due to the nature of the data collected, sampling bias could be an important factor influencing the results obtained (Elith et al., 2010; Fourcade et al., 2014; Syfert, Smith and Coomes, 2013). In this case, sampling bias is most likely correlated with population density and various socioeconomic factors. Because of this, a bias layer was created using the “MASS” package within R 3.4.4 (Venebles and Ripley, 2002; R Core Team, 2018) following the methodology of Rinnan (2015). This method produced a sampling effort raster based on a kernel density estimate of all bat records collected. This bias layer was included in all MaxEnt analyses to ensure sampling bias was corrected for.

2.4.2.2 MaxEnt Settings

Following the framework of Bellamy (2012), mostly default settings were used within the MaxEnt software. Five-fold cross validation was used to evaluate model performance. This approach separates the data set of each species into five randomly selected equal parts. MaxEnt then uses four of the five subsets to train the model and one to test the performance. Jack-knifing was also used to measure variable performance, allowing variables with low contribution and importance to be removed. The combination of features used (linear, quadratic, product, threshold, or hinge) was automatically determined by MaxEnt for each model. In addition, 500 replicates were carried out when calculating all models. Full settings for the final model of each species can be found in appendix VI.

2.4.2.3 Model Selection

Each final species’ model was calculated through the step-wise reduction of variables. Jack-knifing was used to determine variable importance and prune variables from the model until the final iteration was reached. In each iteration, any environmental variable that showed a permutation importance of less than 5% was excluded and the model was re-calculated. This was repeated until there were no environmental variables under 5% and AUC reduced upon further reduction of variables. Akaike’s Information Criterion corrected for small sample size (AICc) values were not calculated for the habitat suitability models of each species due to the low number of variables included in the calculation of models. AICc values are a valuable method for model selection, however will preferentially select the most parsimonious model (Akaike, 1987). This becomes problematic when modelling with few environmental variables as this can lead to the inclusion of only one or two variables, leading to the underfitting of these models (Radosavljevic and Anderson, 2013).

Chapter 3 - Results

3.1 Species Abundances

Within the dataset, some species showed a substantially higher abundance than others. Of the total 2,262 records retained after quality control, *Artibeus lituratus* constituted 676 of these, representing 29.9% of the total. Following this, *Molossus molossus* was recorded on 569 occasions and represented 25.2% of the dataset. *Glossophaga soricina* was the third most recorded species in the study with 291 records, representing 12.7%. *Cynomops planirostris* followed this closely with 236 total recordings, representing 10.4% of the dataset. The fifth most common species in the study, and the final species included in the habitat suitability analysis, was *Platyrrhinus lineatus* with 148 separate recordings over the study period, representing 6.5% of the dataset. In total, the five most common species recorded represent 84.9% of the total records after quality control with 1,920 records combined. The geographic distributions and of each of the focal species can be seen in Figure 4. In comparison, the remaining 342 records (15.3%) of the dataset

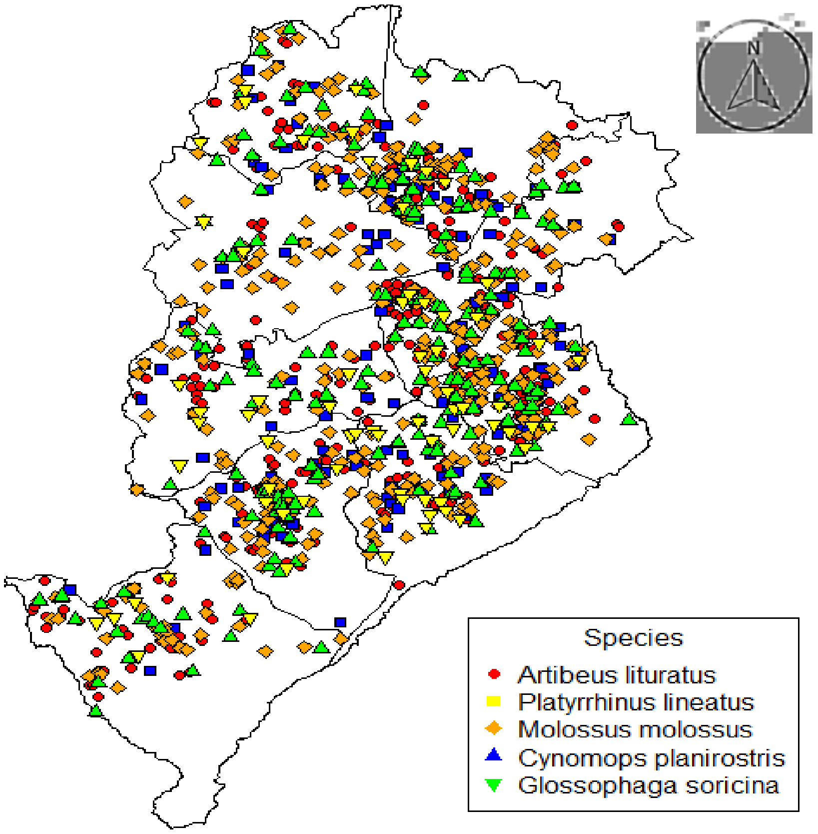

Figure 4. The point occurrences of each of the five most common species in the study. Demonstrating the major overlap in occurrence of these species throughout Belo Horizonte.

consisted of 13 species, with a number of records ranging between 5 and 81. All of these species were either primarily insectivorous or frugivorous in their feeding behaviour. The dominance of the five focal species in the database can be seen in a rank-abundance plot in Figure 5. The plot highlights the substantial differences in prevalence between the most and least common species in Belo Horizonte, with every species, excluding the five most common, representing less than 5% of the total records each.

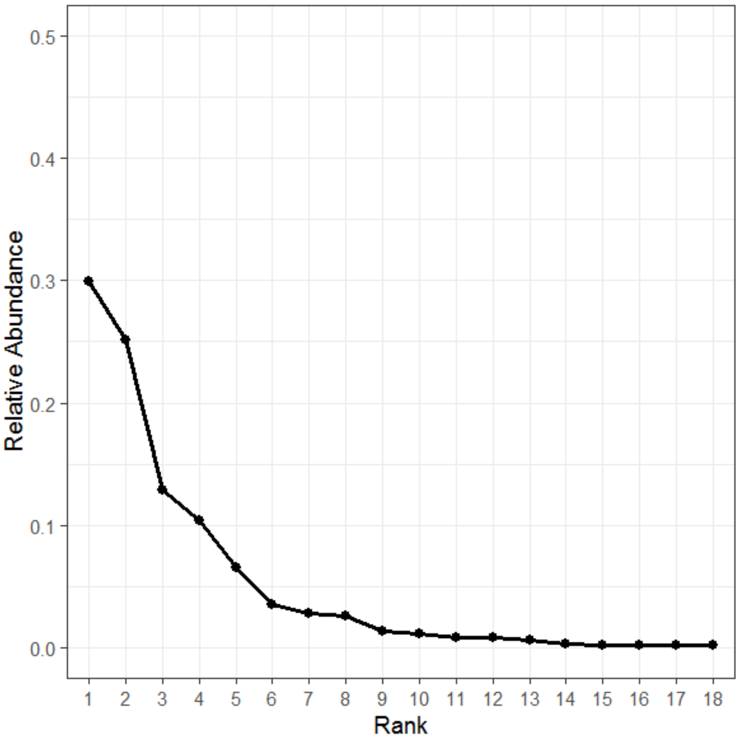

Figure 5. Rank abundance plot for all species recorded in the dataset.

3.2 Temporal Biodiversity Trends

For the purposes of this study, each year and season of the study is considered an individual sampling unit. Alpha diversity quantifies the taxonomic, functional, and phylogenetic diversity of bats within each sampling unit as independent measurements. In contrast, beta diversity, indicates the amount of similarity in taxonomic, functional, and phylogenetic diversity of bats across all sampling units measured. A beta diversity value of zero indicates complete similarity whereas a value of one shows complete dissimilarity between each year of the study.

3.2.1 Taxonomic Diversity

Over the period of 2004 to 2014, a significant positive trend was observed in median bat species richness (Figure 6, $p = 0.02$, adjusted $R^2 = 0.60$), ranging from 10 species in 2004 to 15 species in 2014. There was a high a degree of variation within years throughout the study period (Figure 6). Species richness was lower in the wet season (17 ± 0.5) than dry season (18 ± 1). Despite being no significant difference between seasons, the dry season shows more variable levels of TD than the wet season, however, this is highly likely to be insignificant and should be interpreted with caution.

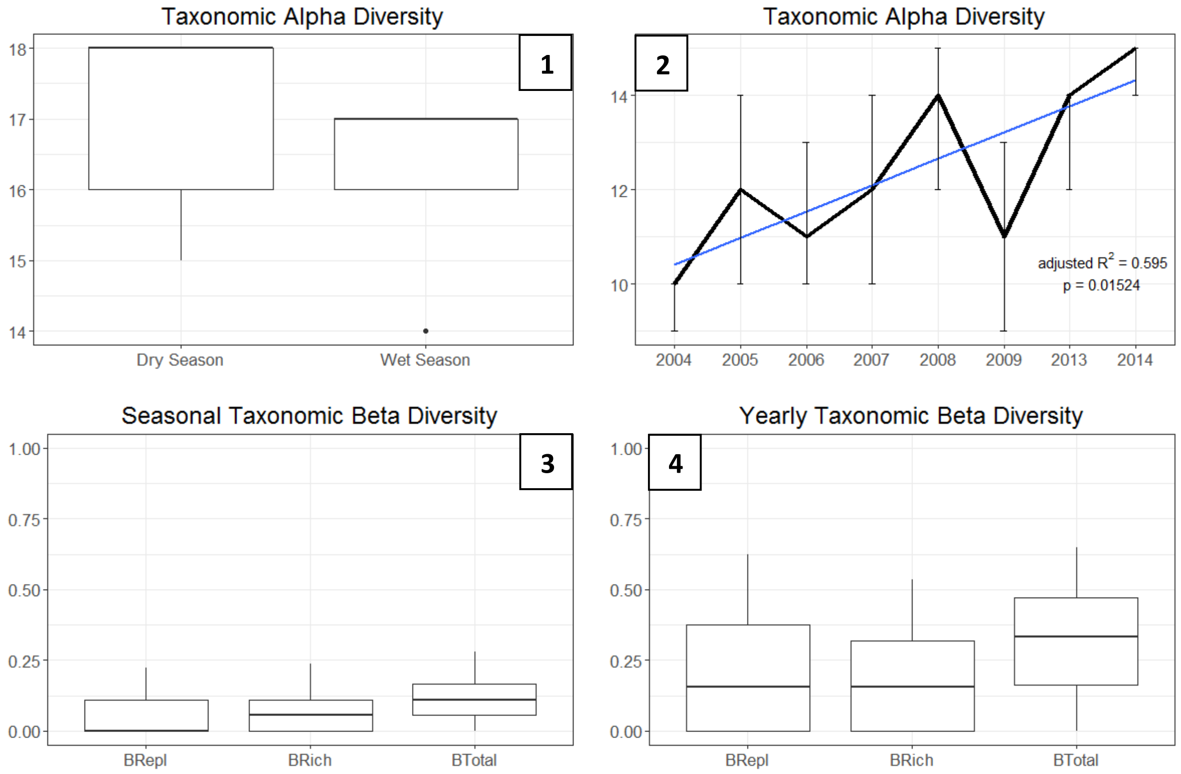

Figure 6. Taxonomic alpha and beta diversity of bats in Belo Horizonte for each year and season of the study period. [1] Horizontal black lines indicate median values. Boxes indicate the first and third quartiles, whiskers indicate the minimum and maximum diversity values obtained, and black dots indicate outlier points of data. [2] Points are median values with error bars, representing the upper and lower 95% confidence intervals, derived from rarefaction of bat records. Linear regression of yearly alpha diversity is shown as a blue line with adjusted R^2 and p-values annotated. [3] Taxonomic beta diversity of bats based on Jaccard’s dissimilarity index. Boxes indicate the first and third quartiles, horizontal black lines show median values, and whiskers indicate minimum and maximum values for each component. “BRepl” shows replacement component of beta diversity whereas “BRich” shows richness. “BTotal” is the sum of BRepl and BRich and indicates the total beta diversity.

When considering taxonomic beta diversity between study years, the replacement component of beta diversity (BRepl) showed a median value of 0.154, the richness component (BRich) also showed a median value of 0.154, and the total beta diversity (BTotal) showed a median value of 0.333 (Figure 6, Table 1). When considering the beta diversity of seasons, BRepl showed a median value of zero, BRich showed a higher median value of 0.056, and BTotal showed a median value of 0.111 (Figure 6, Table 2). This indicates a large amount of similarity in TD of bats between years and seasons of the study with some slight differences between each. When comparing medians, the replacement and richness components of beta diversity are weighted relatively evenly in their contributions towards the total beta diversity of bats in Belo Horizonte. However, species replacement appears to be slightly more variable than the richness component of beta diversity.

3.2.2 Functional Diversity

Similar to TD, linear regression also showed a significant positive trend in functional diversity of bats in the city over the study period ($p = 0.04$, adjusted $R^2 = 0.54$), ranging from 25.5 in 2004 to 30.3 in 2014. The standard deviation of observed FD was highly variable throughout the study period and was much more variable than for taxonomic diversity (Figure 7). Similar to taxonomic diversity, the median functional diversity was also lower in the wet season (32.3 ± 0.8) than the dry season (33.2 ± 1.0).

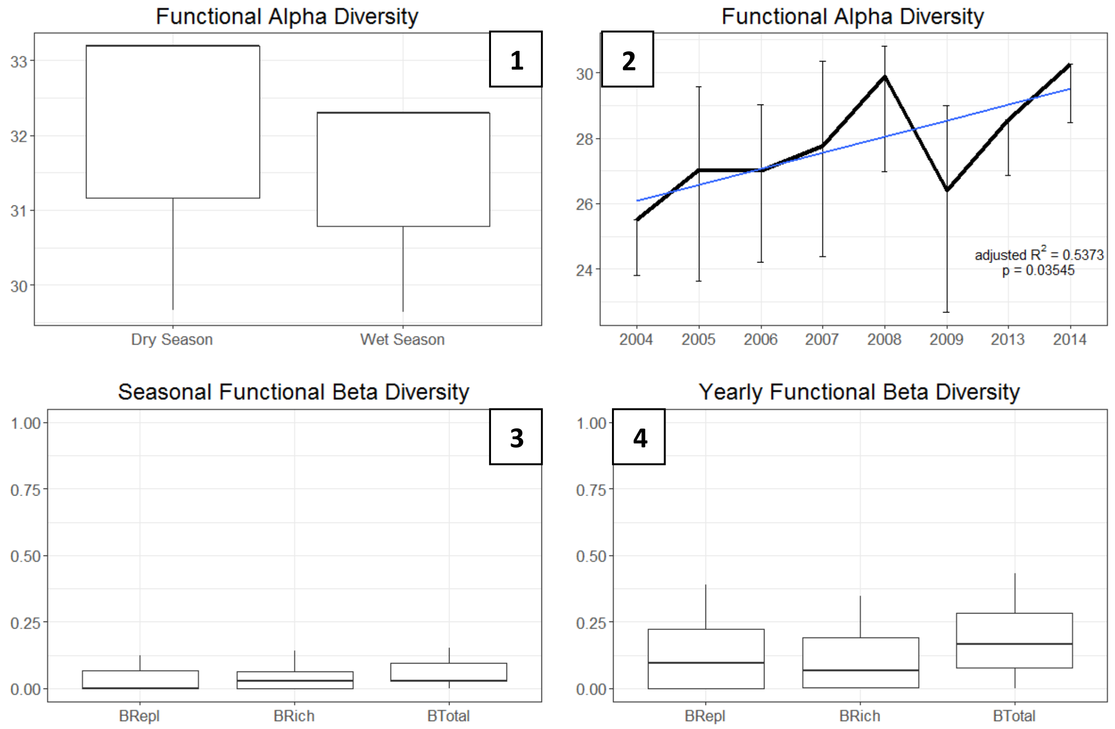

Figure 7. Functional alpha and beta diversity of bats in Belo Horizonte for each year and season of the study period. [1] Horizontal black lines indicate median values. Boxes indicate the first and third quartiles, whiskers indicate the minimum and maximum diversity values obtained, and black dots indicate outlier points of data. [2] Points are median values with error bars, representing the upper and lower 95% confidence intervals, derived from rarefaction of bat records. Linear regression of yearly alpha diversity is shown as a blue line with adjusted R^2 and p-values annotated. [3] Functional beta diversity of bats based on Jaccard's dissimilarity index. Boxes indicate the first and third quartiles, horizontal black lines show median values, and whiskers indicate minimum and maximum values for each component. "BRepl" shows replacement component of beta diversity whereas "BRich" shows richness. "BTotal" is the sum of BRepl and BRich and indicates the total beta diversity.

Functional diversity exhibited the lowest amount of total beta diversity and replacement and richness components of beta diversity for both yearly and seasonal measurements. When considering the functional beta diversity between years, BRepl showed a median value of 0.095, BRich showed a lower median value of 0.068, and BTotal showed a median value of 0.180 (Figure 7, Table 1). In contrast, seasonal beta diversity was lower than the beta diversity between study years. BRepl showed a median value of 0.059, BRich showed a lower median value of 0.027, and BTotal showed a median value of 0.027 (Figure 7, Table 2). There is very high similarity in FD of bats between each season and year. The richness and replacement components of functional beta diversity are very closely weighted when calculating total beta diversity.

3.2.3 Phylogenetic Diversity

In contrast to TD and FD, linear regression showed no significant trend in phylogenetic diversity over the study period ($p = 0.15$, adjusted $R^2 = 0.19$), ranging from 324.6 in 2004 to 444.2 in 2014. As seen with both TD and FD, there is a high degree of variation between years of the study, despite the slower rate of change observed in phylogenetic diversity (Figure 8). Finally, phylogenetic alpha diversity (PD) of bats was also lower in the wet season (503.8 ± 20.9) than the dry season (529.8 ± 61.4), though it was much less variable.

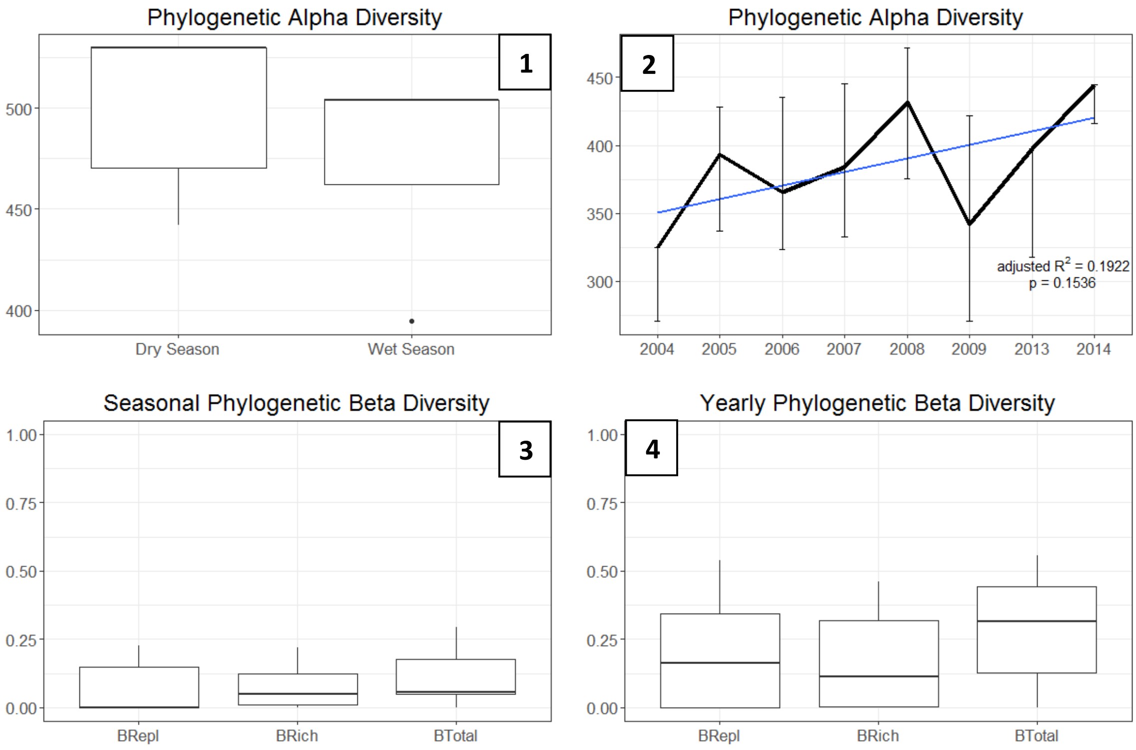

Figure 8. Phylogenetic alpha and beta diversity of bats in Belo Horizonte for each year and season of the study period. [1] Horizontal black lines indicate median values. Boxes indicate the first and third quartiles, whiskers indicate the minimum and maximum diversity values obtained, and black dots indicate outlier points of data. [2] Points are median values with error bars, representing the upper and lower 95% confidence intervals, derived from rarefaction of bat records. Linear regression of yearly alpha diversity is shown as a blue line with adjusted R^2 and p-values annotated. [3] Phylogenetic beta diversity of bats based on Jaccard's dissimilarity index. Boxes indicate the first and third quartiles, horizontal black lines show median values, and whiskers indicate minimum and maximum values for each component. "BRepl" shows replacement component of beta diversity whereas "BRich" shows richness. "BTotal" is the sum of BRepl and BRich and indicates the total beta diversity.

BTotal and BRich was lower for PD than TD between study years. When considering phylogenetic beta diversity between years, BRepl showed a median value of 0.163, BRich showed a lower median value of 0.113, and BTotal showed a median value of 0.312 (Figure 8, Table 1). In contrast, seasonal beta diversity was lower than the beta diversity between study years. BRepl showed a median value of zero, BRich showed a lower median value of 0.057, and BTotal showed a median value of 0.057 (Figure 8, Table 2). This again shows that there is a very high level of similarity between the PD of each season and year. The replacement and richness components of beta diversity are also weighted very closely in their contributions towards the total phylogenetic beta diversity.

Table 1. Median, minimum, maximum, lower confidence level (95%), and upper confidence level (95%) values for beta diversity between years of each biodiversity facet. Beta diversity is divided into total beta diversity as well as richness and replacement components.

BIODIVERSITY FACET	BETA DIVERSITY COMPONENT	MEDIAN	MIN	MAX	LOWCL	HIGHCL
TAXONOMIC	Replacement	0.154	0.000	0.625	0.000	0.375
	Richness	0.154	0.000	0.533	0.000	0.318
	Total	0.333	0.000	0.647	0.182	0.478
PHYLOGENETIC	Replacement	0.163	0.000	0.551	0.000	0.331
	Richness	0.113	0.000	0.491	0.004	0.317
	Total	0.312	0.000	0.580	0.134	0.441
FUNCTIONAL	Replacement	0.095	0.000	0.391	0.000	0.236
	Richness	0.068	0.000	0.321	0.003	0.192
	Total	0.180	0.000	0.431	0.079	0.293

Table 2. Median, minimum, maximum, lower confidence level (95%), and upper confidence level (95%) values for beta diversity between wet and dry seasons for each biodiversity facet. Beta diversity is divided into total beta diversity as well as richness and replacement components.

BIODIVERSITY FACET	BETA DIVERSITY COMPONENT	MEDIAN	MIN	MAX	LOW CL	HIGH CL
TAXONOMIC	Replacement	0.000	0.000	0.222	0.000	0.111
	Richness	0.056	0.000	0.222	0.000	0.111
	Total	0.111	0.056	0.278	0.056	0.167
PHYLOGENETIC	Replacement	0.000	0.000	0.225	0.000	0.149
	Richness	0.049	0.000	0.219	0.010	0.114
	Total	0.057	0.000	0.294	0.049	0.177
FUNCTIONAL	Replacement	0.059	0.000	0.145	0.000	0.066
	Richness	0.027	0.000	0.107	0.001	0.062
	Total	0.027	0.000	0.168	0.027	0.095

3.3 Habitat Suitability Analysis

3.3.1 Model and Variable Performance

The best-performing final model, based on the AUC value of 0.73, was for the species *Cynomops planirostris* (Table 3). Of the seven potential environmental variables, three were included in the final model for this species. Population density was the most important factor, with the lowest habitat suitability index (HSI) at low and high extremes of population density and highest HSI at medium population density (Figure 9a). Population density contributed the majority of information to the final model for this species with 76.3% contribution overall. Distance to the nearest water body and distance to the nearest forest body were also important variables for this *C. planirostris'* final model, contributing 7.0% and 16.6% respectively. *C. planirostris* showed a negative response to increasing distance to both of these natural resources (Figure 9b). Despite both variables contributing relatively low amounts of information to this model, removing either variable significantly reduced the overall AUC value.

The final habitat suitability models for *Platyrrhinus lineatus* and *Glossophaga soricina* were also well-performing with an AUC value of 0.70 and 0.69 for each model respectively (Table 3). Similar to *C. planirostris*, *P. lineatus* included three of the seven possible variables in the final iteration of its habitat suitability model, however, *G. soricina* only included two of the possible seven variables. The final model for both species considered population density an important factor. However, population density was considered of much higher importance for *G. soricina* than *P. lineatus*, with a percent contribution of 92.5% for *G. soricina* and 8.6% for *P. lineatus*. Both species showed a mixed response to increasing levels of human population density. HSI was lowest for both species at both extremes of population density and highest at medium population density (Figure 9a). Distance to the nearest natural resource, whether water or forest, was also important for both species' final models. Distance to the nearest forest body contributed 7.5% of information for *G. soricina*'s final habitat suitability, and distance to the nearest water body contributed 35.2% of information to *P. lineatus*' final model. The response of *P. lineatus* to increasing distance to the nearest water body was mixed, increasing until approximately 2.7 km, then sharply decreasing after this point. However, the response of *G. soricina* to increasing distance to the nearest forest body was positive overall. Road density was only considered an important variable for *P. lineatus*, contributing the majority of information to this habitat suitability model with 56.3% contribution overall. The response of *P. lineatus* to increasing road density was generally uniform, however, was lowest at medium road densities.

Molossus molossus and *Artibeus lituratus* exhibited the poorest performing final models with AUC values of 0.67 and 0.66 respectively (Table 3). Two environmental variables were included in the final model for *M. molossus* whereas five were included for *A. lituratus* (Table 3). Population density was considered an important variable in the final model for both species, with a contribution of 79.5% and 33.6% for *M. molossus* and *A. lituratus* respectively. Both species also showed a mixed response to increasing population density with the highest habitat suitability index observed at medium population densities (Figure 9a). Distance to the nearest forest body was also included in the final model for both species, with a model contribution of 20.5% and 4.3% for *M. molossus* and *A. lituratus* respectively. The response of *M. molossus* to this variable was also mixed, however, *A. lituratus* showed a positive response to increase distance to tree cover (Figure 9b). Lamp post power was the most important for *A. lituratus*, with a model contribution of 41.6%. In contrast, road density and lamp post type, showed low percent contributions to this species' final model, with 16.2% and 4.4% contribution respectively. The response of *A. lituratus* to each of these variables was mixed (Figure 9a and 9b). As seen with *Cynomops planirostris*, removing environmental variables of lower importance still significantly reduced AUC for the final habitat suitability model of *Artibeus lituratus*.

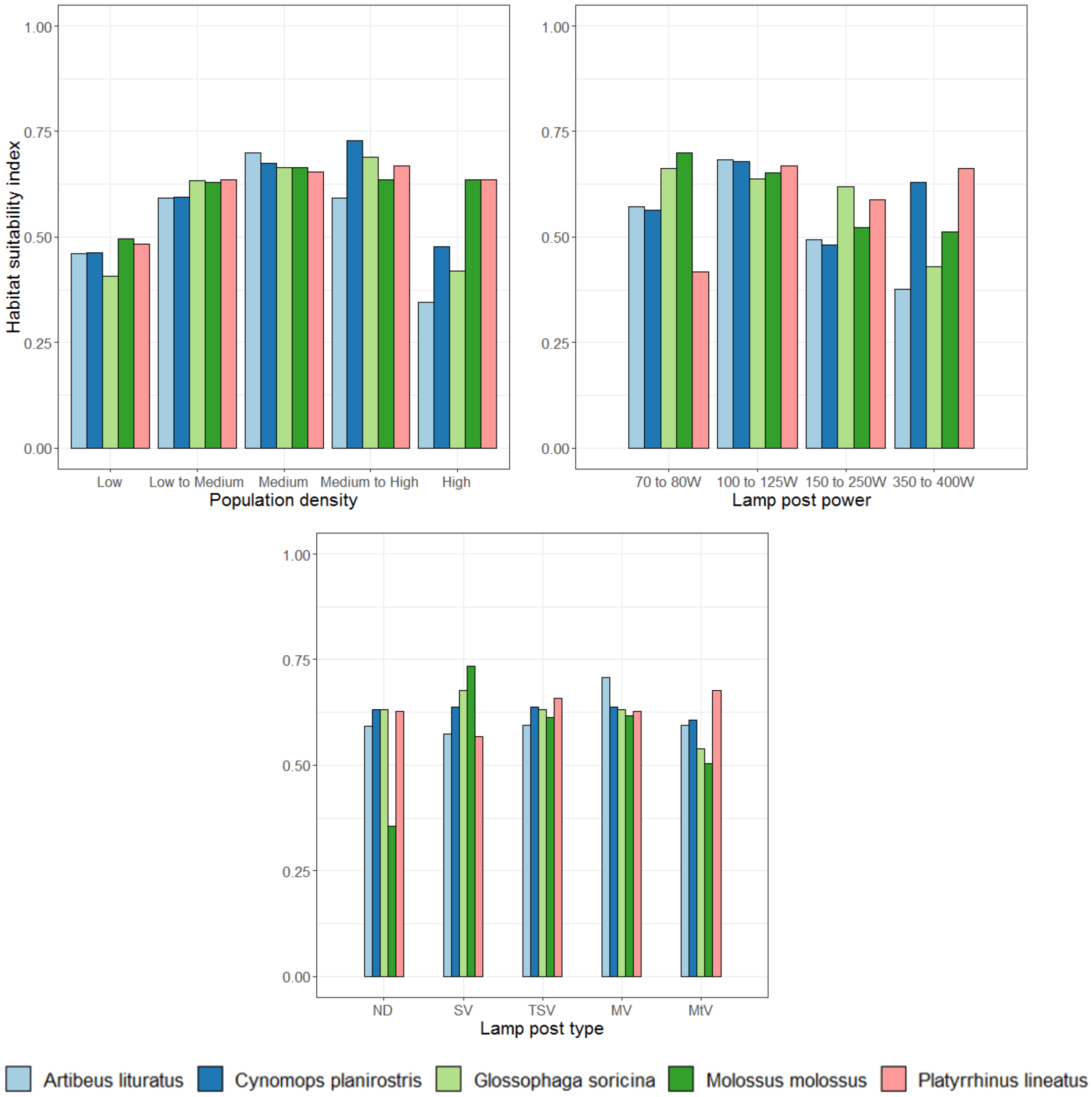

Figure 9a. The responses of each species to population density, lamp post type, and lamp post power in the study. ND = No Data, SV = Sodium Vapor, TSV = Tubular Sodium Vapor, MV = Mercury Vapor, MtV = Metallic Vapor.

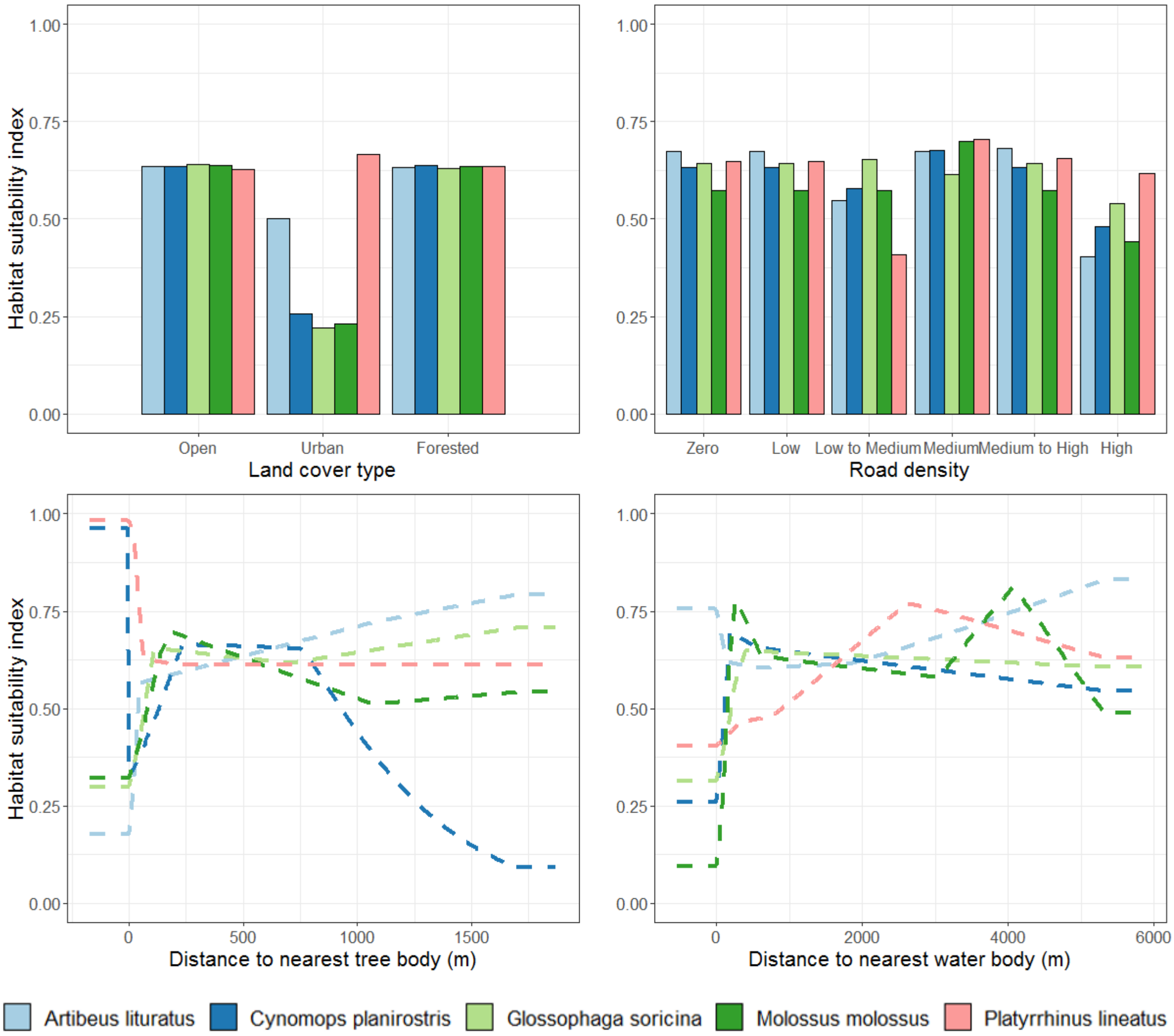

Figure 9b. The responses of each species to land cover type, road density, distance to the nearest forest body, and distance to the nearest body of water.

Table 3. Environmental variables retained in the final iteration of MaxEnt models for each species. Also shows the response of each species increasing levels of individual variables where applicable. Species are grouped by feeding guild, followed by test AUC values. Variables are listed in order of their percent contribution to the model.

SPECIES	GUILD	VARIABLE	CONTRIBUTION	RESPONSE	AUC
Artibeus lituratus	Frugivore	Lamp post power	41.6%	Negative	0.66
		Population density	33.6%	Mixed	
		Road density	16.2%	Mixed	
		Lamp post type	4.4%	N/A	
		Distance to tree cover	4.3%	Positive	
Platyrrhinus lineatus	Frugivore	Road density	56.3%	Mixed	0.70
		Distance to nearest water body	35.2%	Mixed	
		Population density	8.6%	Mixed	
Cynomops planirostris	Insectivore	Population density	76.3%	Mixed	0.73
		Distance to tree cover	16.6%	Negative	
		Distance to nearest water body	7.0%	Negative	
Molossus molossus	Insectivore	Population density	79.5%	Negative	0.67
		Distance to tree cover	20.5%	Mixed	
Glossophaga soricina	Nectarivore	Population density	92.5%	Mixed	0.69
		Distance to tree cover	7.5%	Positive	

Population density and road density were consistently considered highly important variables for determining habitat suitability for all of the common species in this study. Both variables are included in the final iteration of each species' habitat suitability model and contribute the majority of information for all but one species (*Platyrrhinus lineatus*). HSI has a consistent negative response to increasing road density for all species whilst HSI is typically highest for a medium and medium to high population density class. Following these, distance to the nearest water and tree body are the next most important factors in determining bat presence and habitat suitability for the five species included in these models. The response of each species to both environmental factors is highly variable (Table 3, Figure 9b). Finally, lamp post type, lamp post power, and land cover type are the least important of the seven predictors included in this study as they were not included in the final habitat suitability model of any focal species.

3.3.2 Habitat Suitability Maps

Each map that was produced exhibited a large range of low, medium, and high areas of habitat suitability for its representative species (Figure 10). *Artibeus lituratus* and *Platyrrhinus lineatus* are both frugivorous species and their areas of highest habitat suitability are generally most concentrated towards the centre of the city. In contrast, *Cynomops planirostris* exhibits a lower peak habitat suitability index than all other species, however, this species shows a much larger range of medium to high habitat suitability index values throughout Belo Horizonte. Finally, *Glossophaga soricina* and *Molossus molossus* both show the highest peak habitat suitability index of all species modelled. Specifically, *M. molossus* and *G. soricina* show the highest HSI towards to southern outskirts of Belo Horizonte, which is closer to the Atlantic rainforest. However, this is contrasted which a much lower habitat suitability index than other species throughout the majority of the city’s landscape.

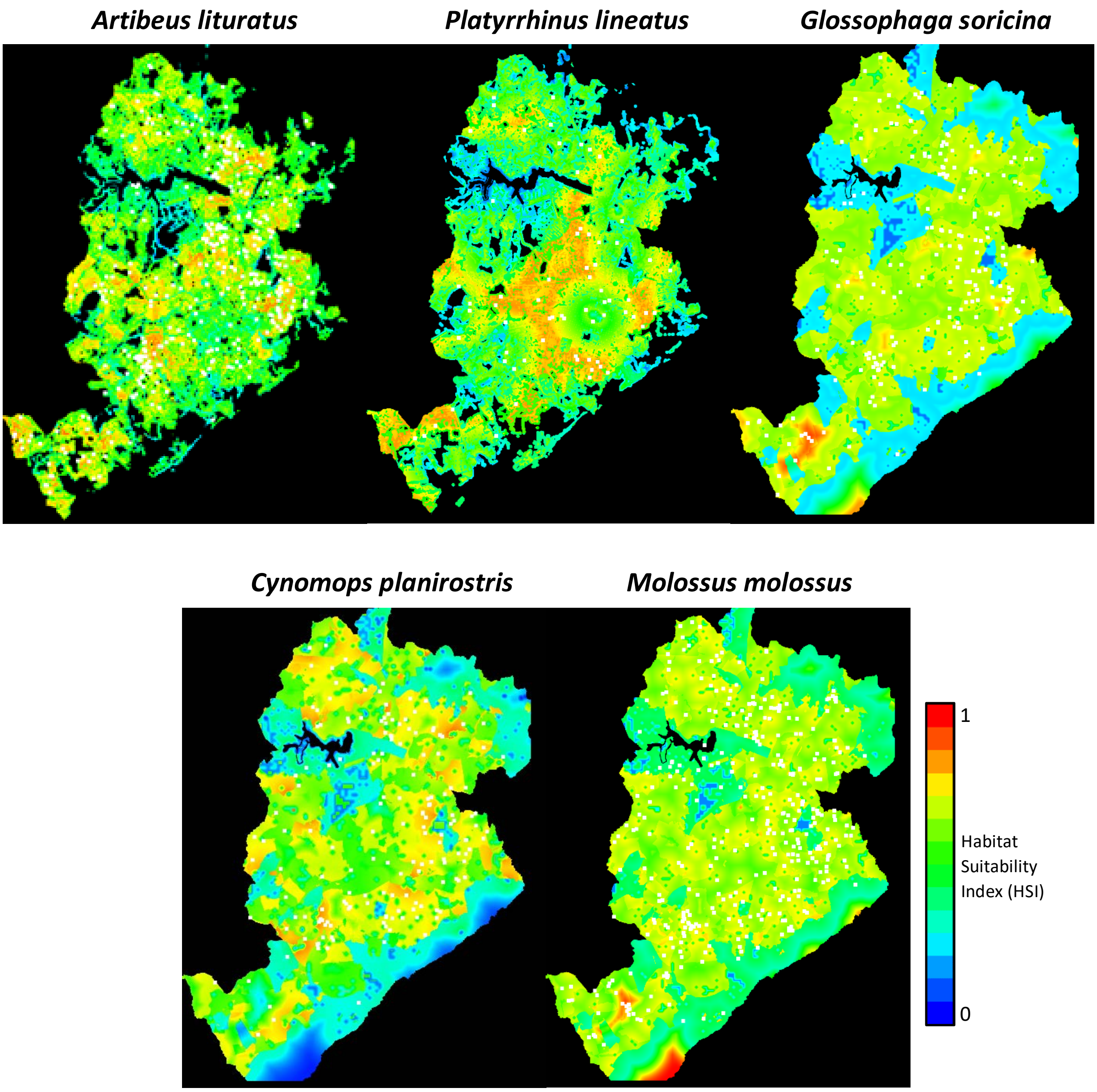

Figure 10. Maps of habitat suitability for each of the five most common species in the study. The habitat suitability index ranges from 0 to 1. Blue map areas, with a value of 0, indicate perfect habitat unsuitability while red map areas, with values of 1 indicate perfect habitat suitability. Black areas show where no background environmental data was available when calculating the final MaxEnt models for each species.

Chapter 4 - Discussion

Overall, the results show that taxonomic and functional diversity of bats is significantly increasing over time, though phylogenetic diversity is not. All dimensions of biodiversity are linked, and over a long enough time frame, phylogenetic diversity may also be considered to have significantly increased over time. Another possible explanation for this may be that urban assemblages are not stable and that urban areas may filter bat species according to phylogeny. This, however, still disagrees with the first hypothesis set out, which states all dimensions of biodiversity will show no significant trends over the study period. Moreover, there was no significant difference in the levels of each biodiversity facet observed between the wet and dry seasons of the study. In contrast to the yearly alpha diversity trends, this agrees with the second hypothesis stated. Population density and distance to the nearest natural resources (forest and water bodies) were important variables for all focal species. However, each species response to these environmental variables included was variable, indicating species-specific habitat requirements and thus species-specific responses to urbanisation. These results are in agreement with the third and fourth hypotheses laid out.

4.1 Species Urban Adaptability

It can be seen from the results of this research that the response of species to urbanisation is highly species-specific, which is in agreement with previous research (Santini et al., 2019; Threlfall et al., 2011; Jung and Kalko, 2011; Gehrt and Chelsvig, 2003; Concepción et al., 2015). Conservation efforts should take this into consideration during planning stages to ensure maximum effectiveness. As such, it may be beneficial to the conservation of biodiversity to classify species as either urban-exploiters, urban-tolerant, or urban-intolerant to better direct conservation strategies to their needs.

Artibeus lituratus is a highly common species in both the study area and throughout its geographical range of Northern Mexico to Southern Brazil (IUCN, 2019), being reported as highly abundant in both natural and urban environments from other studies to date (Silva, Perini and de Oliveira, 2005; Sazima et al., 1994). The high levels of abundance observed for this species is potentially due to its' ability to utilise multiple food resources such as nectar, leaves, or insects, despite being primarily frugivorous (Sazima et al., 1994). The high abundance of *A. lituratus* in Belo Horizonte may also reflect the number and variety of tree species present in the city, which can act as roosting resources for bat species (Perini, Tavares and Nascimento, 2014). *A. lituratus* can be considered a generalist species given its ability to utilise a wide variety of resources in a number of different environments (McCulloch, 2012). Moreover, the dominance of this species in the data suggests that this species can also be considered an urban exploiter.

Platyrrhinus lineatus is the second most common frugivorous species in the study. This species is relatively common in forested habitats and is considered to have a stable population by the IUCN (2019), ranging from Northern Colombia to Uruguay. *P. lineatus* is similar to *A. lituratus* in both its frugivorous diet and its generalist habitat requirements (Silva, Perini and de Oliveira, 2005). This is reflected in its ability to utilise buildings and palm tree canopies as roosting sites in urban environments (Franco Bessa et al., 2010; Mendes et al., 2011). However, the overlap in the niches of *A. lituratus* and *P. lineatus* may potentially lead to competition between these species for resources (Bobrowiec and Cunha, 2010), though testing this was beyond the scope of this study and thus this conclusion is purely speculation by the author. However, if this is the case, competition between these species may partially explain the lower abundance of *P. lineatus* in comparison to *A. lituratus*. Despite *P. lineatus'* habitat preference for forested areas, its ability to exploit roosting resources in urban environments likely classes this species as urban tolerant.

Similar to *Artibeus lituratus*, *Molossus molossus* is also a highly common species in both natural and urban environments, with a large distribution range from Northern Mexico to Southern Brazil (IUCN, 2019; Barros, 2014). However, *M. molossus* occupies a separate niche to *A. lituratus* and is an aerial insectivorous species, whereby it forages primarily by catching insects during flight (Nunes, Rocha and Cordeiro-Estrela, 2016). As well as this, *M. molossus* has been observed to typically roost within buildings in urban environments (Franco Bessa et al., 2010; Nunes, Rocha and Cordeiro-Estrela, 2016), rather than the tree roosting behaviour of *A. lituratus* (Perini, Tavaores and Nascimento, 2014). This species was also highly dominant in the dataset, representing over a quarter of the total records. This is also seen in other studies of bats within cities, often reporting high numbers of abundance and activity of *M. molossus* (Santini et al., 2019; Jung and Kalko, 2011; Franco Bessa et al., 2010; Silva, Perini and de Oliveira, 2005; Cormier, 2014; Jung and Threlfall, 2016). It can be inferred from this prevalence, that *M. molossus* can likely be considered an urban exploiter.

Cynomops planirostris is the second most common of the eight molossid species recorded in this study. This species is common throughout its distribution from Panama to Northern Argentina and is considered of least concern by the IUCN (2019). Species of the Molossidae family are specialised aerial insectivorous bats, and thus *C. planirostris* and *M. molossus* occupy a similar niche. This niche overlap may lead to inter-specific competition between these species for both food and roosting resources. However, *M. molossus* has been observed to exhibit precise emergence times for nightly foraging activities (Holland et al., 2011) which may secondarily serve to reduce the competition between other species competing for similar foraging resources. Furthermore, both *M. molossus* and C*. planirostris* have also been recorded to show higher levels of activity in urban environment than forested (Jung and Kalko, 2011), with the specific exploitation of buildings as roosting resources as well as the increased insect abundance for foraging. It is likely that both *C. planirostris* and *M. molossus* can both be considered urban-exploiters.

Glossophaga soricina is the most common nectarivorous species in this study. Moreover, it exhibits a large distribution range from Northern Mexico to Southern Brazil (IUCN, 2019). As well as feeding on nectar, *G. soricina* is also able to utilise fruit and insect resources as part of their diet (Lemke, 1984; Murphy et al., 2016). However, despite the abundance of this species, the dietary specialisation of *G. soricina* and the adaptations it has developed because of this (i.e. high metabolism) cause it to be highly sensitive to reductions in food resources (Lemke, 1984). With this in mind, *G. soricina* may be considered urban-tolerant. However, the sensitivity of this species to food resource availability may limit it to urban environments with sufficient green space availability.

4.2 Functional Diversity Homogenisation

Biodiversity has been shown to become increasingly homogenised within and surrounding urban environments, depending on the intensity of urbanisation (McKinney, 2006; Schoeman, 2015; Devictor et al., 2007; Luck and Smallbone, 2010). This phenomenon occurs because specific functional traits and adaptations, such as high mobility and tolerance to artificial light, become necessary to persist within these environments (Jung and Threlfall, 2018; Devictor et al., 2007; Schoeman, 2015). Moreover, urban environments are relatively uniform globally, and thus the pressures associated with different urban areas are similar (McKinney, 2006).

Each of the five most common species recorded in this study can be considered either urban-tolerant or an urban-exploiter. As well as this, each of these species was recorded substantially more often than any of the species not included in this list. For example, the fifth most common species, *P. lineatus,* was recorded 148 times and the next most common species, *Nyctinomops laticaudatus*, recorded on only 81 occasions, just over half the records of *P. lineatus*. All of the five aforementioned species are capable of and exhibit both high-speed and highly manoeuvrable flight (Oprea et al., 2009; Rhodes and Catterall, 2008), and the ability to roost in man-made structures (Perini, Tavares and Nascimento, 2003; Nunes, Rocha and Cordeiro-Estrela, 2016). Both of these functional adaptations have been identified as important for persistence within cities (Threlfall et al., 2011; Duchamp, Sparks and Whitaker, Jr., 2004). The dominance of species with these specific functional adaptations within the dataset thus corroborates the hypothesis that urban environments promote the homogenisation of functional diversity within them.

4.3 Biodiversity Trends

4.3.1 Yearly Trends

Linear regressions indicated a significant positive trend in both taxonomic and functional alpha diversity, though no significant trend was found for phylogenetic alpha diversity. However, due to the highly correlated nature of the three biodiversity dimensions (Huang, Stephens and Gittleman, 2012), it can be expected that phylogenetic diversity will also increase over time, if the positive trends in TD and FD continue. Furthermore, analysis of the beta diversity of bats for each biodiversity facet showed very low levels of difference between study years (TD = 0.333, FD = 0.180, PD = 0.312, Table 1). This indicates that biodiversity within Belo Horizonte is remaining relatively stable, with very low amounts of species replacement occurring within the city. It can be concluded from this that the city has become a commonly used habitat for the bat species that able to utilise its resources. However, it is beyond the scope of this study to monitor the fine-scale land use changes in Belo Horizonte over time. Therefore, it is impossible to accurately determine whether the temporal biodiversity trends observed can be linked to specific changes in the city, such as the development of additional green spaces, during the study period. However, the positive trend in functional and taxonomic diversity of bats in Belo Horizonte is an indicator that biodiversity in the city is becoming less homogenised over time, which is a major threat caused by urbanisation on a global scale. Though these trends should be carefully monitored in the future.

4.3.2 Seasonal Trends

Taxonomic, functional, and phylogenetic alpha diversity of bats showed no significant difference between the wet and dry seasons of the study period. However, the median values for each diversity facet were consistently higher in the dry season. This may be due to the increased energy expenditure required to fly and moderate body temperature when wet, and due to the interference of raindrops on echolocation calls (Voigt et al., 2011), which may have led to lower levels of bat activity during the wet season. However, cities are known to act as heat islands and exhibit higher temperatures than surrounding natural habitats (Gago et al., 2013). The increased average temperatures of the city may allow reduced overall energy costs of moderating body temperature during the wet season and can potentially partially explain why bat alpha biodiversity showed no significant difference between the wet and dry seasons of the study period. Quantification of the beta diversity of bats for each biodiversity facet showed incredibly high similarity between seasons of the study (TD = 0.111, FD = 0.027, PD = 0.057, Table 2). Moreover, the species replacement (turnover) component of beta diversity was also incredibly low (TD = 0.000, FD = 0.059, PD = 0.000, Table 2). This indicates that bat community composition and structure is almost identical in both the wet and dry seasons of the study. Furthermore, the low levels of species turnover, combined with the high similarity in community composition of the wet and dry seasons, shows that bats species in Belo Horizonte do not migrate to other regions during specific seasons and utilise the cities resource throughout the year.

4.4 Habitat Suitability

Habitat suitability models and maps were built for the five most common bat species in the dataset. The best performing model, determined by an AUC value of 0.73, was calculated for *Cynomops planirostris*. The poorest performing model, determined by an AUC value of 0.66, was calculated for *Artibeus lituratus*. However, the range in test AUC of the final models developed is small, with the difference in best and worst model being equal to a 0.07 change in test AUC. These models showed test AUC values ranging from 0.66 to 0.73, showing that these models can be of use for predicting the distributions and habitat requirements of these focal species. An AUC value of 0.5 would indicate that predictions based of a model would be no better than random predictions. As such, it can be determined that each of these habitat suitability models are relatively accurate and thus the predictions made from can be applied to both conservation strategies and sustainable urban development plans.

Population density can be considered the most important variable for determining the presence of each of the focal species of this study. This environmental variable was included in every species final HSM. Furthermore, population density contributed over a third of the model information for four of the five species modelled (*A. lituratus, G. soricina, M. molossus,* and *C. planirostris*). All of the focal species have been observed to utilise housing and other man-made constructions for roosting resources (Perini, Tavares and Nascimento, 2003; Nunes, Rocha and Cordeiro-Estrela, 2016). The availability of roosting resources is key to the persistence of bat species within a given habitat, and thus the importance of human population density is most likely due to this fact. Moreover, habitat suitability was typically highest at medium population densities. This level of human population density may balance the high availability of roosting resources and the amount of human-wildlife contact in these areas of the city. Areas of medium population densities or lower may also contain a higher amount of green spaces than areas of higher population densities. However, it is beyond the scope of this study to test this hypothesis. If this is the case, it is also likely that medium population density areas are also preferred due to the increased green space availability.

In contrast to population density, road density was considered to have very low importance for the focal species of this study, only being included in the final HSM for *Artibeus lituratus*. HSI showed very little change in response to increasing road density overall and was only substantially lower at very high road densities. Multiple studies have reported that large and highly active roads significantly reduce bat activity (Berthinussen and Altringham, 2011; Kitzes and Merenlender, 2014) due to the increased anthropogenic noise interfering with foraging activities (Schaub, Ostwald and Siemers, 2008; Altringham and Kerth, 2015). The response of *A. lituratus* to very high levels of road density corroborate the findings of these studies. In contrast, the lack of response to road density by any other focal species could indicate that roads may act as corridors which these species could utilise to access foraging areas. However, testing this is beyond the scope of this research and is speculation of the author.

Distance to the nearest natural water and forest resources were also determined to be highly important from this analysis. Every species' final habitat suitability model contained at least one of these environmental variables, with the final model for *C. planirostris* containing both variables (Table 3). In comparison to population density, these environmental variables contributed less information to each species' habitat suitability model overall. However, the inclusion of at least one of these variables in every species' final model and habitat suitability index decreasing after a threshold distance from each resource (specific to each species), indicates the importance of these resources being within an easily accessible distance for bat species. This corroborates previous findings (Rainho and Palmeirim, 2011; Evelyn, Stiles and Young, 2004) and further highlights the importance of green spaces within urban environments to promote wildlife within them.

Lamp post power, and lamp post type can be considered of low ecological importance for the focal species of this study. Lamp post power and type was only included in the final model for *A. lituratus*. Lamp post type also contributed a very low amount in information to *A. lituratus'* final model. However, Lamp post power contributed the major of information to this model (41.6%), indicating whilst the intensity of artificial lightning is highly important for this species, regardless of the type of lightning used. The negative response of *A. lituratus* could be linked to potential lunar phobic behaviour of this species. However, literature on lunar phobic behaviour of bats is often in disagreement, with multiple studies reporting both lunar phobic and non-lunar phobic behaviour in *Artibeus* species (Appel et al., 2017; Saldaña-Vázquez and Munguía-Rosas, 2013; Gutierrez et al., 2014; Esbérard, 2007; Morrison, 1978). However, a recent meta-analysis of lunar phobia in bats, conducted by Saldaña-Vázquez and Munguía-Rosas (2013), showed a significantly negative response of bats to moonlight intensity, which also correlated with latitude. Lunar phobia is often linked to predation risk (Saldaña-Vázquez and Munguía-Rosas, 2013), which may be the cause of this response due to high numbers of domestic predators such as cats and dogs within urban environments (Russo and Ancillotto, 2015). However, this light avoiding behaviour may also serve to reduce human-wildlife contact with lower human activity in less well-lit areas and thus lower detection rates, though this cannot be objectively tested with this study.

Land cover type can be considered the least important predictor variable used in this study, as it was not included in the final habitat suitability model of any of the focal species. It is likely that this variable was not considered of high importance due to the inclusion of the distance to the nearest natural resource predictors. This was tested by the removal of the distance to natural resource variables from the habitat suitability models of the focal species, which often resulted in the inclusion of land cover type in the final model. However, AUC values of models that did not include the distance to nearest resource predictors were substantially lower than those with them included. From this it can be concluded that urban habitat suitability can be more accurately predicted by the distance to resources, rather than the type of land cover.

The inclusion and importance of distance to natural resources (water and forest bodies) and population density predictors in the final HSM of every species is in agreement with the third hypothesis stated. Furthermore, the response of each focal species to given environmental predictors is highly variable. This is also in agreement with the final hypothesis stated. It is clear that each of the focal species of this study show specific habitat requirements in order for them to thrive within Belo Horizonte and other urban environments. In order to conserve these species effectively, the full extent of these requirements must be understood. Future research should aim to further narrow this knowledge gap. In particular, research into the wider habitat requirements of neotropical bat species would greatly improve conservation efforts.

4.5 Further Considerations

Public databases show substantial potential for remote biodiversity monitoring efforts, especially in developing countries where systematic monitoring schemes are rare (El-Gabbas and Dormann, 2017). However, the methods of data collection typically employed by these systems are highly susceptible to changes in public policy and funding availability. This can lead to drastic changes in sampling effort and thus inter-year or inter-season comparisons may no longer be statistically accurate. This scenario occurred in this study between the years 2010 to 2012, where a change in governance drastically reduced the capabilities of the Zoonosis Control Centre to respond to callouts. Because of this, these years were not representative of the true bat biodiversity within the city and were not comparable with other years and were thus removed from the analyses. Significant trends were still able to be determined as the trends were present prior to the change in governance, however, this may be problematic for future studies where it may be impossible to determine if there was a change in trend during this period.

Urban green spaces are known to be of great benefit for both human populations and urban wildlife and can act as refuges within these environments (Kong et al., 2010; Goddard, Dougill and Benton, 2010). Moreover, green spaces may also house high levels of biodiversity and species abundance under certain landscape configurations (Aronson et al., 2017), especially for species which are not as adapted to urban environments and are unable to migrate to other habitats (Goddard, Dougill and Benton, 2010). An example of this can be seen with arthropod and small mammalian species, which thrive in adequately sized urban green spaces (Goddard, Dougill and Benton, 2010; Beninde, Veith and Hochkirch, 2015). A limitation of the dataset used in this analysis and many other databases, is that green spaces within the city are not included as part of the monitoring scheme. Although bat species are likely to utilise areas outside of these green spaces due to their high mobility, studies utilising databases to monitor less mobile and less conspicuous taxa may under-represent the true diversity of urban communities and should be corrected for (Schmeller et al., 2009). In the future, attempts to incorporate green spaces into local monitoring schemes may prove incredibly useful for accurately representing biodiversity within urban environments.

Although the habitat suitability models calculated in this study can at least partially explain the responses of the focal species of this study to urbanisation, they are limited by the amount of environmental information which was available to predict them. Each of the predictor variables included show ecological importance for bat species, however they are not exhaustive of the anthropogenic pressures associated with persisting in urban environments. Other factors such as ambient noise levels may significantly affect bat distributions (Schaub, Ostwald and Siemers, 2008), however, information regarding factors such as these is often sparse, despite potentially significant effects on species distributions and biodiversity. In order to effectively conserve biodiversity within urban environments, as much information regarding the anthropogenic pressure associated with them should be obtained and incorporated into studies such as this.

4.6 Conclusion

The global threat posed by unmoderated urbanisation continues to be a major challenge for the conservation of biodiversity worldwide (Jung & Threlfall, 2016; Russo and Ancillotto, 2015). Moreover, the neotropics are still undergoing major amounts of urbanisation and the proportion of the population living in urban environments is expected to further increase over the next century (UNPD, 2017). Therefore, it is imperative that the effects of urbanisation on bat species and other taxa, and the specific habitat requirements of these species are fully understood. With this knowledge, conservationists may have the tools and information necessary to develop the critical conservation measures needed to conserve global biodiversity over the coming century.

As shown in this study, public access databases can provide critical information for the long-term monitoring of biodiversity. With rigorous quality control, these databases are a potentially untapped resource for global conservation efforts, particularly in areas of the world where large-scale monitoring programs have not been organised. Moreover, species distribution modelling and the MaxEnt algorithm have previously and continue to show substantial potential for identifying the habitat requirements of many taxa, including bats. The ability to determine these habitat preferences and requirements on the local, regional, and continental geographic scales greatly improves the ability of conservationists to adapt management and conservation strategies based on previously unavailable information. In addition to this, species distribution modelling has the ability to predict the impacts of environmental change on these taxa. The combination of public access databases, such as the one used in this study, and species distribution modelling will aid in mitigation of the impacts of urbanisation and other global challenges such as climate change and fragmentation and should be utilised to their full potential.

This study has monitored the taxonomic, functional, and phylogenetic diversity of bats in Belo Horizonte using a long-term public access database and has found that bat taxonomic and functional diversity showed a significant positive trend over the study period, though phylogenetic diversity did not. Furthermore, this study has identified some of the key factors affecting the persistence and distribution of the five most common species in the dataset used. Population density and distance to the nearest natural resources, whether water and forest bodies, were highly important for these species. Lamp post power and road density were of medium importance in predicting the distribution and persistence of these species, and lamp post type and land cover type were of low importance for these species. We have attempted to contribute to the knowledge regarding how bats are affected by urbanisation and highlight the use of public access databases for remote biodiversity monitoring efforts.

Chapter 5 - References

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Chapter 6 - Appendix

6.1 Appendix I

The functional trait values and the number of total recordings for each species within the dataset after the quality control protocol was carried out. Wing morphology trait data was could not be obtained for *Nyctinomops laticaudatus*.

Species	**Feeding Guild**	**Log body mass (grams base e)**	**Aspect Ratio**	**Wing Loading**	**Total Records**
Artibeus lituratus	Frugivorous	4.087	6.1	44.89	676
Molossus molossus	Insectivorous	2.785	8.7	62.37	569
Glossophaga soricina	Nectivorous	2.2513	6.4	47.08	291
Cynomops planirostris	Insectivorous	2.6027	8.3	78.98	236
Platyrrhinus lineatus	Frugivorous	3.3322	6.1	44.9	148
Nyctinomops laticaudatus	Insectivorous	2.5257	N/A	N/A	81
Eumops glaucinus	Insectivorous	3.6376	9.6	52.77	63
Nyctinomops macrotis	Insectivorous	2.9014	9.71	35.26	58
Lasiurus ega	Insectivorous	2.3702	7.6	32.18	31
Tadarida brasiliensis	Insectivorous	2.5257	8.2	48.83	26

Promops centralis	Insectivorous	3.6243	9.41	72.99	20
Eumops perotis	Insectivorous	3.9797	9.5	65.97	18
Myotis nigricans	Insectivorous	1.4351	6.5	37.12	14
Eptesicus brasiliensis	Insectivorous	2.2565	6.33	33.56	8
Artibeus planirostris	Frugivorous	3.9982	6.33	41.18	6
Lasiurus cinereus	Insectivorous	3.4965	8.1	50.86	6
Phyllostomus discolor	Insectivorous	3.7424	6.6	44.91	6
Carollia perspicillata	Frugivorous	2.9497	6.1	34.56	5

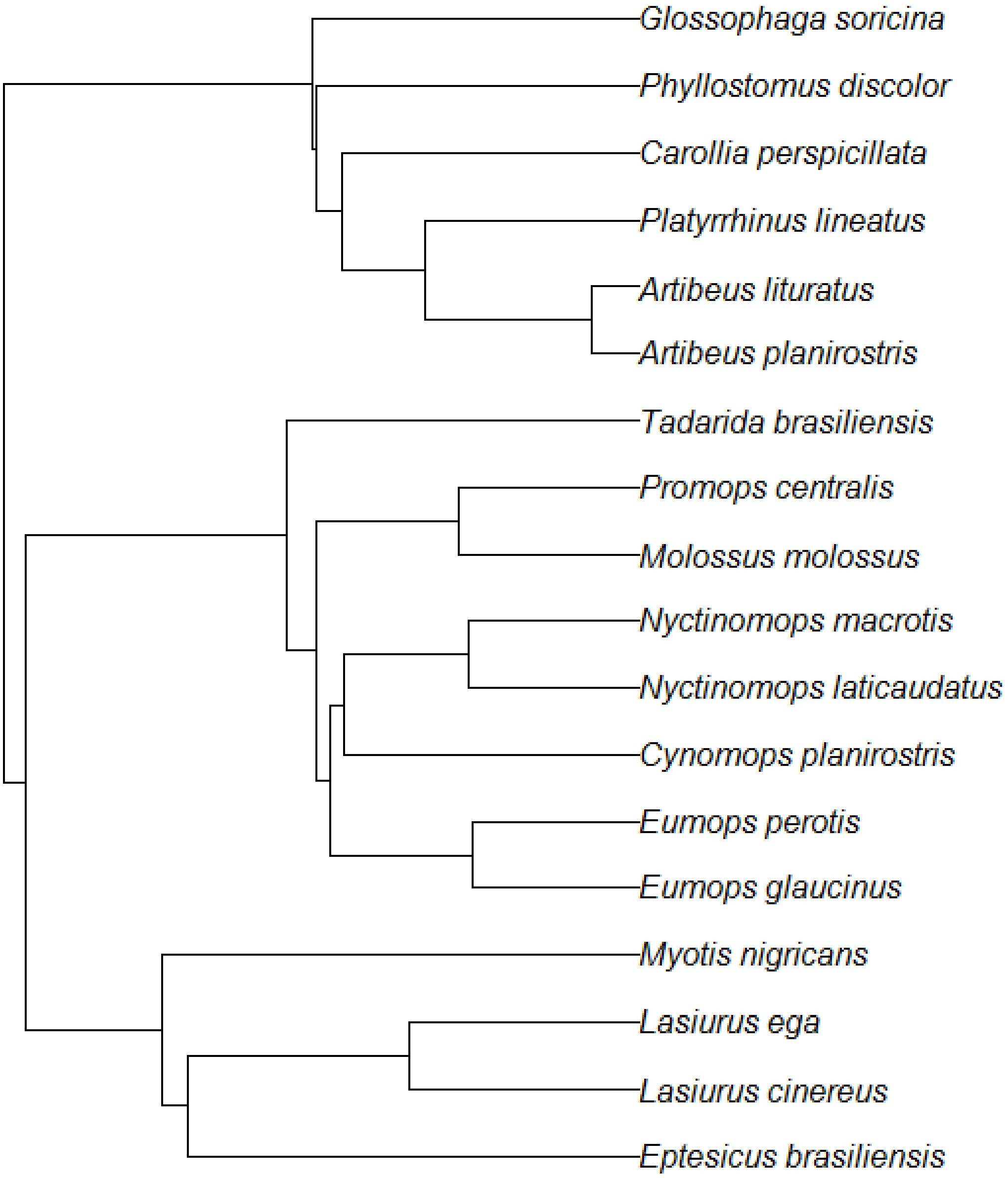
6.2 Appendix II

Literature sources for the functional trait data of all species within the dataset after the quality control process.

Species	Functional Trait Data Source
Artibeus lituratus	Norberg and Rayner, 1987; Farneda et al., 2018; Tavares, 2013;
Artibeus planirostris	Farneda et al., 2018
Carollia perspicillata	Norberg and Rayner, 1987; Farneda et al., 2018; Tavares, 2013
Cynomops planirostris **(*C. paranus* traits used)**	Marinello and Bernard, 2014
Eumops glaucinus	Best, Kiser and Rainey, 1997
Eumops perotis	Norberg and Rayner, 1987
Glossophaga soricina	Norberg and Rayner, 1987; Farneda et al., 2018; Tavares, 2013
Lasiurus cinereus	Norberg and Rayner, 1987
Lasiurus ega	Rydell et al., 2002b
Molossus molossus	Norberg and Rayner, 1987; Farneda et al., 2018
Myotis nigricans	Norberg and Rayner, 1987
Nyctinomops laticaudatus	Avila-Flores, Flores-Martínez and Ortega, 2002
Nyctinomops macrotis	Norberg and Rayner, 1987; Milner, Jones and Jones, 1990
Phyllostomus discolor	Norberg and Rayner, 1987; Farneda et al., 2018
Platyrrhinus lineatus	Tavares, 2013
Promops centralis	Norberg and Rayner, 1987; Bowles, Heideman and Erickson, 1990
Sturnira lilium	Norberg and Rayner, 1987; Farneda et al., 2018
Tadarida brasiliensis	Norberg and Rayner, 1987

6.3 Appendix III

Shi and Rabosky's (2015) bat phylogeny after pruning to include only the species recorded in this study. This was the phylogeny used for all phylogenetic diversity measurements.



6.4 Appendix IV

Variance Inflation Factors (VIFs) for all of the environmental variables available for this study.

Environmental Variable	**Variance Inflation Factor (VIF)**
Population density	1.181747
Road Density	1.234122
Land cover type	1.037377
Lamp post type	1.446413
Lamp post power	1.089021
Distance to nearest forest body	1.067824
Distance to nearest water body	1.134854

6.5 Appendix V

Pearson's correlation coefficients for all of the environmental variables available for this study.

	Pop. Dens.	Road Dens.	Land Cover	Lamp Type	Lamp Power	Distance to Forest	Distance to Water
Pop. Dens.		0.249	-0.157	0.524	0.140	- 0.090	0.005
Road Dens.	0.249		-0.139	0.431	0.128	0.055	0.096
Land Cover	-0.157	-0.139		-0.176	-0.001	- 0.109	- 0.0634
Lamp Type	0.524	0.431	-0.176		0.145	- 0.080	0.211
Lamp Power	-0.140	0.128	-0.001	0.145		- 0.010	0.077
Distance to Forest	-0.090	0.055	-0.109	-0.080	-0.010		0.120
Distance to Water	0.005	0.096	-0.063	0.211	0.077	0.119	

6.6 Appendix VI

Maxent settings (feature types, regularization multiple, number of maximum iterations, and number of background points) used for all species in the habitat suitability analysis.

Species	Features used	Regularization multiplier	Maximum iterations	Number of background points
Artibeus lituratus	hinge (H), linear (L), quadratic (Q)	0.500 (H), 0.050 (L/Q)	5,000	10,000
Platyrrhinus lineatus	hinge (H), linear (L), quadratic (Q)	0.500 (H), 0.136 (L/Q)	5,000	10,000
Molossus molossus	hinge (H), linear (L), quadratic (Q)	0.500 (H), 0.050 (L/Q)	5,000	10,000
Cynomops planirostris	hinge (H), product (P), linear (L), quadratic (Q)	0.500 (H), 0.050 (P/L/Q)	5,000	10,000
Glossophaga soricina	Hinge (H), linear (L), quadratic (Q)	0.500 (H), 0.050 (L/Q)	5,000	10,000

6.7 Appendix VII

Raster maps of each of the environmental variables used in the MaxEnt habitat suitability analysis.