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Taxonomic, phylogenetic and functional diversity of an urban Amazonian avifauna

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Abstract Amazonia is undergoing rapid urbanisation, but nothing has been published on the structure and function of urban Amazonian avifaunas. Here we present the results of a year-long survey of the avifauna of an Amazonian city, exploring temporal variation in its taxonomic, phylogenetic and functional diversity. We found urban bird communities to be taxonomically depauperate and dominated by a small subset of common species typical of second growth and river-edge habitats. Broad patterns of phylogenetic community similarity typically resembled those found in other studies on urban Neotropical bird assemblages, with insectivores the dominant guild. There was significant temporal variation in taxonomic and phylogenetic structure owing to the seasonal arrival and departure of a regionally over-represented minority of migratory species. Although the urban avian assemblage is of limited regional conservation value, it may still offer significant biodiversity services and represent one of few points of contact for local people with biodiversity.

Keywords City birds · Brazil · Habitat associations · Non-native species · Migrants · Breeding

Introduction

Over half of the world's human population now resides in cities covering less than 3% of the planet's terrestrial surface (United Nations 2014). This urbanisation is increasing most dramatically in the tropics fuelled by high birth rates and rural-urban migration (United Nations 2014). Although the conservation of biodiversity in urban areas is intrinsically important (Niemelä 1999), retaining biodiversity is also crucial to minimally maintain important ecosystem services (Dearborn and Kark 2010). Despite recognition by the Convention on Biological Diversity (United Nations Environment Programme 2007) of the importance of biodiversity in cities, our understanding of the impacts of urbanisation on biodiversity in many regions is lacking (Ortega-Álvarez and MacGregor-Fors 2011).

Amazonia is experiencing rapid urbanisation; between 1970 and 2010, the urban population within the Brazilian Amazon experienced a growth rate of over 500% and urban residents now represent around 75% of the total regional population (IBGE - Instituto Brasileiro de Geografia e Estatística 2016). Despite the proliferation of research into the impacts of other forms of land-cover change on Amazonian biodiversity (Peres et al. 2010) and birds in particular (e.g. Moura et al. 2013) our knowledge of how its biota is adapting to urban areas is very limited (Ortega-Álvarez and MacGregor-Fors 2011). Understanding how Amazonian bird species respond to urban areas ought to give insight into both the resilience and adaptability of different avian lineages (Bonier et al. 2007) and shed light on what ecosystem services might be retained in urban areas. Moreover, there are

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specific provisions for considering the importance of urban biodiversity within the Global Cities Covenant on Climate (Mexico City Pact) and at present Manaus is the only Amazonian municipality signatory (Inoue 2012).

Here we investigate the spatio-temporal structure and function of an urban Amazonian avian assemblage for the first time. We explore variation in taxonomic, phylogenetic and functional diversity through the full annual cycle, identifying migrants and transients and their geographical origins, as well as permanent residents and breeding species. We also identify habitat associations of species within the assemblage based on published classifications to understand the source habitats for colonists of this novel Amazonian habitat.

Methods

Study area

The city of Belém is located in Pará state in north-east Brazil (approximately 1°S, 48°W) and is the second largest in the Brazilian Amazon with a population of approximately 1.5 million people at a density of 1351.8 people/km² (IBGE - Instituto Brasileiro de Geografia e Estatística 2016). The city lies in the 243,000 km² Belém Center of Endemism (BCE) which has been subject to the highest proportion of forest loss of any Amazonian interfluvial region and retains less than 24% of its original primary forest cover (Almeida and Vieira 2010). Founded on 12 January 1616 the city replaced the natural climax vegetation of dense ombrophilous terra firma and várzea (seasonally flooded) forests. The climate is hot and humid with annual precipitation of 2834 mm.

We sampled a 5 km transect (Fig. S1) in the SW of the city that traverses representative sections of habitats in a district of the city with only 4.3% vegetative cover (Luz and Rodrigues 2014). The route passes both high and low rent housing areas along the Rua dos Mundurucus, a 5.2 ha urban park (the Praça Batista Campos), a stretch of the Rio Guamá along a recently gentrified promenade (Portal da Amazonia) backed by derelict 'waste ground' and finishes outside the Mangal das Garças park. The first half of the transect includes 1 km of tree-lined section (mostly *Mangifera indica*) in a more affluent suburb, whilst the Praça Batista Campos has a more diverse tree community also including *Ceiba pentandra*, *Euterpe oleracea*, *Minquartia guianensis*, *Caesalpinia echinata* and *Platonia insignis*. The poorer suburbs have very little tree cover, whilst the abandoned area by the Portal da Amazonia is mostly grassland with some encroaching scrub. The foreshore in front of the promenade is mudflats exposed at high tide and backed by short grassland, with some tall monodominant stands of *Montrichardia linifera* towards the Mangal das Garças.

Bird sampling

We sampled birds along this 5 km transect from August 2014 to July 2015, surveys were undertaken from dawn (between 0535 and 0600) and lasted two hours. This transect was travelled 54 times, between one and eight times per month dependent on meteorological conditions, totalling 270 km. We recorded all species seen and heard along this route, obtaining voucher images of any unusual taxa, which, along with the raw data were deposited online at www.ebird.org. We paid special attention for any signs of breeding behaviour and used the eBird breeding codes (Supporting Information Table S1) to define the likelihood of breeding, scoring evidence as confirmed, probable and possible.

Functional classification of bird species

Bird species were classified to trophic guild based on (Wilman et al. 2014), we divided the community into the broad categories 'plant/seed eaters', 'insectivores', 'omnivores', 'frugivores/nectarivores', and 'vertebrate/fish/scavenger' feeders. Data on body mass was also extracted from Wilman et al. (2014) or genus level averages where no data was available ($n = 2$). We assigned species native or non-native status based on Novaes and Lima (1998). Migratory status was extracted from the Birdlife Datazone database <http://www.birdlife.org/datazone/index.html> and Parker et al. (1996). We assigned species to the categories 'resident' for species which remain in the Belém area throughout the year; 'Boreal migrant' for Nearctic-Neotropical migrants breeding in North America and migrating south to the Neotropics; 'Austral migrant/partial austral migrant' for species for which part or all of their population migrate north from breeding areas in southern South America to winter in Amazonia and 'Intratropical migrant' for species which undertake seasonal movements within Amazonia (categories sensu Faaborg et al. 2010 based on classifications from the Birdlife Datazone). We used the Parker et al. (1996) database to look at habitat affinities of the community, where species may have more than one occupied habitat type. We also used the Birdlife Datazone database to classify the threat status of species on the IUCN Global Red List.

Data analysis

We extracted phylogenetic trees from a global avian phylogeny (Jetz et al. 2012) based on the Hackett backbone (Hackett et al. 2008) using 500 phylogenies. The resulting phylogram was visualized and edited using the FigTree v 1.4.1 software (<http://tree.bio.ed.ac.uk/software/figtree/>). We calculated six measures of phylogenetic diversity monthly: phylogenetic diversity (PD), sesPD (the standard effect size (SES) of PD), MPD (mean pairwise

distance), sesSMPD (adjusted for species richness, MNTD (mean nearest taxon distance), sesMNTD (MNTD adjusted for species richness). We performed these metrics using the ‘picante’ (Kembel et al. 2010). To check if there was difference among months we performed the ANOVA function and type III sums of squares in the ‘car’ package in R version 3.2.3 (R Core Development Team 2014).

Results

Community structure and traits

We recorded 99 bird species during our survey (Fig. 1), of which five were non-native: Feral Pigeon (*Columba livia* var. *domestica*), Jandaya Parakeet (*Aratinga jandaya*), Common Waxbill (*Estrilda astrild*), House Sparrow (*Passer domesticus*) and Campo Troupial (*Icterus jamacaii*). Although representing only 5.1% of the total species richness, exotics accounted for 19.0% of total bird abundance and included 100% of the regional species pool of exotic species (Table 1). Species abundance and biomass was heavily skewed to a few numerically dominant species (Table 1, Fig. 1a, Supporting Information Table S2). The most frequently recorded of which was Black Vulture (*Coragyps atratus*) with 1732 individuals counted. There were more records of the most abundant eight species combined than all remaining 91 species; fewer than five individuals were recorded of 28 of these species.

Breeding evidence was ‘confirmed’ for 31 species, ‘probable’ for 20 species and ‘possible’ for 13, there was no evidence for breeding activity for the remaining 35 species (Supporting Information Table S3). Most of the species recorded were resident (66), of the remainder, nine were Boreal migrants from North America, 12 were austral/partial austral migrants and 12 intratropical migrants (Fig. 2b).

However migrant species were over-represented in the totals in comparison with the total regional species pool (Table 1). Among the guilds, insectivores dominated the community with 53 species (53.3% of the total), although this included a long-tail of rarely-recorded species, a distribution not reflected in the remaining guilds. Omnivores (17 species) were the next commonest guild followed by vertebrate/fish/scavenger feeders (16), fruit/nectar feeders (10) and plant/seed eaters (7). However, as a function of the regional species pool, insectivores were in fact under-represented in comparison to omnivores, which were represented by proportionately more species (Table 1). The guild of vertebrate, scavenger and piscivorous feeders dominated by weight, accounting for 40.4% of total avian biomass. All species were globally ‘Least Concern’ with the exception of the Near-Threatened Semipalmated Sandpiper (*Calidris pusilla*).

Spatio-temporal structure

The taxonomic diversity of birds in our study region varied throughout the annual cycle, driven by the arrival and departure of different cohorts of migrating birds. Species richness was highest in January–April when Boreal migrants were present alongside intratropical migrants. Taxonomic diversity subsequently decreased with the departure of these species, a change which was not offset by the arrival of smaller numbers of Austral migrants and partial Austral migrants. This difference in taxonomic diversity over the annual cycle was mirrored and accentuated in terms of phylogenetic diversity given the higher phylogenetic diversity of many of the migrant taxa resulting in higher values of mean pairwise differences (Fig. 2, S2, S3). The temporal trend in mean pairwise distance also mirrored the pattern of PD with significant differences between the Boreal ‘summer’ and ‘winter periods. This loss of large phylogenetically divergent waterbirds distributed across a wide range of clades, was not temporary compensated for by

Fig. 1 Relative abundance (a) and phylogenetic structure (b) of an urban Amazonian bird community

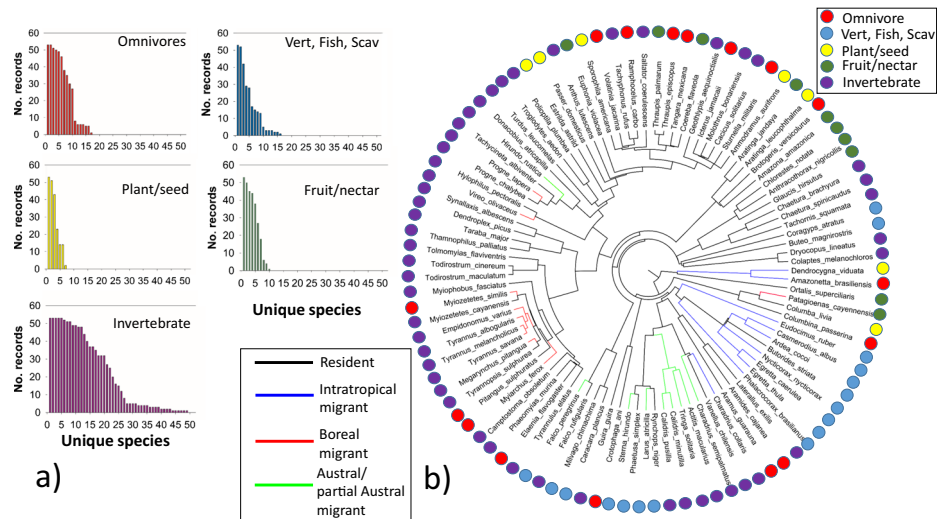


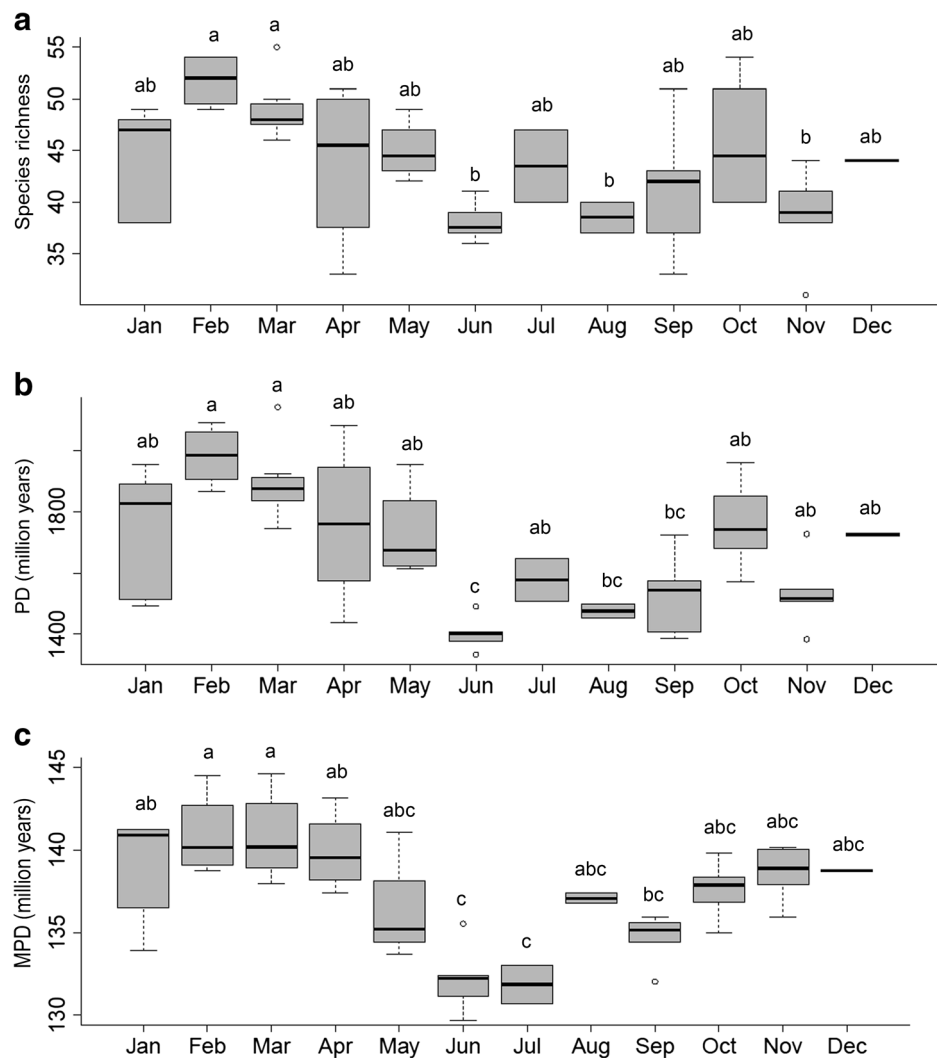
Table 1 Species richness, total abundance and total biomass of species with different migratory statuses and different diet guilds. The total number of species in the regional species pool, extracted from Novaes and Lima (1998) and percentage of the total is given in parentheses

	No. species	Total # individuals	Estimated total biomass (kg)
Migratory status			
Resident native	61 (437, 13%)	9210	197.85
Resident introduced	5 (5, 100%)	3212	20.89
Austral migrant	12 (17, 71%)	757	12.34
Boreal migrant	9 (29, 31%)	1215	12.33
Intratropical migrant	12 (35, 34%)	2537	93.94
Diet Guild			
Omnivore	17 (60, 28.3%)	3497	47.02
Vert fish scav	16 (63, 25.4%)	4510	93.94
Plant/seed	7 (40, 17.5%)	3163	29.36
Fruit/nectar	10 (97, 10.3%)	923	17.42
Insectivore	53 (263, 20.1%)	4838	44.21

the gain in Austral and partial migrants which were phylogenetically clustered. These changes resulted in changes in trophic structure through the annual cycle (Fig. 3) as fewer piscivores and more insectivores were present during the

austral winter. We did not however find significant differences in the mean nearest taxon distance throughout the annual cycle (Fig. S2, S3) suggesting that despite migration there is still relative phylogenetic evenness.

Fig. 2 Species richness (a), Phylogenetic diversity (PD: b) and mean pairwise difference (MPD: c) of bird communities throughout the annual cycle. Non-significant pairwise differences between months are indicated by the presence of the same letter



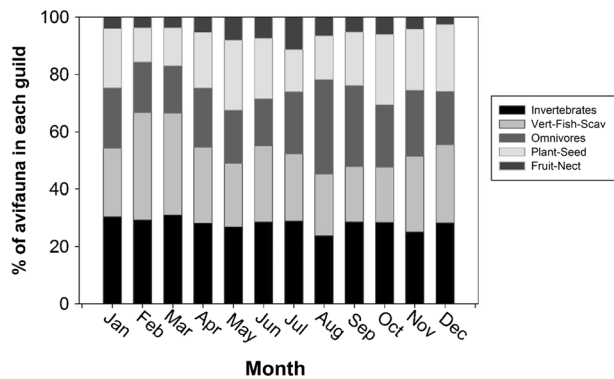


Fig. 3 Variation over the annual cycle of the percentage of individuals within five different foraging guilds

Habitat affinities

Comparison of habitat affinities with the Parker et al. classifications show that the community is most similar to that occupying other ‘secondary’ habitats with 44.4% of species occurring in secondary forest, 37.3% in ‘second growth scrub’ and 19.1% in pastures/agricultural lands (Table 2). The strongest affiliation for a ‘primary habitat’ was ‘river edge forest’ which was occupied by 24% of species, followed by freshwater marshes (19.1%) and ‘riparian thickets’ (10.1%). Only 9.1% of species were typically found in ‘tropical lowland evergreen forest’ which is the region’s dominant natural climax habitat.

Table 2 Habitat associations of species according to their listing in the Parker et al. database

Parker et al. habitat category	No. species	% species
Secondary forest	44	44.4
Second-growth scrub	37	37.4
River-edge forest	24	24.2
Pastures/agricultural lands	19	19.2
Freshwater marshes	19	19.2
Riparian thickets	10	10.1
Tropical lowland evergreen forest	9	9.1
Arid lowland scrub	9	9.1
Low, seasonally wet grassland	9	9.1
River island scrub	9	9.1
Flooded tropical evergreen forest	7	7.1
Mangrove forest	7	7.1
Saltwater/brackish	7	7.1
Coastal sand beaches/mudflats	7	7.1
Riverine sand beaches	2	2.0
Palm forest	1	1.0

Discussion

Our survey is the first ever undertaken of an urban Amazonian avifauna; we found the urban assemblage to be depauperate retaining only 99 species, representing 20.5% of the regional pool of 482 species (Novaes and Lima 1998) although 14% of these species are now potentially locally extinct (Moura et al. 2014). Previous studies in Neotropical cities have reported similarly proportionately low totals e.g. 55 species in 5 months at Xalapa, Mexico (Escobar-Ibáñez and MacGregor-Fors 2016), 143 species in 20 months in Porto Alegre, Brazil (Fontana et al. 2011), 66 species in ten months in Uberlândia, Brazil (Torga et al. 2007) and 57 species in 6 months at La Paz, Bolivia (Villegas and Garitano-Zavala 2010).

This Amazonian assemblage in Belém was taxonomically and phylogenetically seasonally dynamic, composed principally of resident species associated with secondary habitats, with a small number of species numerically dominant. These broad patterns mirror those found in other human-dominated Amazonian land-uses (e.g. Moura et al. 2013) which generally retain few forest-associated species. A maximum of 64 species (64.6%) of the community were suspected of breeding behaviour, with the remainder as migrants or transients. This is still a surprisingly high number considering the ostensibly ‘harsh’ anthropogenic environment and we did find some nests in surprising locations, such as one of Short-crested Flycatcher (*Myiarchus ferox*) in a traffic light for example. Insectivores were the dominant trophic guild followed by frugivores, whilst plant/seed eaters were very rare, in contrast with most studies of urban avifaunas (Ortega-Álvarez and MacGregor-Fors 2011).

The dominance of the community by insectivorous birds hint at a potential role for these species in the control of insect pests including disease vectors; a research avenue that has largely been overlooked (Wenny et al. 2011). The potential role of this ecosystem service and that conducted by the numerically dominant Black Vultures in waste removal and disease regulation ought to be subject to future research. The relative rarity of granivores and frugivores is presumably a reflection of the relative rarity of suitable foodplants in urban systems given the high vagility of these groups (Lees and Peres 2009). Identifying and then planting keystone food plants would likely be a relatively easy way of increasing urban avian biodiversity (Stagoll et al. 2010). The pattern of disproportionate abundance of non-native species we observed has also been reported from other urban regions of the Neotropics (e.g. Ortega-Álvarez and MacGregor-Fors 2011). Non-native species only seem to manage to gain a toe-hold in Amazonia in urban systems; our own exhaustive inventories of rural agricultural regions failed to find evidence of colonisation of exotic species (e.g. Mahood et al. 2012; Moura et al. 2013).

Broad patterns of phylogenetic community similarity mirror that observed in other studies on urban Neotropical bird assemblages which were also numerically dominated by

members of the Tyrannidae (Ortega-Álvarez and MacGregor-Fors 2011). However, the 18 species recorded in our study still only represent 33.3% of all the Tyrannidae recorded in the metropolitan region (Novaes and Lima 1998). Other clades within the suboscine passerine group were even more under-represented; the species of antbirds make up just 8.3% of the total species richness (24) of that group which is typically numerically dominant in Neotropical forests.

Phylogenetic diversity varied significantly through the annual cycle owing to the impacts of migration, highlighting the importance of temporal sampling in assessing phylogenetic diversity within communities with high numbers of migrants. The dynamism of both taxonomic and phylogenetic diversity within this system is also notable given the pervasive assumption of residency in Neotropical avifaunas (Faaborg et al. 2010) and is a strong argument for sampling across the annual cycle, particularly when communities include migrant waterbirds.

Although, urban avian biodiversity in Belém was impoverished, it should still be valued given the ecosystem services, such as predation on phytophagous and biting insects (Whelan et al. 2015) that the community provides. These improve the urban environment and enhance the wellbeing and quality of life of urban dwellers (Savard et al. 2000). Charismatic members of the urban avifauna, like the nesting Great Egrets (*Casmerodius albus*) in the Praça Batista Campos may provide one of few connections that many Amazonian urban residents have to the natural world; reinforcing the importance of Amazonian conservation far beyond the city's boundaries.

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