Left Running Head: Hayes *et al.*

Right Running Head: Neotropical urban bird communities

Bird communities across varying landcover types in a Neotropical city

William Michael Hayes[1*], Jessica Claris Fisher[1], Meshach Andres Pierre[2], Jake Emmerson Bicknell[1], Zoe Georgina Davies[1]

[1]Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury, Kent, CT2 7NR, UK

[2]60 Atlantic Ville, Georgetown, Guyana

[*]Corresponding Author Email Address: willhayes373@gmail.com

Received_____; revision accepted___.

Abstract

Urbanization poses a serious threat to local biodiversity, yet towns and cities with abundant natural features may harbor important species populations and communities. While the contribution of urban greenspaces to conservation has been demonstrated by numerous studies within temperate regions, few consider the bird communities associated with different landcovers in Neotropical cities. To begin to fill this knowledge gap, we examined how the avifauna of a wetland city in northern Amazonia (Georgetown, Guyana) varied across six urban landcover types (coastal bluespace; urban bluespace; managed greenspace; unmanaged greenspace; dense urban; sparse urban). We measured detections, species richness and a series of ground cover variables that characterized the heterogeneity of each landcover, at 114 locations across the city. We recorded >10% (98) of Guyana's bird species in Georgetown, including taxa of conservation interest. Avian detections, richness, and community composition differed with landcover type. Indicator species analysis identified 29 species from across dietary guilds, which could be driving community composition. Comparing landcovers, species richness was highest in managed greenspaces and lowest in dense urban areas. The canal network had comparable levels of species richness to greenspaces. The waterways are likely to play a key role in enhancing habitat connectivity as they traverse densely urbanized areas. Both species and landcover information should be integrated into urban land-use planning in the rapidly urbanizing Neotropics to maximize the conservation value of cities. This is imperative in the tropics, where anthropogenic pressures on species are growing significantly, and action needs to be taken to prevent biodiversity collapse.

Key words: avian; bluespace; diversity; greenspace; Guyana; indicator species; species richness; urban planning

RAPID URBANIZATION IS A GLOBAL PHENOMENON (United Nations 2014) THAT POSES A POTENTIALLY SERIOUS THREAT TO LOCAL BIODIVERSITY (Dearborn & Kark 2010; Sol *et al.* 2014). During urbanization, natural habitats are modified, fragmented or lost and are replaced by a novel ecosystem characterized by a mosaic of natural, semi-natural and anthropogenic features (McDonnell & Pickett 1990; Kowarik 2011; Beninde *et al.* 2015). This high degree of heterogeneity changes the composition of ecological communities, creating opportunities for some species to thrive, while others may decline or go extinct (Concepción *et al.* 2015; Seress & Liker 2015).

Greenspaces are often viewed as the principal habitat in towns and cities, providing the most favorable resources for biodiversity (Kong *et al.* 2010) and acting as dispersal corridors throughout the urban matrix (Murgui 2009). However, natural or artificial waterbodies (‘bluespaces’), buildings and other human-made structures with diverse forms and functions can also provide food, shelter and breeding sites (Farinha-Marques *et al.* 2017), helping to maintain species diversity when there is no natural habitat in close proximity (Savard *et al.* 2000). In developed regions of the world, where intensive agricultural use of the wider landscape has resulted in population declines of species, urban areas are becoming progressively more important in sustaining regional abundances. Indeed, substantial proportions of the populations of some previously widespread and common species now occur in urban environments (e.g. Bland *et al.* 2004; Peach *et al.* 2004; Shochat *et al.* 2010; Kowarik 2011; Kowarik *et al.* 2013). Therefore, a clearer understanding of how species assemblages vary between different landcover types within towns and cities is important, if decision-makers are to reduce the potentially detrimental impacts of urbanization on biodiversity through evidence-based land-use planning and proactive conservation interventions (Goddard *et al.* 2010; Wu 2014; Oliveira-Hagen *et al.* 2017; Parris *et al.* 2018).

Birds are one of the most-studied taxonomic groups in urban areas, as they can be monitored inexpensively and are highly responsive to environmental change (Koskimies 1989; Gardner *et al.* 2008). As such, they are used extensively as bio-indicators of ecosystem health (Herrando *et al.* 2017). Avian communities in towns and cities can exist independently of neighboring rural ones (Chiari *et al.* 2010) and, in general, are typified by greater abundances but lower species richness than those in more natural habitats (Ortega-Álvarez & MacGregor-Fors 2009). Nonetheless, most of the studies conducted on urban bird communities to date have been located in the temperate zones of Europe, Canada and the USA (Ortega-Álvarez & MacGregor-Fors 2011). Moreover, many have primarily examined the conservation benefits of greenspace and vegetation (Fontana *et al.* 2011; Ferenc *et al.* 2014; Rupprecht *et al.* 2015), overlooking the contribution that urban bluespaces may play in harboring avian communities and species abundances (Andrade *et al.* 2018).

The Neotropics are highly biodiverse and undergoing rapid urbanization, yet there is a paucity of urban ecological studies undertaken in the region (Ortega-Álvarez & MacGregor-Fors 2011; Pauchard & Barbosa 2013). This is despite the fact that urbanization is likely to be a contributing factor to species extinctions in the tropics (Laurance & Useche 2009). Neotropical towns and cities are often characterized by extreme social and economic inequality, which in turn, may relate to the distribution and quality of urban greenspace (Boulton *et al.* 2018). What little research there is on Neotropical urban birds has indicated that urbanization leads to reduced species richness (Reynaud & Thioulouse 2000; Amaya-Espinel *et al.* 2019), an increase in overall abundance (Reis *et al.* 2012; Amaya-Espinel *et al.* 2019), and larger populations of non-native species (Ortega-Álvarez & MacGregor-Fors 2011; Amaya-Espinel *et al.* 2019). However, very few studies have examined the bird communities associated with different types of greenspace and bluespace within towns and cities.

Here, we assess how bird species detections vary across a range of urban landcover types in Georgetown, Guyana. Specifically, we examine differences in the number of bird detections, species richness and community composition among managed greenspaces (e.g. parks, cemeteries), unmanaged greenspaces (e.g. abandoned grazing sites, meadows, wastelands), waterways (e.g. canals, drainage ditches), coastline and built up areas within the urban boundary. We also conduct an indicator species analysis to determine whether specific species typify particular landcover types and investigate how dietary guild composition changes across the urban landscape.

METHODS

STUDY AREA. —This study was conducted in the city of Georgetown, the capital of Guyana, located on the North Atlantic coast of tropical South America, 6° N, 58° W (Fig. S1). The human population was estimated to be ~118,000 in 2012 (Bureau of Statistics 2012), and the area extent of the city is ~70 km^2 (Edwards *et al.* 2005). Guyana has an average temperature of 26°C, and two rainy seasons during April-August and November-January (Edwards *et al.* 2005).

Georgetown is situated in the Upper Amazonia/Guyana Shield 'major tropical wilderness area', which represents one of the most globally pristine terrestrial forest ecoregions (Cincotta *et al.* 2000). The city lies below sea level, interlaced by a network of canals and drains to prevent flooding, as well as a sea wall providing protection during high tide. (Edwards *et al.* 2005). Although Georgetown is situated in a country of high rainforest cover, the landscape surrounding the city is dominated by agriculture and the ocean, with the nearest primary forest approximately 35 km south. Landcover type within Georgetown varies from heavily urbanized (areas with a high density of multi-storied buildings) in the city center, to greenspace in the form of parks and grassland, and bluespace along canals and coast. Many residential houses in the city have private gardens that contain a diversity of vegetation, including fruit and flowering trees, as well as shrubs and grasses.

SURVEY DESIGN.—During May and June 2017, the bird community of Georgetown was sampled across 114 point-count locations, 19 per landcover type, of which there were six (Fig. S1). The six landcover types were: 'managed greenspace', 'unmanaged greenspace', 'urban bluespace', 'coastal bluespace', 'dense urban' and 'sparse urban' (see Table S1 for definitions). The point-count locations were determined by digitally overlaying a 250 m x 250 m grid over the city via GIS. The predominant landcover type within a 50 m radius buffer of every grid line intersection, and potential point count location, was evaluated using Google Earth 2017 satellite imagery and maps obtained from the local authorities. A random sample of point count locations for each landcover type was then generated. When we assessed a point count location on the ground, prior to conducting the bird surveys, we verified whether our landcover categorization was correct by ground truthing. If a point was inaccessible (e.g. it was private property and permission to survey was not granted, it was covered by a building), or incorrectly categorized, it was replaced with another from the random sample. All point count locations were at least 250 m apart from one another to ensure independence (Silva *et al.* 2015) and, to avoid potential edge effects, they were all more than 250 m away from the agricultural fields bordering the city (see Ikin *et al.* 2014).

To describe the landcover type at each point count location, the percentage (%) ground-cover of a number of variables (Table 1) was assessed within a 50 m radius (matching that of the point count area – see below). We also recorded the presence or absence of fruiting and flowering trees (fruiting only, flowering only, both, or neither) which are likely to influence bird communities, as each tree type offers different resources such as food and shelter (Jankowski *et al.* 2013).

Each point count location was surveyed once on a clear day between 05:30 and 08:30 (Verner & Ritter 1986). All birds seen or heard within the 50 m radius were recorded during a 15-minute interval (O'Neal Campbell 2008). If birds were interacting with the landcover type, or flying within 25 m of the highest structure within the 50 m radius, they were recorded (Huff *et al.* 2000). Any individuals flying above this height threshold were not noted as they were deemed to be flyovers. Our bird taxonomy follows Remsen *et al.* (2019).

STATISTICAL ANALYSES.—Species accumulation curves and their 95% confidence intervals were generated to investigate whether the sampling effort was sufficient to represent the bird community of Georgetown. Error was measured using the CHAO1 function (Chao 1984) in EstimateS 8.2.0, which calculates true estimated species diversity based on the number of rare species found in a sample (Colwell 2006).

As point count locations that are geographically closer together may naturally harbor more similar communities than those further apart, we tested our dataset for spatial autocorrelation. We did this using a Mantel test to examine the Bray-Curtis coefficients of the bird communities against geographic distance, conducted in PC-ORD from 999 permutations. The test revealed that any effect of spatial autocorrelation was weak and non-significant ($r=0.006$; $p=0.88$), meaning that differences in assemblage patterns can be attributed reliably to landcover type.

We first $\log_{10}$ transformed the bird detection data, as is standard practice, when conducting community and ordination analyses (McCune & Grace 2002; Suarez-Rubio *et al.* 2011). To investigate differences in the bird communities between landcover types, we conducted non-metric multi-dimensional scaling (NMDS; Shepard 1962) from Bray-Curtis dissimilarity coefficients of the number of detections per species in each point count location. The NMDS was conducted in PC-ORD v6.0 (McCune & Mefford 1999). A final ordination of minimum stress on two axes was generated through a random starting configuration of 500 iterations, split into 250 runs of both randomized and real data (Bicknell *et al.* 2014). Kendall's tau rank correlation coefficient (McCune & Grace 2002) was used to assess the strongest associations between landcover variables and the bird community. We undertook this procedure twice, once with all point count locations included, and once with the coastal bluespace sites removed. The latter was done to facilitate closer visual inspection of the remaining data.

To assess whether the bird communities were statistically different between landcover types, we used a multi-response permutations procedure of Euclidean distances (MRPP; McCune & Grace 2002) between the number of detections per species in each landcover. This was also carried out in PC-ORD. The analysis was repeated three times: first with the entire assemblage included in the dataset, second with species removed if they only occurred once and, finally, with species removed if they occurred twice or less. All three approaches gave consistent results and, therefore, the results are reported for the entire assemblage.

Kruskal-Wallis H tests in IBM SPSS Statistics (version 24) were used to determine whether the proportional coverage of each landcover variable differed across the landcover types. 'Coastal bluespace' was dominated by the landcover variable '*ocean*', which was observed only in this landcover type and thus excluded from analyses. *Post-hoc* pairwise comparisons between landcover types were conducted using Dunn's (1964) procedure for Bonferroni corrections.

Each species was grouped according to its primary dietary guild, according to Restall *et al.* (2006): piscivore, carnivore, frugivore, granivore, insectivore, omnivore and nectarivore. To examine whether the number of species from each dietary guild varied across landcover types we conducted Kruskal-Wallis H tests.

Indicator species analyses (IndVal) in PC-ORD were used to identify species that typify the bird communities associated with the six broad landcover types, following the method described in Dufrêne and Legendre (1997). An indicator value was assigned to each species as a result of a random reallocation process (4999 permutations), and these were then tested for significance using a Monte Carlo procedure, with species considered indicators if this was significant ($p < 0.05$). High indicator values reflect both high abundance and prevalence within a landcover type; *p*-values represent the probability of a similar observation relative to a randomized dataset. Species that occurred in all landcover types were excluded from the analysis as they are ubiquitous.

RESULTS

LANDCOVER TYPES.—There were significant differences in the percentage ground-cover of eight of the 10 landcover variables occurring across the six landcover types (Table S2; Fig. 1). None of the landcover variables differed between managed and unmanaged greenspaces, both of which were dominated by vegetation (Fig. S2). Sparse urban was the only landcover type that contained fruiting and/or flowering trees in all point count locations (Fig. S3), while coastal bluespace point locations did not support any fruiting or flowering trees.

BIRD COMMUNITIES.—Across the 114 point count locations, 3,408 detections from 98 bird species were recorded (Table S3). The overall species accumulation curve tended toward an asymptote, indicating that sampling effort was sufficient, and the 95% confidence intervals of estimated species richness overlapped with the observed species richness (Fig. S4). In Georgetown, we recorded over 10% of Guyana's total avian species. The landcover type with both the highest bird species richness and detections was managed greenspace, followed by urban bluespace (Table 2). The lowest species richness was observed in coastal bluespace, while the lowest detections were recorded in the dense urban landcover. Six species were found in all six landcover types and accounted for 23% of all individuals recorded (Fig. 2): greater kiskadee (*Pitangus sulphuratus*), rock pigeon (*Columba livia*), ruddy ground dove (*Columbina talpacoti*), gray-breasted martin (*Progne chalybea*), blue-gray tanager (*Thraupis episcopus*) and shiny cowbird (*Molothrus bonariensis*).

The 2-dimensional NMDS ordination with minimal stress accounted for 64% (Fig. 3A) and 54% (Fig. 3C) of the variability in the bird data (with and without the inclusion of coastal bluespace point count locations respectively). This, in combination with the MRPP, showed that the bird communities differed significantly between landcover types (global MRPP: $p < 0.001$). The assemblage in the coastal bluespace was significantly different from all other landcover types. The differences between landcover types remained, even when the procedure was repeated with coastal bluespace removed (global MRPP with coastal bluespace removed $p < 0.001$). Pairwise comparisons of the bird communities within landcover types revealed statistically significant differences between 12 of the 15 landcover type pairings (Table 3). Plotting vectors of the landcover variables revealed that NMDS axis 1 was significantly associated with *Ocean* and *Tree*, while axis 2 was correlated with *Shrub*, *Building* and *Road* (Fig. 3B; Table S4).

Insectivorous species were the most abundant, accounting for at least 40% of birds in each landcover type (Fig. 4), and there were significant differences between the median number of species in each dietary guild across the six landcovers (Table S5). No significant differences in dietary guild composition were found between managed greenspace and urban bluespace, managed greenspace and unmanaged greenspace, and dense urban and sparse urban landcover types.

Indicator species were identified for each landcover type (Fig 3B; Table 4). The number per landcover type ranged from one indicator species for sparse urban, through to 12 for the coastal bluespace.

DISCUSSION

As urbanization is progressing rapidly throughout the biodiverse Neotropics (Pauchard & Barbosa 2013), research on biodiversity assemblages in the urban areas of this region is growing increasingly important to inform local conservation priorities (Socolar *et al.* 2016). Our study, one of only a few with an urban focus conducted in the Neotropics, demonstrates that many species are found within towns and cities, and reaffirms that urban bird assemblages are influenced by landcover type (Villegas & Garitano-Zavala 2010; Fontana *et al.* 2011; de Toledo *et al.* 2012; Pellissier *et al.* 2012; Kang *et al.* 2015; Leveau & Leveau 2016; MacGregor-Fors *et al*. 2016; Dale 2018; Amaya-Espinel *et al.* 2019). As the majority of land around Georgetown is agricultural, drawing comparisons with bird communities inhabiting natural landcovers in close proximity to the city was not possible. However, our study detected 98 species, more than half the number detected via point counts in the primary forests of Iwokrama in central Guyana (Bicknell *et al.* 2015). Indeed, we recorded over 10% of Guyana's bird species in the city of Georgetown, including one endemic to the Guianas, the blood-colored woodpecker (*Veniliornis sanguineus*), and the IUCN Near Threatened semipalmated sandpiper (*Calidris pusilla*) (Braun *et al*. 2007; IUCN 2018). Urban landscapes in the Neotropics can, therefore, provide suitable habitat for high bird diversity and species of conservation concern (Beninde *et al.* 2015). By using the same bird survey techniques within each landcover, we could compare their relative contributions to avifauna of Georgetown. Although the landcover variables and bird community composition showed some levels of similarity across landcover types, they differed significantly between six different landcover types, with urban greenspaces and bluespaces being the most diverse.

Georgetown is heterogeneous in form, comprising a mosaic of greenspaces, built up areas and waterways. Our results clearly demonstrate that landcover type can influence bird abundance and community composition, and a range of landcover types in a city is key to maximizing species richness (Kowarik 2011). Greenspaces are generally expected to be the most important landcover type for urban biodiversity because they often have the highest tree cover (Rupprecht *et al.* 2015; Ferenc *et al.* 2014). Indeed, Georgetown's managed greenspaces are the most species rich and have greater numbers of detections. This finding is consistent with two other urban bird studies conducted in the Neotropics (e.g. Carbó-Ramírez & Zuria 2011; MacGregor-Fors *et al.* 2016). Sufficient amounts of vegetation, such as trees and shrubs, are thus integral to maintaining diverse urban bird communities, and efforts should be made to protect existing greenspaces from development (Sandström *et al.* 2006). However, variables that were not characterized in this study, such as greenspace patch area, proximity of landcovers to the city centre, and vegetation structure, could also influence avian diversity in the landcover types assessed (Khera *et al.* 2005). For example, Sandström *et al.* (2006) demonstrated that greenspaces further from the city centre, were more species rich than those located in the city centre.

Georgetown's canal network is interlaced through areas of relatively low species diversity (i.e. dense urban and sparse urban landcovers), yet our results highlight that urban bluespaces had a bird community with a similar species richness and number of detections to that of managed greenspace. There have been a number of studies that have found evidence of an increase in the number of individuals in more urbanized sites (Seress & Liker 2015; Mikami & Mikami 2014). However, this was not the case in our study. The low number of birds detected in the dense landcover type may reflect bird preference for the bluespaces that dissect the city, and that Georgetown has a relatively low number of invasive species. Although the canals in the city may be subject to relatively high anthropogenic pressure, the presence of a diverse avian community is encouraging, particularly as waterbird populations are declining globally (Wetlands International 2012). These waterbird species (e.g. wattled jacana, pied water tyrant and limpkin, *Aramus guarauna*) use the waterways for food, shelter, nesting sites and breeding (Ma *et al.* 2010). Likewise, vegetation along the canal banks appears to be important for species usually found in forests (e.g. roadside hawk, violaceous euphonia, *Euphonia violacea*, and yellow oriole, *Icterus nigrogularis*) (Scott *et al.* 2003; Fletcher & Hutto 2008). This finding concurs with those reported in Domínguez-López & Ortega-Álvarez (2014) and López-Pomares *et al.* (2015), suggesting that riparian corridors can facilitate species movement and support populations within urban landscapes. As such, we strongly encourage urban planners, both locally and regionally, to recognize the potential of urban waterways for bird conservation in towns and cities. In contrast, the coastal bluespace landcover type had the lowest bird species diversity, but was distinct from the rest of Georgetown's bird community because it was home to maritime species not found in any of the other landcover types.

As expected, landcover types dominated by roads and buildings had lower species richness than those with greater vegetation cover (Tratalos *et al.* 2007; Gagné & Fahrig 2011;

Silva *et al.* 2015). The relatively lower levels of diversity may additionally reflect the intensity of human activities and pollution, which represent a hazard to species sensitive to such disturbances (Herrera-Duenas *et al.* 2014). The limited variety of feeding resources available in the dense urban landcover, as highlighted by the low percentage of fruiting and flowering trees, may have promoted the over dominance of generalist species that are tolerant to anthropogenic disturbance (e.g. the invasive rock pigeon, and native carib grackle, *Quiscalus lugubris*) (Dunn *et al.* 2006). Increasing urbanization, specifically the replacement of natural habitat with built-up features and the development of human-related infrastructures, globally may continue to favor generalist species over specialist species, which are susceptible to significant changes in their environment (Devictor *et al.* 2007). Furthermore, it is possible that urban pressures are causing some of the landcovers assessed in this study to become an ecological trap (Garmendia *et al.* 2016). We cannot, however, determine whether or not this is the case, as we only recorded numbers of detections and have not examined variables such as breeding success. Where this has been studied explicitly elsewhere in the world, authors have concluded that urban habitats do not act as ecological traps for their study species (e.g. northern cardinal, *Cardinalis cardinalis*, & northern mockingbird, *Mimus polyglottos*) (Leston & Rodewald 2006; Stracey & Robinson 2012).

Species from all dietary guilds were observed in almost every landcover type. Omnivorous and granivorous species, such as the rock pigeon (Dunn *et al.* 2006), are known to be successful at adapting to urban landscapes, due to the relative abundance of food resources (e.g. human refuse) (Kark *et al.* 2007; Croci *et al.* 2008; Møller 2009). This plasticity is also epitomized by species from other dietary guilds; for example, the insectivorous greater kiskadee (Echeverria & Vassallo 2008) and frugivorous blue-gray tanager (Sanz & Cuala 2015), both recorded in our research. Indeed, where more heavily frugivorous bird species are absent in urban areas, the greater kiskadee can also be an important seed disperser (Emer *et al*. 2018). However, in accordance with another Neotropical urban bird study (Reynaud & Thiolouse 2000), insectivorous species were the most numerous in Georgetown. This is likely to be because of the fruiting and flowering trees occurring across the city which are typically rich in arthropods (Vehviläinen *et al.* 2008), and because of the insect communities associated with the many waterways. Moreover, insectivorous bird species prefer edges (Helle 1983), which characterize most urban landscapes (Alberti 2005). Nonetheless, Glennon & Porter (2005) assert that the development of a human-dominated matrix negatively affects insectivorous species. O'Connell *et al.* (2000) attribute this negative effect to the loss of specific feeding opportunities as a result of greater disturbance. Therefore, if development of Georgetown intensifies, leading to canal culverting or tree removal, it is probable that insectivorous bird species will decline. Additionally, urban areas offering increased feeding opportunities may act as a sink for species from the surrounding rainforest (Schreiber & Kelton 2005).

Indicator species analysis identified landcover type preferences for 29 of the bird species recorded in Georgetown, from across different dietary guilds. This could be driving avian species richness in the city (Tews *et al.* 2004). Species with high indicator values for urban bluespace landcover, such as wattled jacana and pied water tyrant, were uncommon or absent from built up areas containing little to no freshwater, further suggesting that these species heavily rely on the canal system in the city. The high number of indicator species found in the coastal bluespace landcover, all of which were seabirds, can be attributed to coastal habitat preference of these species. Furthermore, in accordance with our findings, snowy egret and whimbrel have been previously recorded having a strong association with coastal urban habitats (Seigel *et al.* 2005; Tejera & Rodríguez 2014). Aside from coastal bluespace, the managed greenspace landcover had the highest number of indicator species, including tropical kingbird and cattle egret, both of which have previously been observed in urban greenspaces (Phalen *et al.* 2010; Leveau & Leveau 2016). Moreover, the high indicator value of blue-black grassquit within unmanaged greenspace is not surprising, given that they are typically found within high grass and scrubland throughout the Neotropics (Wilczynski *et al.* 1989).

Studies such as this are useful within the wider context of growing anthropogenic pressure on tropical ecosystems and the urgent calls being made to take action to prevent biodiversity collapse (Barlow *et al.* 2018). As a coastal settlement, Georgetown is highly susceptible to the threat of sea level rise as a result of climate change. Damage to urban infrastructure, permanent inundation and shifts in salinity gradients as a result of flooding, will probably alter the landcover type quality, putting bird communities under increasing pressure to adapt to these changes (Solecki & Marcotullio 2013).

Both species and landcover information should be integrated into urban land-use planning processes to maximize bird conservation in the rapidly urbanizing Neotropics. As urban bird species richness is influenced by both local and landscape characteristics (Savard *et al.* 2006), generating an integrated, but differentiated management plan for Georgetown's landcover types could prove a useful tool for maintaining native birdlife. Enhancement of biodiversity in towns and cities can improve the quality of life of urban residents and, in turn, increase support for biodiversity conservation (Soga *et al.* 2016; Schebella *et al.* 2019). This is particularly important for Georgetown and other coastal cities located in relatively pristine ecoregions like the Guiana Shield (Mittermeier *et al.* 2011), where the adverse effects of urbanization and climate change on bird communities are likely to increase dramatically in the coming decades (de Toledo *et al.* 2012: Solecki & Marcotullio 2013).

ACKNOWLEDGEMENTS

We thank Brian O'Shea for useful discussions, Leon Moore who provided invaluable field assistance, and Annalise Bayney and Denise Fraser of Guyana's Protected Areas Commission (PAC) for providing logistical help and work space. JCF was supported by grants from the Royal Geographical Society (with the Institute of British Geographers) Dudley Stamp Memorial Award, Gilchrist Educational Foundation, and the UK Economic and Social Research Council (ESRC scholarship ES/J500148/1).

DATA AVAILABILITY STATEMENT

The data used in this study will be archived at the Dryad Digital Repository upon acceptance.

LITERATURE CITED

ALBERTI, M. 2005. The effects of urban patterns on ecosystem function. Int. Reg. Sci. Rev. 28: 168-192.

AMAYA-ESPINEL, J. D., M. HOSTETLER, C. HENRÍQUEZ, AND C. BONACIC. 2019. The influence of building density on Neotropical bird communities found in small urban parks. Landsc. Urban Plan. 190: 103578.

ANDRADE, R., H. L. BATEMAN, J. FRANKLIN, AND D. ALLEN. 2018. Waterbird community composition, abundance, and diversity along an urban gradient. Landsc. Urban Plan. 170: 103-111.

ANGOLD, P. G., J. P. SADLER, M. O. HILL, A. PULLIN, S. RUSHTON, K. AUSTIN, E. SMALL, B. WOOD, R. WADSWORTH, R. SANDERSON, AND K. THOMPSON. 2006. Biodiversity in urban habitat patches. Sci. Total Environ. 360: 196-204.

BARLOW, J., F. FRANÇA, T. A. GARDNER, C. C. HICKS, G. D. LENNOX, E. BERENGUER, L. CASTELLO, E. P. ECONOMO, J. FERREIRA, B. GUÉNARD, AND C. G. LEAL. 2018. The future of hyperdiverse tropical ecosystems. Nature 559: 517-526.

BENINDE, J., M. VEITH, AND A. HOCHKIRCH. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol. Lett. 18: 581-592.

BICKNELL, J. E., M. J. STRUEBIG, AND Z. G. DAVIES. 2015. Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. J. Appl. Ecol. 52: 379-388.

BICKNELL, J. E., S. P. PHELPS, R. G. DAVIES, D. J. MANN, M. J. STRUEBIG, AND Z. G. DAVIES. 2014. Dung beetles as indicators for rapid impact assessments: evaluating best practice forestry in the neotropics. Ecol. Indic. 43: 154-161.

BLAND, R. L., J. TULLY, AND J. J. GREENWOOD. 2004. Birds breeding in British gardens: an underestimated population?. Bird Study 51: 97-106.

BOLGER, D. T., T. A. SCOTT, AND J. T. ROTENBERRY. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. Conserv. Biol. 11: 406-421.

BOULTON, C., A. DEDEKORKUT-HOWES, AND J. BYRNE. 2018. Factors shaping urban greenspace provision: a systematic review of the literature. Landsc. Urban Plan. 178: 82-101.

BRAUN, M. J., D. W. FINCH, M. B. ROBBINS, AND B. K. SCHIMDT. 2007. A field checklist of the birds of Guyana. Smithsonian Institution, Washington, DC, USA.

BUREAU OF STATISTICS. 2012. National Population and Housing Census 2012. Guyana Bureau of Statistics, Guyana. Available at http://www.statisticsguyana.gov.gy/census.html (accessed 1 December 2018).

CARBÓ-RAMÍREZ, P., AND I. ZURIA. 2011. The value of small urban greenspaces for birds in a Mexican city. Landsc. Urban Plan. 100: 213-222.

CHAO, A. 1984. Nonparametric estimation of the number of classes in a population. Scand. Stat. Theory Appl. 11: 265-270.

CHIARI, C., M. DINETTI, C. LICCIARDELLO, G. LICITRA, AND M. PAUTASSO. 2010. Urbanization and the more-individuals hypothesis. J. Anim. Ecol. 79: 366-371.

CINCOTTA, R. P., J. WISNEWSKI, AND R. ENGELMAN. 2000. Human population in the biodiversity hotspots. Nature 404: 990.

COLWELL, R. 2006. EstimateS: statistical estimation of species richness and shared species from simples, version 8.0. http://purl. oclc. org/estimates.

CONCEPCIÓN, E. D., M. MORETTI, F. ALTERMATT, M. P. NOBIS, AND M. K. OBRIST. 2015. Impacts of urbanization on biodiversity: the role of species mobility, degree of specialization and spatial scale. Oikos 124: 1571-1582.

CROCI, S., A. BUTET, AND P. CLERGEAU. 2008. Does urbanization filter birds on the basis of their biological traits. The Condor 110: 223-240.

DALE, S. 2018. Urban bird community composition influenced by size of urban green spaces, presence of native forest, and urbanization. Urban Ecosyst. 21: 1-14.

DE TOLEDO, M. C. B., R. J. DONATELLI, AND G. T. BATISTA. 2012. Relation between green spaces and bird community structure in an urban area in Southeast Brazil. Urban Ecosyst. 15: 111-131.

DEARBORN, D. C., AND S. KARK. 2010. Motivations for conserving urban biodiversity. Conserv. Biol. 24: 432-440.

DEVICTOR, V., R. JULLIARD, D. COUVET, A. LEE, AND F. JIGUET. 2007. Functional homogenization effect of urbanization on bird communities. Conserv. Biol. 21: 741-751.

Domínguez-López, M. E., and R. Ortega-Álvarez. 2014. The importance of riparian habitats for avian communities in a highly human-modified Neotropical landscape. Revista Mexicana de Biodiversidad 85: 1217-1227.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345-366.

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6: 241-252.

Dunn, R. R., M. C. Gavin, M. C. Sanchez, and J. N. Solomon. 2006. The pigeon paradox: dependence of global conservation on urban nature. Conserv. Biol. 20: 1814-1816.

Echeverría, A. I., and A. I. Vassallo. 2008. Novelty responses in a bird assemblage inhabiting an urban area. Ethology 114: 616-624.

Edwards, R., S. C. Wu, S.C. and J. Mensah. 2005. Georgetown, Guyana. Cities 22: 446-454.

Emer, C., M. Galetti, M. A. Pizo, P. R. Guimaraes Jr, S. Moraes, A. Piratelli, and P. Jordano. 2018. Seed-dispersal interactions in fragmented landscapes–a metanetwork approach. Ecol. Lett. 21: 484-493.

Farinha-Marques, P., C. Fernandes, F. Guilherme, J. M. Lameiras, P. Alves, and R. G. Bunce. 2017. Urban Habitats Biodiversity Assessment (UrHBA): a standardized procedure for recording biodiversity and its spatial distribution in urban environments. Landsc. Ecol. 32: 1-18.

Ferenc, M., O. Sedláček, and R. Fuchs. 2014. How to improve urban greenspace for woodland birds: site and local-scale determinants of bird species richness. Urban Ecosyst. 17: 625-640.

Fletcher, R. J., and R. L. Hutto. 2008. Partitioning the multi-scale effects of human activity on the occurrence of riparian forest birds. Landsc. Ecol. 23: 727-739.

FONTANA, S., T. SATTLER, F. BONTADINA, AND M. MORETTI. 2011. How to manage the urban green to improve bird diversity and community structure. Landsc. Urban Plan. 101: 278-285.

GAGNÉ, S. A., AND L. FAHRIG. 2011. Do birds and beetles show similar responses to urbanization? Ecol. Appl. 21: 2297-2312.

GARAFFA, P. I., J. FILLOY, AND M. I. BELLOCQ. 2009. Bird community responses along urban–rural gradients: does the size of the urbanized area matter? Landsc. Urban Plan. 90: 33-41.

GARDNER, T. A., J. BARLOW, I. S. ARAUJO, T. C. AVILA-PIRES, A. B. BONALDO, J. E. COSTA, M. C. ESPOSITO, L. V. FERREIRA, J. HAWES, M. I. M. HERNANDEZ, M. S. HOOGMOED, R. N. LEITE, N. F. LO-MAN-HUNG, J. R. MALCOLM, M. B. MARTINS, L. A. M. MESTRE, R. MIRANDA-SANTOS, W. L. OVERAL, L. PARRY, S. L. PETERS, M. A. RIBEIRO-JUNIOR, M. N. F. DA SILVA, C. D. S. MOTTA, AND C. A. PERES. 2008. The cost-effectiveness of biodiversity surveys in tropical forests. Ecol. Lett. 11: 139-150.

GARMENDIA, E., E. APOSTOLOPOULOU, W. M. ADAMS, AND D. BORMPOUDAKIS. 2016. Biodiversity and Green Infrastructure in Europe: Boundary object or ecological trap?. Land use policy 56:315-319.

GLENNON, M. J., AND W. F. PORTER. 2005. Effects of land use management on biotic integrity: an investigation of bird communities. Biol. Conserv. 126: 499-511.

GODDARD, M. A., A. J. DOUGILL, AND T. G. BENTON. 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends Ecol. Evol. 25: 90-98.

GRAÇA, M., P. ALVES, J. GONÇALVES, D. J. NOWAK, R. HOEHN, P. FARINHA-MARQUES, AND M. CUNHA. 2018. Assessing how green space types affect ecosystem services delivery in Porto, Portugal. Landsc. Urban Plan. 170: 195-208.

HELLE, P. 1983. Bird communities in open ground-climax forest edges in northeastern Finland. Oulanka Reports 3: 39-46.

HERRANDO, S., L. BROTONS, M. ANTON, M. FRANCH, J. QUESADA, AND X. FERRER. 2017. Indicators of the effects of the urban greening on birds: the case of Barcelona. *In* E. Murgui, and M. Hedblom (Eds). Ecology and Conservation of Birds in Urban Environments, pp. 449-463. Springer, Cham, Switzerland.

HERRERA-DUENAS, A., J. PINEDA, M. T. ANTONIO, AND J. I. AGUIRRE. 2014. Oxidative stress of house sparrow as bioindicator of urban pollution. Ecol. Indic. 42: 6-9.

HUFF, M. H., K. A. BETTINGER, H. L. FERGUSON, M. J. BROWN, AND B. ALTMAN. 2000. A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon. Gen. Tech. Rep. PNW-GTR-501. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station 39: 501.

IKIN, K., P. S. BARTON, E. KNIGHT, B. LINDENMAYER, J. FISCHER, AND A. D. MANNING. 2014. Bird community responses to the edge between suburbs and reserves. Oecologia 174: 545-557.

IUCN. 2014. The IUCN red list of threatened species. Version 2018.2. Available at: https://www.iucnredlist.org/species/22693373/93400702 (accessed 1 December, 2018).

JANKOWSKI, J. E., C. L. MERKORD, W. F. RIOS, K. G. CABRERA, N. S. REVILLA, AND M. R SILMAN. 2013. The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. J. Biogeogr. 40: 950-962.

KANG, W., E. S. MINOR, C. R. PARK, AND D. LEE. 2015. Effects of habitat structure, human disturbance, and habitat connectivity on urban forest bird communities. Urban Ecosyst. 18: 857-870.

KARK, S., A. IWANIUK, A. SCHALIMTZEK, AND E. BANKER. 2007. Living in the city: can anyone become an 'urban exploiter'?. J. Biogeogr. 34: 638-651.

KHERA, N., V. MEHTA, AND B. C. SABATA. 2009. Interrelationship of birds and habitat features in urban greenspaces in Delhi, India. Urban For Urban Green 8:187-196.

KONG, F., N. YIN, N. NAKAGOSHI, AND Y. ZONG. 2010. Urban green space network development for biodiversity conservation: Identification based on graph theory and gravity modeling. Landsc. Urban Plan. 95: 16-27.

KOSKIMIES, P. 1989. Birds as a tool in environmental monitoring. Annales Zoologici Fennici 26: 153-166.

KOWARIK, I. 2011. Novel Urban Ecosyst, biodiversity, and conservation. Environ. Pollut. 159: 1974-1983.

KOWARIK, I., M. LIPPE, AND A. CIERJACKS. 2013. Prevalence of alien versus native species of woody plants in Berlin differs between habitats and at different scales. Preslia 85: 113-132.

LAURANCE, W. F., AND D. C. USECHE. 2009. Environmental synergisms and extinctions of tropical species. Conserv. Biol. 23: 1427-1437.

LESTON, L. F., AND A. D. RODEWALD. 2006. Are urban forests ecological traps for understory birds? An examination using Northern cardinals. Biol. Conserv. 131: 566-574.

LEVEAU, L. M., AND C. M. LEVEAU. 2016. Does urbanization affect the seasonal dynamics of bird communities in urban parks?. Urban Ecosyst. 19: 631-647.

LÓPEZ-POMARES, A., G. M. LÓPEZ-IBORRA, AND C. MARTÍN-CANTARINO. 2015. Irrigation canals in a semi-arid agricultural landscape surrounded by wetlands: their role as a habitat for birds during the breeding season. J. Arid Environ. 118: 28-36.

MA, Z., Y. CAI, B. LI, AND J. CHEN. 2010. Managing wetland habitats for waterbirds: an international perspective. Wetlands 30: 15-27.

MACGREGOR-FORS, I., F. ESCOBAR, R. RUEDA-HERNÁNDEZ, S. AVENDAÑO-REYES, M. L. BAENA, V. M. BANDALA, S. CHACÓN-ZAPATA, A. GUILLÉN-SERVENT, F. GONZÁLEZ-GARCÍA, F. LOREA-HERNÁNDEZ, AND E. MONTES DE OCA. 2016. City "green" contributions: The role of urban greenspaces as reservoirs for biodiversity. Forests 7: 146.

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities. MJM Software Design, Oregon, USA.

MCCUNE, B., AND M. J. MEFFORD. 1999. PC-ORD 5.0. Multivariate analysis of ecological data. Gleneden Beach, Oregon, USA.

MCDONNELL, M. J., AND S. T. PICKETT. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71: 1232-1237.

MIKAMI, O. K., AND K. MIKAMI. 2014. Structure of the Japanese avian community from city centers to natural habitats exhibits a globally observed pattern. Lansc. Ecol. Eng. 10: 355-360.

MITTERMEIER, R. A., W. R. TURNER, F. W. LARSEN, T. M. BROOKS, AND C. GASCON. 2011. Global biodiversity conservation: the critical role of hotspots. *In* F. Zachos, and J. Habel (Eds). Biodiversity Hotspots, pp. 3-22. Springer, Berlin, Heidelberg.

MØLLER, A. P. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologia 159: 849-858.

MURGUI, E. 2009. Influence of urban landscape structure on bird fauna: a case study across seasons in the city of Valencia (Spain). Urban Ecosyst. 12: 249.

O'CONNELL, T. J., L. E. JACKSON, AND R. P. BROOKS. 2000. Bird guilds as indicators of ecological condition in the central Appalachians. Ecol. Appl. 10: 1706-1721.

OLIVEIRA HAGEN, E., O. HAGEN, J. D. IBÁÑEZ-ÁLAMO, O. L. PETCHEY, AND K. L. EVANS. 2017. Impacts of urban areas and their characteristics on avian functional diversity. Front. Ecol. Evol. 5: 84.

O'NEAL CAMPBELL, M. 2008. The impact of vegetation, river, and urban features on waterbird ecology in Glasgow, Scotland. J. Coast Res. 24: 239-245.

ORTEGA-ÁLVAREZ, R., AND I. MACGREGOR-FORS. 2009. Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. Landsc. Urban Plan. 90: 189-195.

ORTEGA-ÁLVAREZ, R., AND I. MACGREGOR-FORS. 2011. Spreading the word: the ecology of urban birds outside the United States, Canada, and Western Europe. The Auk 128: 415-418.

PARRIS, K. M., M. AMATI, S. A. BEKESSY, D. DAGENAIS, O. FRYD, A. K. HAHS, D. HES, S. J. IMBERGER, S. J. LIVESLEY, A. J. MARSHALL, AND J. R. RHODES. 2018. The seven lamps of planning for biodiversity in the city. Cities 83: 44-53.

PAUCHARD, A., AND O. BARBOSA. 2013. Regional assessment of Latin America: rapid urban development and social economic inequity threaten biodiversity hotspots. *In* T. Elmqvist at al. (Eds.). Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities, pp. 589-608. Springer, Dordrecht, Netherlands.

PEACH, W. J., M. DENNY, P. A. COTTON, I. F. HILL, D. GRUAR, D. BARRITT, A. IMPEY, AND J. MALLORD. 2004. Habitat selection by song thrushes in stable and declining farmland populations. J. Appl. Ecol. 41: 275-293.

PELLISSIER, V., M. COHEN, A. BOULAY, AND P. CLERGEAU. 2012. Birds are also sensitive to landscape composition and configuration within the city center. Landsc. Urban Plan. 104: 181-188.

Phalen, D. N., M. L. Drew, B. Simpson, K. Roset, K. Dubose, and M. Mora. 2010. Salmonella enterica subsp. enterica in cattle egret (Bubulcus ibis) chicks from central Texas: prevalence, serotypes, pathogenicity, and epizootic potential. J. Wildl. Dis. 46: 379-389.

Reis, E., G. M. López-Iborra, and R. T. Pinheiro. 2012. Changes in bird species richness through different levels of urbanization: Implications for biodiversity conservation and garden design in Central Brazil. Landsc. Urban Plan. 107: 31-42.

Remsen, J. V., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, D. F. Stotz, AND K. J. Zimmer. 2019. A classification of the bird species of South America. American Ornithologists' Union. (Version: September 2019). Available at: http://www.museum.lsu.edu/~Remsen/SACCBaseline.html (accessed September 2019).

Restall, R., C. Rodner, and R. Lentino. 2006. Birds of northern South America. Christopher Helm, London, UK.

Reynaud, P. A., and J. Thioulouse. 2000. Identification of birds as biological markers along a neotropical urban–rural gradient (Cayenne, French Guiana), using co-inertia analysis. J. Environ. Manage. 59: 121-140.

Rupprecht, C. D., J. A. Byrne, J. G. Garden, and J. M. Hero. 2015. Informal urban green space: A trilingual systematic review of its role for biodiversity and trends in the literature. Urban For. Urban Green. 14: 883-908.

Sandström, U. G., P. Angelstam, and G. Mikusiński. 2006. Ecological diversity of birds in relation to the structure of urban green space. Landsc. Urban Plan. 77: 39-53.

Sanz, V., and S. Caula. 2015. Assessing bird assemblages along an urban gradient in a Caribbean island (Margarita, Venezuela). Urban Ecosyst. 18: 729-746.

SAVARD, J. P. L., P. CLERGEAU, AND G. MENNECHEZ. 2000. Biodiversity concepts and urban ecosystems. Landsc. Urban Plan. 48: 131-142

SCHEBELLA, M. F., D. WEBER, L. SCHULTZ, AND P. WEINSTEIN. 2019. The Wellbeing Benefits Associated with Perceived and Measured Biodiversity in Australian Urban Green Spaces. Sustainability 11: 802.

SCHREIBER, S. J., AND M. KELTON. 2005. Sink habitats can alter ecological outcomes for competing species. J. Anim. Ecol. 74: 995-1004.

SCOTT, M. L., S. K. SKAGEN, AND M. F. MERIGLIANO. 2003. Relating geomorphic change and grazing to avian communities in riparian forests. Conserv. Biol. 17: 284-296.

SEIGEL, A., C. HATFIELD, AND J. M. HARTMAN. 2005. Avian response to restoration of urban tidal marshes in the Hackensack Meadowlands, New Jersey. Urban Habitats 3: 87-116.

SERESS, G., AND A. LIKER. 2015. Habitat urbanization and its effects on birds. Acta Zool. Academ. Sci. Hung. 61: 373-408.

SHEPARD, R. N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. Psychometrika 27: 125-140.

SHOCHAT, E., S. B. LERMAN, J. M. ANDERIES, P. S. WARREN, S. H. FAETH, AND C. H. NILON. 2010. Invasion, competition, and biodiversity loss in urban ecosystems. BioScience 60: 199-208.

SILVA, C. P., C. E. GARCÍA, S. A. ESTAY, AND O. BARBOSA. 2015. Bird richness and abundance in response to urban form in a latin American City: Valdivia, Chile as a case study. PloS ONE 10: e0138120.

SOCOLAR, J. B., J. J. GILROY, W. E. KUNIN, AND D. P. EDWARDS. 2016. How should beta-diversity inform biodiversity conservation?. Trends Ecol. Evol. 31: 67-80.

Soga, M., K. J. Gaston, T. F. Koyanagi, K. Kurisu, and K. Hanaki. 2016. Urban residents' perceptions of neighbourhood nature: Does the extinction of experience matter?. Biol. Conserv. 203: 143-150.

Sol, D., C. González-Lagos, D. Moreira, J. Maspons, and O. Lapiedra. 2014. Urbanization tolerance and the loss of avian diversity. Ecol. Lett. 17: 942-950.

Solecki, W. and P. J. Marcotullio. 2013. Climate Change and Urban Biodiversity Vulnerability. In T. Elmqvist, M. Fragkias, J. Goodness, B. Güneralp, P. J. Marcotullio, R. I. McDonald, S. Parnell, M. Schewenius, M. Sendstad, K. C. Seto, and C. Wilkinson (Eds.). Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities, pp. 485-504. Springer, Dordrecht.

Stracey, C. M., and S. K. Robinson. 2012. Are urban habitats ecological traps for a native songbird? Season-long productivity, apparent survival, and site fidelity in urban and rural habitats. J. Avian Biol. 43: 50-60.

Suarez-Rubio, M., P. Leimgruber, and S. C. Renner. 2011. Influence of exurban development on bird species richness and diversity. J. Ornithol. 152: 461-471.

Tejera, G., and B. Rodríguez. 2014. Quantifying the importance for waterbirds of an urban rocky coastal site in Lanzarote, Canary Islands. Wader Study Group Bulletin, 121: 1.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31: 79-92.

Tratalos, J., R. A. Fuller, K. L. Evans, R. G. Davies, S. E. Newson, J. J. Greenwood, and K. J. Gaston. 2007. Bird densities are associated with household densities. Glob. Chang. Biol. 13: 1685-1695.

UNITED NATIONS. 2014. World urbanization prospects: the 2014 revision. United Nations, New York. Available at https://esa.un.org/unpd/wup/publications/files/wup2014-report.pdf (accessed 1, December 2018).

VEHVILÄINEN, H., J. KORICHEVA, AND K. RUOHOMÄKI. 2008. Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos 117: 935-943.

VERNER, J., AND L. V. RITTER. 1986. Hourly variation in morning point counts of birds. The Auk 103: 117-124.

VILLEGAS, M., AND A. GARITANO-ZAVALA. 2010. Bird community responses to different urban conditions in La Paz, Bolivia. Urban Esocyst. 13: 375-391.

VÖLKER, S., AND T. KISTEMANN. 2015. Developing the urban blue: comparative health responses to blue and green urban open spaces in Germany. Health & Place 35: 196-205.

WETLANDS INTERNATIONAL. 2012. Waterbird population estimates. Summary report (5th ed.). Wetlands International, Wageningen, Netherlands. Available at https://www.wetlands.org/wp-content/uploads/2015/11/Waterbird-Populations-Estimates-Fifth-Edition.pdf (accessed 1 December, 2018).

WILCZYNSKI, W., M. J. RYAN, AND E. A. BRENOWITZ. 1989. The display of the blue-black grassquit: the acoustic advantage of getting high. Ethology 80: 218-222.

WU, J. 2014. Urban ecology and sustainability: The state-of-the-science and future directions. Landsc. Urban Plan. 125.

TABLES

TABLE 1. *Description of the variables used to assess the vegetation, waterbody and impervious surface ground-cover of six landcover types in Georgetown, Guyana*.

Ground cover surface	Landcover variable name	Definition
Vegetation	*Tree*	Woody vegetation above 2 m.
	Shrub	Woody vegetation below 2 m.
	Grass	Herbaceous vegetation.
Impervious surface	*Building*	A structure standing permanently in one place. Includes houses, factories, walls and fences.
	Road	An area that has been paved for vehicles to travel along. Also includes off-road tracks used for vehicular transport on a regular basis.
	Pavement	A hard or highly compacted surface. Includes pedestrian walkways, hard court recreation facilities, vehicle parking, cemetery infrastructure and the sea wall promenade.
Waterbodies	*Ocean*	Coastal waters. Includes mudflats that are exposed during low tide.
	Pond	Permanent (human-made) and ephemeral (flooded areas) standing bodies of water.
	Canal	Artificial waterways, wider than 2 m in width, which have been constructed as a defense against flooding.
	Drain	Artificial channels, less than 2 m in width, which have been constructed as a defense against flooding.

TABLE 2. *Total and mean bird species richness, and total and mean number of detections, for the six landcover types surveyed within Georgetown, Guyana.*

Landcover type	**Total species richness**	**Mean species richness (±SE)**	**Total species detections**	**Mean species detections**
Managed greenspace	72	16.30 (1.08)	846	44.52
Unmanaged greenspace	56	13.50 (1.08)	590	31.05
Urban bluespace	60	13.30 (1.18)	710	37.36
Coastal bluespace	26	6.37 (0.45)	440	23.15
Sparse urban	46	7.79 (0.67)	475	25.00
Dense urban	29	7.79 (0.66)	347	18.26
Total	98		3408	

TABLE 3. *MRPP pairwise comparisons of the bird communities within the six landcover types in Georgetown, Guyana. Significant differences, after Bonferonni corrections for multiple comparisons, are shown in bold.*

Bird community pairwise comparisons	***t*-statistic**	***p*-value**
Coastal bluespace vs. Dense urban	**-13.85**	**<0.001**
Coastal bluespace vs. Urban bluespace	**-14.52**	**<0.001**
Coastal bluespace vs. Managed greenspace	**-13.73**	**<0.001**
Coastal bluespace vs. Unmanaged greenspace	**-14.45**	**<0.001**
Coastal bluespace vs. Sparse urban	**-11.82**	**<0.001**
Dense urban vs. Urban bluespace	**-7.16**	**<0.001**
Dense urban vs. Managed greenspace	**-8.85**	**<0.001**
Dense urban vs. Unmanaged greenspace	**-4.06**	**<0.01**
Dense urban vs. Sparse urban	-0.35	0.29
Urban bluespace vs. Managed greenspace	-1.71	0.06
Urban bluespace vs. Unmanaged greenspace	**-4.49**	**<0.001**
Urban bluespace vs. Sparse urban	**-4.46**	**<0.001**
Managed greenspace vs. Unmanaged greenspace	**-2.54**	**<0.01**
Managed greenspace vs. Sparse urban	**-4.57**	**<0.001**
Unmanaged greenspace vs. Sparse urban	-0.74	0.20

TABLE 4. *Indicator species for each of the six landcover types in Georgetown, Guyana, determined using IndVal (Dufrêne & Legendre 1997). Only species with indicator values (Obs IV) significantly larger than random, based on Monte Carlo tests (4,999 permutations, p<0.05), are listed. High indicator values reflect both high species abundance and prevalence within a landcover type.*

Landcover type	**Common name**	**Latin name**	**Dietary guild**	***Obs IV***	***p-value***
Managed greenspace	Wing-barred seedeater	*Sporophila americana*	Granivore	25.0	0.001
	Tropical kingbird	*Tyrannus melancholicus*	Insectivore	24.4	0.003
	Lesser kiskadee	*Pitangus lictor*	Insectivore	21.1	0.004
	Orange-winged amazon	*Amazona amazonica*	Frugivore	18.9	0.008
	Violaceous euphonia	*Euphonia violacea*	Omnivore	15.8	0.025
	Silver-beaked tanager	*Ramphocelus carbo*	Omnivore	15.3	0.027
	Cattle egret	*Bubulcus ibis*	Omnivore	24.4	0.041
Unmanaged greenspace	Blue-black grassquit	*Volatinia jacarina*	Granivore	39.9	0.001
	Short-crested flycatcher	*Myiarchus ferox*	Insectivore	18.9	0.004
Urban bluespace	Wattled jacana	*Jacana jacana*	Insectivore	34.7	0.000
	Pied water-tyrant	*Fluvicola pica*	Insectivore	25.1	0.001
	Striated heron	*Butorides striata*	Piscivore	20.1	0.012
	Yellow-chinned spinetail	*Certhiaxis cinnamomues*	Insectivore	19.1	0.014
	Snail kite	*Rostrhamus sociabilis*	Carnivore	18.9	0.014
Coastal bluespace	Black skimmer	*Rynchops niger*	Piscivore	36.8	0.001
	Collared plover	*Charadrius collaris*	Insectivore	36.8	0.001
	Snowy egret	*Egretta thula*	Insectivore	68.0	0.001
	Scarlet ibis	*Eudocimus ruber*	Insectivore	36.8	0.001
	Little blue heron	*Egretta caerulea*	Carnivore	57.5	0.001
	Neotropical cormorant	*Phalacrocorax brasilianus*	Piscivore	26.3	0.001
	Tricolored heron	*Egretta tricolor*	Carnivore	35.1	0.001

	Sanderling	*Calidris alba*	Insectivore	28.7	0.001
	Common tern	*Sterna hirundo*	Piscivore	21.1	0.003
	Magnificent frigatebird	*Fregata magnificens*	Piscivore	21.1	0.005
	Brown pelican	*Pelecanus occidentalis*	Piscivore	15.8	0.023
	Whimbrel	*Numenius phaeopus*	Insectivore	15.8	0.026
Sparse urban	Roadside hawk	*Rupornis magnirostris*	Carnivore	18.9	0.015
Dense urban	House wren	*Troglodytes aedon*	Insectivore	19.3	0.045
	Pale-breasted thrush	*Turdus leucomelas*	Omnivore	15.4	0.046

FIGURE LEGENDS

FIGURE 1. Boxplots showing percentage cover of the eight landcover variables across five landcover types: unmanaged greenspace (UGR), managed greenspace (MGR), urban bluespace (UBL), sparse urban (SUR) and dense urban (DUR) in Georgetown, Guyana. Thick black horizontal lines in the boxes indicate median values, unfilled circles are moderate outliers, and stars show extreme outliers. Significant differences (indicated by blue lines) were apparent in the percentage ground cover in eight of the 10 landcover variables occurring across the six landcover types.

FIGURE 2. Comparison of the total number of detections for the ten most common bird species recorded in the six different landcover types in Georgetown, Guyana. Species such as the greater kiskadee, ruddy ground dove and blue-gray tanager were common in all landcovers apart from coastal bluespace.

FIGURE 3. (A) Non-metric multidimensional scaling (NMDS) ordination of bird species community composition, based on 98 species of birds from 114 point count locations across six landcover types in Georgetown, Guyana. (B) As in A, but bird images show the two species with the highest indicator values (IndVal) within each landcover type (NB: only one species was an indicator of sparse urban), positioned on their centroid within the ordination. The direction of black lines indicates the strongest associations between labeled landcover variables and landcover types. (C) As in A, but with the coastal bluespace point count location data removed from the analysis (95 point count locations in total). Apart from the coastal bluespace community, all the bird communities from each landcover showed substantial levels of overlap on the NMDS ordination. However, pairwise comparison

analysis revealed significant differences between these bird communities. Each landcover had at least one indicator species.

FIGURE 4. Composition of the avian dietary guilds represented in the bird communities of six landcover type in Georgetown, Guyana, estimated from sample means. Insectivores were the most common dietary guild in all landcovers.