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Left Running Head: Hayes *et al.*

Right Running Head: Neotropical urban bird communities

**Bird communities across varying landcover types in a
Neotropical city**

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23 Received____; revision accepted____.

24 **Abstract**

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

45

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

48

49 RAPID URBANIZATION IS A GLOBAL PHENOMENON (United Nations 2014) THAT POSES A
50 POTENTIALLY SERIOUS THREAT TO LOCAL BIODIVERSITY (Dearborn & Kark 2010; Sol *et al.*
51 2014). During urbanization, natural habitats are modified, fragmented or lost and are replaced
52 by a novel ecosystem characterized by a mosaic of natural, semi-natural and anthropogenic
53 features (McDonnell & Pickett 1990; Kowarik 2011; Beninde *et al.* 2015). This high degree
54 of heterogeneity changes the composition of ecological communities, creating opportunities
55 for some species to thrive, while others may decline or go extinct (Concepción *et al.* 2015;
56 Seress & Liker 2015).

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

73 Birds are one of the most-studied taxonomic groups in urban areas, as they can be
74 monitored inexpensively and are highly responsive to environmental change (Koskimies
75 1989; Gardner *et al.* 2008). As such, they are used extensively as bio-indicators of ecosystem
76 health (Herrando *et al.* 2017). Avian communities in towns and cities can exist independently
77 of neighboring rural ones (Chiari *et al.* 2010) and, in general, are typified by greater
78 abundances but lower species richness than those in more natural habitats (Ortega-Álvarez &
79 MacGregor-Fors 2009). Nonetheless, most of the studies conducted on urban bird
80 communities to date have been located in the temperate zones of Europe, Canada and the
81 USA (Ortega-Álvarez & MacGregor-Fors 2011). Moreover, many have primarily examined
82 the conservation benefits of greenspace and vegetation (Fontana *et al.* 2011; Ferenc *et al.*
83 2014; Rupprecht *et al.* 2015), overlooking the contribution that urban bluespaces may play in
84 harboring avian communities and species abundances (Andrade *et al.* 2018).

85 The Neotropics are highly biodiverse and undergoing rapid urbanization, yet there is a
86 paucity of urban ecological studies undertaken in the region (Ortega-Álvarez & MacGregor-
87 Fors 2011; Pauchard & Barbosa 2013). This is despite the fact that urbanization is likely to be
88 a contributing factor to species extinctions in the tropics (Laurance & Useche 2009).
89 Neotropical towns and cities are often characterized by extreme social and economic
90 inequality, which in turn, may relate to the distribution and quality of urban greenspace
91 (Boulton *et al.* 2018). What little research there is on Neotropical urban birds has indicated
92 that urbanization leads to reduced species richness (Reynaud & Thioulouse 2000; Amaya-
93 Espinel *et al.* 2019), an increase in overall abundance (Reis *et al.* 2012; Amaya-Espinel *et al.*
94 2019), and larger populations of non-native species (Ortega-Álvarez & MacGregor-Fors
95 2011; Amaya-Espinel *et al.* 2019). However, very few studies have examined the bird
96 communities associated with different types of greenspace and bluespace within towns and
97 cities.

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

106

107 **METHODS**

108

109 **STUDY AREA.**—This study was conducted in the city of Georgetown, the capital of Guyana,
110 located on the North Atlantic coast of tropical South America, 6° N, 58° W (Fig. S1). The
111 human population was estimated to be ~118,000 in 2012 (Bureau of Statistics 2012), and the
112 area extent of the city is ~70 km² (Edwards *et al.* 2005). Guyana has an average temperature
113 of 26°C, and two rainy seasons during April-August and November-January (Edwards *et al.*
114 2005).

115 Georgetown is situated in the Upper Amazonia/Guyana Shield ‘major tropical
116 wilderness area’, which represents one of the most globally pristine terrestrial forest
117 ecoregions (Cincotta *et al.* 2000). The city lies below sea level, interlaced by a network of
118 canals and drains to prevent flooding, as well as a sea wall providing protection during high
119 tide. (Edwards *et al.* 2005). Although Georgetown is situated in a country of high rainforest
120 cover, the landscape surrounding the city is dominated by agriculture and the ocean, with the
121 nearest primary forest approximately 35 km south. Landcover type within Georgetown varies
122 from heavily urbanized (areas with a high density of multi-storied buildings) in the city

123 center, to greenspace in the form of parks and grassland, and bluespace along canals and
124 coast. Many residential houses in the city have private gardens that contain a diversity of
125 vegetation, including fruit and flowering trees, as well as shrubs and grasses.

126

127 SURVEY DESIGN.—During May and June 2017, the bird community of Georgetown was
128 sampled across 114 point-count locations, 19 per landcover type, of which there were six
129 (Fig. S1). The six landcover types were: ‘managed greenspace’, ‘unmanaged greenspace’,
130 ‘urban bluespace’, ‘coastal bluespace’, ‘dense urban’ and ‘sparse urban’ (see Table S1 for
131 definitions). The point-count locations were determined by digitally overlaying a 250 m x
132 250 m grid over the city via GIS. The predominant landcover type within a 50 m radius
133 buffer of every grid line intersection, and potential point count location, was evaluated using
134 Google Earth 2017 satellite imagery and maps obtained from the local authorities. A random
135 sample of point count locations for each landcover type was then generated. When we
136 assessed a point count location on the ground, prior to conducting the bird surveys, we
137 verified whether our landcover categorization was correct by ground truthing. If a point was
138 inaccessible (e.g. it was private property and permission to survey was not granted, it was
139 covered by a building), or incorrectly categorized, it was replaced with another from the
140 random sample. All point count locations were at least 250 m apart from one another to
141 ensure independence (Silva *et al.* 2015) and, to avoid potential edge effects, they were all
142 more than 250 m away from the agricultural fields bordering the city (see Ikin *et al.* 2014).

143 To describe the landcover type at each point count location, the percentage (%)
144 ground-cover of a number of variables (Table 1) was assessed within a 50 m radius (matching
145 that of the point count area – see below). We also recorded the presence or absence of fruiting
146 and flowering trees (fruiting only, flowering only, both, or neither) which are likely to

147 influence bird communities, as each tree type offers different resources such as food and
148 shelter (Jankowski *et al.* 2013).

149 Each point count location was surveyed once on a clear day between 05:30 and 08:30
150 (Verner & Ritter 1986). All birds seen or heard within the 50 m radius were recorded during a
151 15-minute interval (O'Neal Campbell 2008). If birds were interacting with the landcover
152 type, or flying within 25 m of the highest structure within the 50 m radius, they were
153 recorded (Huff *et al.* 2000). Any individuals flying above this height threshold were not noted
154 as they were deemed to be flyovers. Our bird taxonomy follows Remsen *et al.* (2019).

155

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

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

168 We first \log_{10} transformed the bird detection data, as is standard practice, when
169 conducting community and ordination analyses (McCune & Grace 2002; Suarez-Rubio *et al.*
170 2011). To investigate differences in the bird communities between landcover types, we
171 conducted non-metric multi-dimensional scaling (NMDS; Shepard 1962) from Bray-Curtis

172 dissimilarity coefficients of the number of detections per species in each point count location.
173 The NMDS was conducted in PC-ORD v6.0 (McCune & Mefford 1999). A final ordination
174 of minimum stress on two axes was generated through a random starting configuration of 500
175 iterations, split into 250 runs of both randomized and real data (Bicknell *et al.* 2014).
176 Kendall's tau rank correlation coefficient (McCune & Grace 2002) was used to assess the
177 strongest associations between landcover variables and the bird community. We undertook
178 this procedure twice, once with all point count locations included, and once with the coastal
179 bluespace sites removed. The latter was done to facilitate closer visual inspection of the
180 remaining data.

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

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

194 Each species was grouped according to its primary dietary guild, according to Restall
195 *et al.* (2006): piscivore, carnivore, frugivore, granivore, insectivore, omnivore and

196 nectarivore. To examine whether the number of species from each dietary guild varied across
197 landcover types we conducted Kruskal-Wallis H tests.

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

207

208 **RESULTS**

209

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

216

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

229 The 2-dimensional NMDS ordination with minimal stress accounted for 64% (Fig.
230 3A) and 54% (Fig. 3C) of the variability in the bird data (with and without the inclusion of
231 coastal bluespace point count locations respectively). This, in combination with the MRPP,
232 showed that the bird communities differed significantly between landcover types (global
233 MRPP: $p < 0.001$). The assemblage in the coastal bluespace was significantly different from
234 all other landcover types. The differences between landcover types remained, even when the
235 procedure was repeated with coastal bluespace removed (global MRPP with coastal
236 bluespace removed $p < 0.001$). Pairwise comparisons of the bird communities within
237 landcover types revealed statistically significant differences between 12 of the 15 landcover
238 type pairings (Table 3). Plotting vectors of the landcover variables revealed that NMDS axis
239 1 was significantly associated with *Ocean* and *Tree*, while axis 2 was correlated with *Shrub*,
240 *Building* and *Road* (Fig. 3B; Table S4).

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

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

250

251 **DISCUSSION**

252

253 As urbanization is progressing rapidly throughout the biodiverse Neotropics (Pauchard &
254 Barbosa 2013), research on biodiversity assemblages in the urban areas of this region is
255 growing increasingly important to inform local conservation priorities (Socolar *et al.* 2016).
256 Our study, one of only a few with an urban focus conducted in the Neotropics, demonstrates
257 that many species are found within towns and cities, and reaffirms that urban bird
258 assemblages are influenced by landcover type (Villegas & Garitano-Zavala 2010; Fontana *et*
259 *al.* 2011; de Toledo *et al.* 2012; Pellissier *et al.* 2012; Kang *et al.* 2015; Leveau & Leveau
260 2016; MacGregor-Fors *et al.* 2016; Dale 2018; Amaya-Espinel *et al.* 2019). As the majority
261 of land around Georgetown is agricultural, drawing comparisons with bird communities
262 inhabiting natural landcovers in close proximity to the city was not possible. However, our
263 study detected 98 species, more than half the number detected via point counts in the primary
264 forests of Iwokrama in central Guyana (Bicknell *et al.* 2015). Indeed, we recorded over 10%
265 of Guyana's bird species in the city of Georgetown, including one endemic to the Guianas,

266 the blood-colored woodpecker (*Veniliornis sanguineus*), and the IUCN Near Threatened
267 semipalmated sandpiper (*Calidris pusilla*) (Braun *et al.* 2007; IUCN 2018). Urban landscapes
268 in the Neotropics can, therefore, provide suitable habitat for high bird diversity and species of
269 conservation concern (Beninde *et al.* 2015). By using the same bird survey techniques within
270 each landcover, we could compare their relative contributions to avifauna of Georgetown.
271 Although the landcover variables and bird community composition showed some levels of
272 similarity across landcover types, they differed significantly between six different landcover
273 types, with urban greenspaces and bluespaces being the most diverse.

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

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

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

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

332 Species from all dietary guilds were observed in almost every landcover type.
333 Omnivorous and granivorous species, such as the rock pigeon (Dunn *et al.* 2006), are known
334 to be successful at adapting to urban landscapes, due to the relative abundance of food
335 resources (e.g. human refuse) (Kark *et al.* 2007; Croci *et al.* 2008; Møller 2009). This
336 plasticity is also epitomized by species from other dietary guilds; for example, the
337 insectivorous greater kiskadee (Echeverria & Vassallo 2008) and frugivorous blue-gray
338 tanager (Sanz & Cuala 2015), both recorded in our research. Indeed, where more heavily
339 frugivorous bird species are absent in urban areas, the greater kiskadee can also be an

340 important seed disperser (Emer *et al.* 2018). However, in accordance with another
341 Neotropical urban bird study (Reynaud & Thioulouse 2000), insectivorous species were the
342 most numerous in Georgetown. This is likely to be because of the fruiting and flowering trees
343 occurring across the city which are typically rich in arthropods (Vehviläinen *et al.* 2008), and
344 because of the insect communities associated with the many waterways. Moreover,
345 insectivorous bird species prefer edges (Helle 1983), which characterize most urban
346 landscapes (Alberti 2005). Nonetheless, Glennon & Porter (2005) assert that the development
347 of a human-dominated matrix negatively affects insectivorous species. O’Connell *et al.*
348 (2000) attribute this negative effect to the loss of specific feeding opportunities as a result of
349 greater disturbance. Therefore, if development of Georgetown intensifies, leading to canal
350 culverting or tree removal, it is probable that insectivorous bird species will decline.
351 Additionally, urban areas offering increased feeding opportunities may act as a sink for
352 species from the surrounding rainforest (Schreiber & Kelton 2005).

353 Indicator species analysis identified landcover type preferences for 29 of the bird
354 species recorded in Georgetown, from across different dietary guilds. This could be driving
355 avian species richness in the city (Tews *et al.* 2004). Species with high indicator values for
356 urban bluespace landcover, such as wattled jacana and pied water tyrant, were uncommon or
357 absent from built up areas containing little to no freshwater, further suggesting that these
358 species heavily rely on the canal system in the city. The high number of indicator species
359 found in the coastal bluespace landcover, all of which were seabirds, can be attributed to
360 coastal habitat preference of these species. Furthermore, in accordance with our findings,
361 snowy egret and whimbrel have been previously recorded having a strong association with
362 coastal urban habitats (Seigel *et al.* 2005; Tejera & Rodríguez 2014). Aside from coastal
363 bluespace, the managed greenspace landcover had the highest number of indicator species,
364 including tropical kingbird and cattle egret, both of which have previously been observed in

365 urban greenspaces (Phalen *et al.* 2010; Leveau & Leveau 2016). Moreover, the high indicator
366 value of blue-black grassquit within unmanaged greenspace is not surprising, given that they
367 are typically found within high grass and scrubland throughout the Neotropics (Wilczynski *et*
368 *al.* 1989).

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

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

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398 **DATA AVAILABILITY STATEMENT**

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

400

401 **LITERATURE CITED**

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705 **TABLES**

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

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

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

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Landcover type	Total species richness	Mean species richness (\pmSE)	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	

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

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Bird community pairwise comparisons	<i>t</i>-statistic	<i>p</i>-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

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742 **TABLE 4.** *Indicator species for each of the six landcover types in Georgetown, Guyana,*
743 *determined using IndVal (Duf r ne & Legendre 1997). Only species with indicator values*
744 *(Obs IV) significantly larger than random, based on Monte Carlo tests (4,999 permutations,*
745 *p<0.05), are listed. High indicator values reflect both high species abundance and*
746 *prevalence within a landcover type.*
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Landcover type	Common name	Latin name	Dietary guild	Obs IV	p-value
Managed greenspace	Wing-barred seedeater	<i>Sporophila americana</i>	Granivore	25.0	0.001
	Tropical kingbird	<i>Tyrannus melancholicus</i>	Insectivore	24.4	0.003
	Lesser kiskadee	<i>Pitangus lictor</i>	Insectivore	21.1	0.004
	Orange-winged amazon	<i>Amazona amazonica</i>	Frugivore	18.9	0.008
	Violaceous euphonia	<i>Euphonia violacea</i>	Omnivore	15.8	0.025
	Silver-beaked tanager	<i>Ramphocelus carbo</i>	Omnivore	15.3	0.027
	Cattle egret	<i>Bubulcus ibis</i>	Omnivore	24.4	0.041
Unmanaged greenspace	Blue-black grassquit	<i>Volatinia jacarina</i>	Granivore	39.9	0.001
	Short-crested flycatcher	<i>Myiarchus ferox</i>	Insectivore	18.9	0.004
Urban bluespace	Wattled jacana	<i>Jacana jacana</i>	Insectivore	34.7	0.000
	Pied water-tyrant	<i>Fluvicola pica</i>	Insectivore	25.1	0.001
	Striated heron	<i>Butorides striata</i>	Piscivore	20.1	0.012
	Yellow-chinned spinetail	<i>Certhiaxis cinnamomues</i>	Insectivore	19.1	0.014
	Snail kite	<i>Rostrhamus sociabilis</i>	Carnivore	18.9	0.014
Coastal bluespace	Black skimmer	<i>Rynchops niger</i>	Piscivore	36.8	0.001
	Collared plover	<i>Charadrius collaris</i>	Insectivore	36.8	0.001
	Snowy egret	<i>Egretta thula</i>	Insectivore	68.0	0.001
	Scarlet ibis	<i>Eudocimus ruber</i>	Insectivore	36.8	0.001
	Little blue heron	<i>Egretta caerulea</i>	Carnivore	57.5	0.001
	Neotropical cormorant	<i>Phalacrocorax brasilianus</i>	Piscivore	26.3	0.001
	Tricolored heron	<i>Egretta tricolor</i>	Carnivore	35.1	0.001

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

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766 **FIGURE LEGENDS**

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

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

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

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

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

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