1 **Primary productivity in cities and their influence over subtropical bird assemblages**

2

3 **Introduction**

4   Urban areas have significantly expanded in the last decades, becoming one of the

5 most important and permanent components of global land cover change (Hepinstall et al.,

6 2008; Pickett et al., 2011; Wu 2014). Even though cities occupy less than 3% of the land

7 area (Alberti 2010, Fengsong et al., 2013) more than 50% of human population is currently

8 concentrated in cities (Wu 2014) and this proportion is expected to increase in the future.

9 This implies a strong pressure over natural resources, which affects ecosystems and

10 biodiversity (Croci et al. 2008, Vitousek et al. 2008). The expansion and densification of

11 urban areas involve the replacement of natural and semi-natural areas (e.g., agriculture) by

12 impervious surfaces (roads, buildings; Alberti et al. 2008). As a result, the main patches of

13 vegetation are clumped in green areas surrounded by a human built matrix and minor

14 vegetation components are interspersed in this matrix (Marzluff and Ewing, 2001). These

15 spatial structure of vegetation affect the functioning and provision of its ecological services,

16 with significant consequences for both, local biodiversity and human well-being (Alberti et al.,

17 2008a; Vitousek et al., 2008; Niemela et al., 2010; Wu 2013; Alberti 2015).

18   One of the main effects of urban expansion over ecosystems is the modification of

19 spatial and temporal patterns of net primary productivity (from now on, productivity; Gallo et

20 al., 1993; Figueirola and Mazzeo, 1998, White et al., 2002; Imhoff et al., 2004; Zhang et al.,

21 2004; Faeth et al., 2005; Shochat et al., 2006; Buyantuyev and Wu 2009; Fengsong et al.,

22 2013; Wu 2013). Since productivity is directly linked to photosynthetic activity, it is a good

23 indicator of ecosystem functioning, and it plays an important role as resource supply (i.e.

24 habitat and food) for different animal groups (Loreau et al., 2001; Hawkins et al., 2003;

25 Morales-Castilla et al., 2012; Alberti 2015). Even though urban ecology studies increased

26 significantly during the last decades in Latin America (Faggi and Perepelizin, 2006; Villegas

27 and Garitano-Zavala, 2010; Bellocq et al., 2011; Ortega-Álvarez and MacGregor-Fors, 2011;

28 Leveau and Leveau, 2012; Reis et al., 2012), the relation between productivity and other

29   organisms in urban settlements is unclear. Birds are sensitive species which respond to

30   environmental shifts by moving rapidly to adequate sites so they constitute a good indicator

31   of the functioning and ecological conditions of the environment (Jokimaki and Fernández-

32   Juricic, 2001; Croci et al., 2008). Moreover, human beings appraise the presence of birds in

33   urban areas due to their cultural, emotional and recreational values, (among other ecological

34   services that they provide; Sekercioglu 2006, Whelan et al., 2008; Dearborn & Kark 2009;

35   Belaire et al., 2015; Tryjanowski et al., 2015). Since bird species depend on vegetation for

36   food and shelter supply (Reis et al., 2012), they are an appropriate group for assessing

37   interactions with productivity as a surrogate of resource availability associated to vegetation.

38   The spatial arrangement of vegetation-related resources in urban landscapes is

39   determined by human activity (Faeth et al., 2005; Alberti 2015). Assessing the spatial

40   association between vegetation productivity and bird biodiversity will permit understanding

41   the functioning of urban ecosystems, and it can inform urban planning strategies. Despite

42   the negative effects of urban expansion over biodiversity, particularly for birds (i.e. reduction

43   of biodiversity, homogenization; Blair and Johnson, 2008; Marzluff, 2008; Vitousek et al.,

44   2008; Morelli et al., 2016) some species or ecological groups tolerate and adapt or even

45   thrive in these environments (Shochat et al., 2006; Williams et al., 2009). While certain bird

46   species may become threatened, others may benefit from urbanization processes, when

47   some habitat conditions are preserved or new ones are created (Alberti et al., 2008b;

48   Hepinstall, 2008; Haedo et al., 2010; Bellocq et al., 2011; Reis et al., 2012). As a

49   consequence, species assemblages in urban settlements may be composed by a mixture of

50   native species which remain from the original landscape (specialists or avoiders); species

51   which expand their distribution area, favoured by the environmental modifications

52   (generalists or tolerant species), and new exotic species which thrive in urban systems

53   (Donnelly and Marzluff, 2006; Alberti et al., 2008a; Minor and Urban, 2010).

54   The main objective of this study is to assess the responses of bird assemblages to

55   spatial patterns of urban vegetation productivity and to assess the effect of different

56   environmental variables of urban structures which might influence bird assemblages. In

57 order to achieve this, we analysed whether productivity, urban cover (percentage of built-up

58 area), vegetation cover and distance to native forest explained the abundance, richness and

59 diversity of avian assemblages. We also examined the responses of three ecological groups

60 of birds (classified according to their use of the environment in: birds of modified landscapes

61 ML; birds of edges and secondary forests ESF; and birds of native Yungas mature forests

62 YMF) to the same set of variables. Given the particular characteristics of these ecological

63 groups, their use can provide information to understand varying responses to urban

64 environmental changes, which would remain hidden if birds were considered as a single

65 homogeneous group.

66   We expect a positive association between productivity (i.e. indicator of resource

67 availability) and the number of individuals (abundance), species richness and diversity. We

68 expect to find a similar association with vegetation cover, but a negative association with

69 urban cover. Finally, distance to native forest might negatively relate to species richness and

70 diversity, due to a source-sink effect. At the level of ecological groups, we expect that

71 abundance and richness of ML and ESF birds will be positively associated with productivity

72 and vegetation cover, since these groups prioritize sites with high food abundance, nesting

73 and protection sites within the urban matrix. Birds of YMF will respond to vegetation cover

74 and to the distance to native forests, due to their high dependence on the environmental

75 characteristics provided by native vegetation. To assess these predictions, we 1)

76 reconstructed the primary productivity of the system, and determined the percentage of

77 urban/vegetation cover and distance to the main native forest; 2) estimated the abundance,

78 richness and diversity of bird species; classifying bird species in the three ecological groups

79 mentioned before (ML, ESF and YMF); and 3) tested different models to analyse the

80 relationship between environmental variables and bird assemblages.
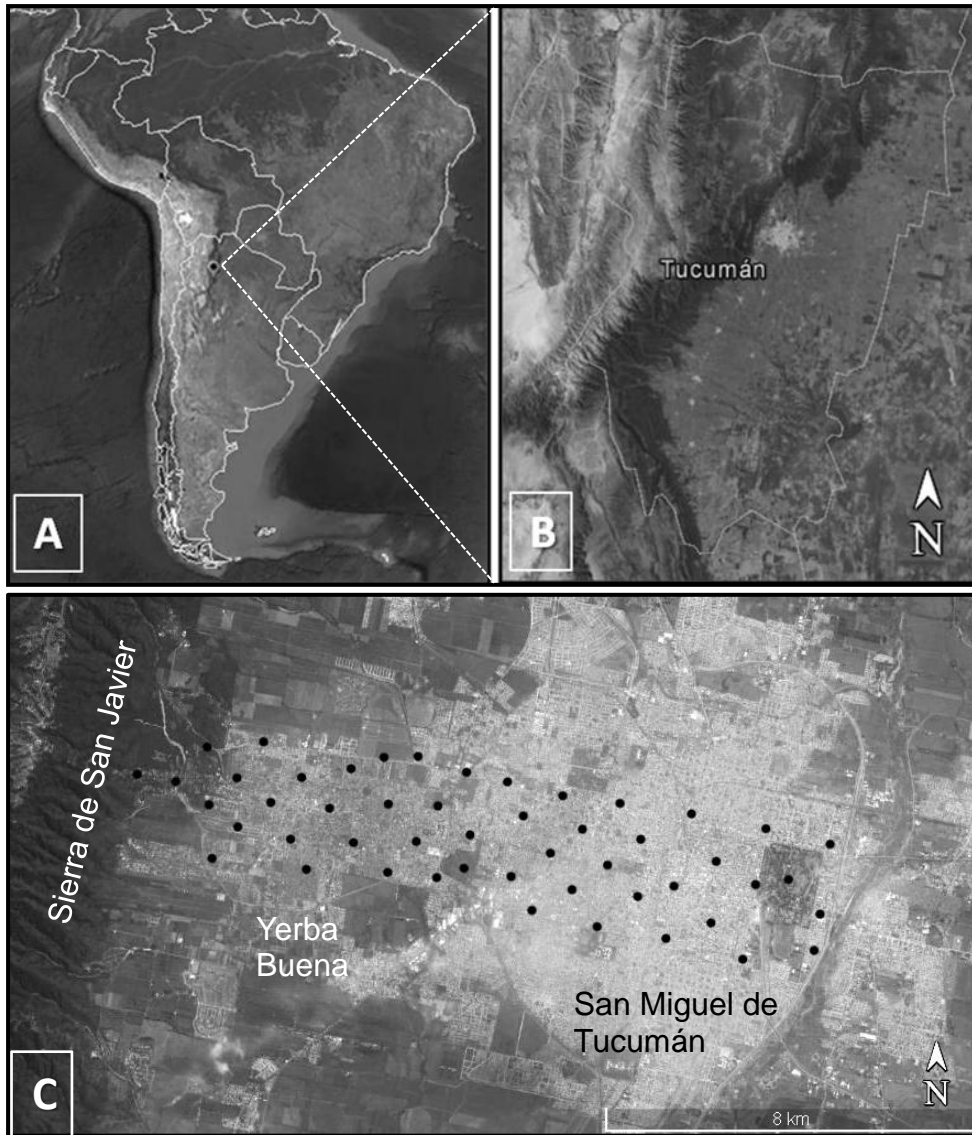
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Methods

Study area

We carried out this study in a metropolitan area of South America: Gran San Miguel de Tucumán (GSMT) 26°49' S and 65°13' W (Fig.1 A), in Tucumán province. This area constitutes the major urban ecosystem of NW Argentina, with more than 1.4 million people living in the foothills of sub-Andean mountains. The two main cities, San Miguel de Tucumán (SMT) and Yerba Buena (YB) represent an east-west urbanization gradient, with the Salí river towards the east end, and Sierra de San Javier (SSJ) mountains at the west (Fig. 1 B - C). SSJ is a natural reserve of about 14000 has of well conserved Yungas forest. Rises in human population and rapid urban growth have promoted the expansion of the urban matrix (3400 hectares between 1986 and 2006; Gutiérrez Angonese 2010), exerting strong pressure towards natural areas such as the foothills of the Yungas forests mountain. This configuration is representative of urban and peri-urban landscapes of other foothill cities of Latin America, such as NW Argentina (i.e. Salta and Jujuy) Bolivia, Colombia and Mexico (Grau, 2010; Parés-Ramos et al., 2013; Gioia et al., 2014; Gutierrez Angonese and Grau 2014). Climate is subtropical with a marked seasonality (hot-wet summers and cool-dry winters), with an annual mean temperature of 18°C and 1000 mm of annual precipitation, mainly concentrated in summer (December-March; Brown et al. 2005). Natural vegetation corresponds to Yungas phytogeographic province (Cabrera, 1976). In peri-urban areas, Yungas forests in the lowlands have been totally replaced by agriculture and urbanization, while forests located at the mountainous area of SSJ are well preserved (Grau et al. 2010).

Fig. 1. (A-B) Location of Tucumán province, Argentina in South America. (C) Cities of Yerba Buena and San Miguel de Tucumán, and location of sampling sites in the study area. Images taken from Google Earth.

Bird surveys

To quantify the abundance, richness and diversity of bird assemblages, we performed point-count surveys (Ralph et al., 1995). Surveys took place from October to December of two consecutive years (2010 and 2011). These months correspond to austral spring, when breeding activity of most species in the region occur (Auer et al. 1997, Lomáscolo et al. 2010, Blendinger et al. 2015). We traced a regular grid of 50 sites, placed 750 m from each other (Fig. 1 C). In each site, we performed two bird surveys per year separated from each other by 250 m. Each survey consisted in recording all species seen or

122 heard from a fixed point during 8 minutes (making a total of 16 minutes in each sampling

123 site). We used 8 minutes per survey point instead of the 5 minutes suggested by Ralph and

124 colleagues (1995) to increase the probability of capturing infrequently encountered species

125 in highly disturbed areas (e.g. traffic, pedestrians). However, most bird species were

126 detected within five-minute point counts (Lynch 1995). Although some distant individuals

127 were recorded, only those detected at less than 50 m from the survey point were considered

128 in the analyses to reduce the differential detectability due to the spatial structure of plants

129 and buildings associated to urban gradients. All bird surveys were conducted by one single

130 observer (HJ) between 6 and 9 am (the time of highest bird activity) on non-rainy and

131 windless days (Ralph et al., 1995). Birds flying were not recorded except those that made

132 use of airspace for food, such as insectivorous species. In each case, the cumulative data

133 was used for each counting site.

134   Bird species were classified in three ecological groups according to the use of

135 Yungas forest and associated transformed environments following the classification of

136 Blendinger and Álvarez (Blendinger and Álvarez, 2009). However, given that this

137 classification takes into account only Yungas native birds, we adapted it to an urban context

138 by including two synanthropic species (see below). Species were classified in the following

139 groups: species of Yungas mature forest (YMF), which occupy forests with a complex

140 structure; edge and secondary forest species (ESF), which inhabit edges and young or

141 secondary Yungas forests; and modified landscape species (ML), which inhabit highly

142 modified and disturbed landscapes, such as urban settlements, generally avoiding mature

143 forests. Two exotic species frequently observed in cities (*Passer domesticus* and *Columba*

144 *livia*), were added to this group, since they exhibit higher affinity to these landscapes. In

145 each site we estimated abundance and species richness for the entire bird assemblage by

146 direct counting and we estimated its biodiversity using the Shannon-Wiener diversity index

147 (H'). We also estimated the species richness and abundance for each of the ecological

148 groups.

149   *Environmental variables*

150   In order to be able to survey public and private vegetation cover and functioning we

151   used remotely sensed data. To measure urban and vegetation cover, we used Google Earth

152   2010 and 2011 images available for the study area. In each site, we traced a buffer area,

153   consisting on a 250m x 250m quadrant around their central point. Within these quadrants,

154   we manually digitized and classified polygons in two cover types: urban (built-up area), and

155   vegetation (herbs and trees). Then, we calculated the area of each cover type. Since these

156   variables (urban and vegetation cover) were inversely related (i.e., sites with higher built-up

157   cover exhibit their reciprocal inverse vegetation cover), we only used vegetation cover. We

158   used Google Earth tools to quantify the distance (in kilometres) from the beginning of the

159   native forests (SSJ) to the central point of each sampling site. We interpreted this variable as

160   the distance from the natural environment (SSJ) which could act as a source of native bird

161   species.

162   In order to reconstruct the vegetation productivity of the growing seasons of years

163   analysed, we used 16-day composites (MOD13Q1) Normalized Difference Vegetation Index

164   (NDVI) estimated from Moderate Resolution Imaging Spectroradiometer (MODIS) images to

165   describe temporal patterns of vegetation phenology. For every year, phenological

166   reconstructions were based on 23 images, 250 x 250 m spatial resolution with NDVI

167   rescaled values ranging from 0 to 1. A compound time series of NDVI images were analysed

168   using TIMESAT software (Jonsson and Eklundh, 2004). TIMESAT quantifies phenological

169   signals from time series of satellite image data, adjusts local functions for each time series

170   point and combines these functions in a model of phenological patterns. Based on these

171   functions, TIMESAT provides statistical descriptors of the seasonal pattern of the analysed

172   variable (NDVI in this case) through the year. For this study, we selected the phenological

173   variables that best describes the annual dynamics of the Growing Season of the vegetation.

174   We analysed the seasonal total integral, an index of absorbed photosynthetically active

175   energy accumulated in one growing season (Running et al., 2004), as a proxy of gross

176   primary productivity. This way we can match the primary productivity of the growing season

177 with the breeding period of birds. Although productivity and vegetation cover might hold

178 common information, we consider that productivity integrates the information from different

179 vegetation strata and from sparse vegetation that cannot be mapped, while vegetation cover

180 represents only the presence or absence of vegetation patches. The availability of

181 quantitative tools to analyse and interpret spatial processes, such as satellite images, allow

182 us for a full study of the area, which cannot be carried out in situ due to limitations of the

183 observer as visual barriers and logistical aspects related to private property, in an urban

184 environment context.

185 *Data analysis*

186 To evaluate the associations between the environmental variables, Pearson

187 correlation analyses were performed (R Core Team 2016). We used Generalized Linear

188 Models (GLMs) to evaluate the responses of the assemblages attributes (abundance,

189 richness and diversity of species) to the combination of the environmental variables

190 (productivity, vegetation cover and distance to native forest). GLMs are a type of regression

191 that allows the response variables to have error distributions other than normal. Thus, they

192 are suitable for count variables (i.e. abundance and richness), which were modelled through

193 a Poisson distribution using a log-link function. This allows modelling the expected number

194 of species or individuals, restraining to the positive range of numbers (Mangeaud and Videla,

195 2005; Gelman and Hill, 2007). We used normal distribution to model species diversity

196 because Shannon-Wienner index is a continuous variable. The use of multivariate models

197 enabled us to assess the individual effect of each explanatory variable, at the time we can

198 control the effects of the other variables included in the model. The proposed models were

199 fitted using their maximum likelihood and the comparative performances of the different

200 models were evaluated through their Akaike Information Criteria (AIC) which combines the

201 fitness of the model to the data (i.e., the likelihood) with the complexity of the model,

202 measured as the quantity of estimated parameters (Burnham et al., 2011). The comparison

203 between models was quantified through the differences in the AIC of the models (dAIC)

204 using the AIC of the best model as reference (dAIC=0). The combination of the three

205 explanatory variables (productivity, vegetation cover and distance) generated seven

206 plausible combinations to explain abundance, richness and diversity of the entire community

207 and of the three birds groups.

208 **Results**

209   We registered a total of 53 bird species (see Appendix 1), from which 39.62%

210 corresponded to modified landscape species (ML), 24.53% to edge and secondary forest

211 species (ESF) and 35.85% to mature Yungas forest species (YMF; Table 1). The proportions

212 were different when individuals were taken into account: most of the 3186 observed

213 individuals belonged to ML birds (65.8%), followed by ESF species (27.3%), while YMF birds

214 were the less abundant (6.9%).

215

216 **Table 1**
217 Groups of bird species registered in San Miguel de Tucumán and Yerba Buena cities, in
218 Argentina. Classification of species was made according to their occupation of Yungas
219 forest environments (modified from Blendinger and Alvarez 2009)

Bird groups	Total Abundance	Total Richness
Modified landscape species	2098	21
Edges and secondary forests species	869	13
Yungas mature forests species	219	19

220

221   In relation to environmental variables, productivity showed a positive association with

222 vegetation cover (ρ= 0.41, $p<0.001$) and a negative association with urban cover ($\rho = -0.57$,

223 $p<0.001$); but it was not associated with distance to SSJ ($\rho < 0.01$, $p=0.97$). On the other

224 hand, vegetation cover was negatively related to the distance to SSJ ($\rho = -0.69$ $p<0.001$).

225 Thus, sites near to SSJ have more vegetation cover than farther sites.

226

227 **Table 2**
228 Performance of GLMs linking spatial variables and attributes of bird assemblages.
229 Dependent variables: abundance (Ab.), richness (R.) and diversity (H'); and abundance and
230 richness of birds of the different groups (ML: modified landscapes species, ESF: edges and
231 secondary forests species, YMF: Yungas mature forests species; modified from Blendinger
232 and Alvarez, 2009). Values in bold indicate the best model (lowest values of dAIC).
233

Models	T. Ab.	T. R.	H'	Ab. ML	R. ML	Ab. ESF	R. ESF	Ab. YMF	R. YMF
Productivity	25.3	47.0	37.6	9.3	3.9	43.8	22.7	267.9	56.3
Veg. Cover	0.7	14.2	13.1	8.2	1.7	13.8	12.3	70.6	10.3
Distance	5.9	1.2	0.7	0.6	1.9	5.8	**0.0**	13.2	3.8
Prod + Veg	**0.0**	15.5	12.8	2.8	2.7	0.6	12.8	33.2	7.5
Prod + Dist	7.6	**0.0**	0.6	**0.0**	**0.0**	6.0	2.0	15.0	4.7
Dist + Veg	0.9	1.1	**0.0**	2.3	2.7	5.0	1.9	**0.0**	**0.0**
Prod + Veg + Dist	1.5	1.6	1.5	1.6	2.0	**0.0**	3.7	1.3	2.0

234

235   GLMs provided different models to explain assemblages attribute responses

236 (abundance, richness and diversity) to explanatory environmental variables (productivity,

237 vegetation cover and distance to SSJ) (Table 2, Fig. 2). Total abundance of bird

238 assemblages was explained by the combination of productivity and vegetation cover, with a

239 negative association with productivity and a positive one with vegetation cover. Total

240 richness was positively related to productivity and negatively related to distance to SSJ;

241 while diversity was explained by vegetation cover and distance, with a positive association

242 with vegetation and a negative association with distance.

243

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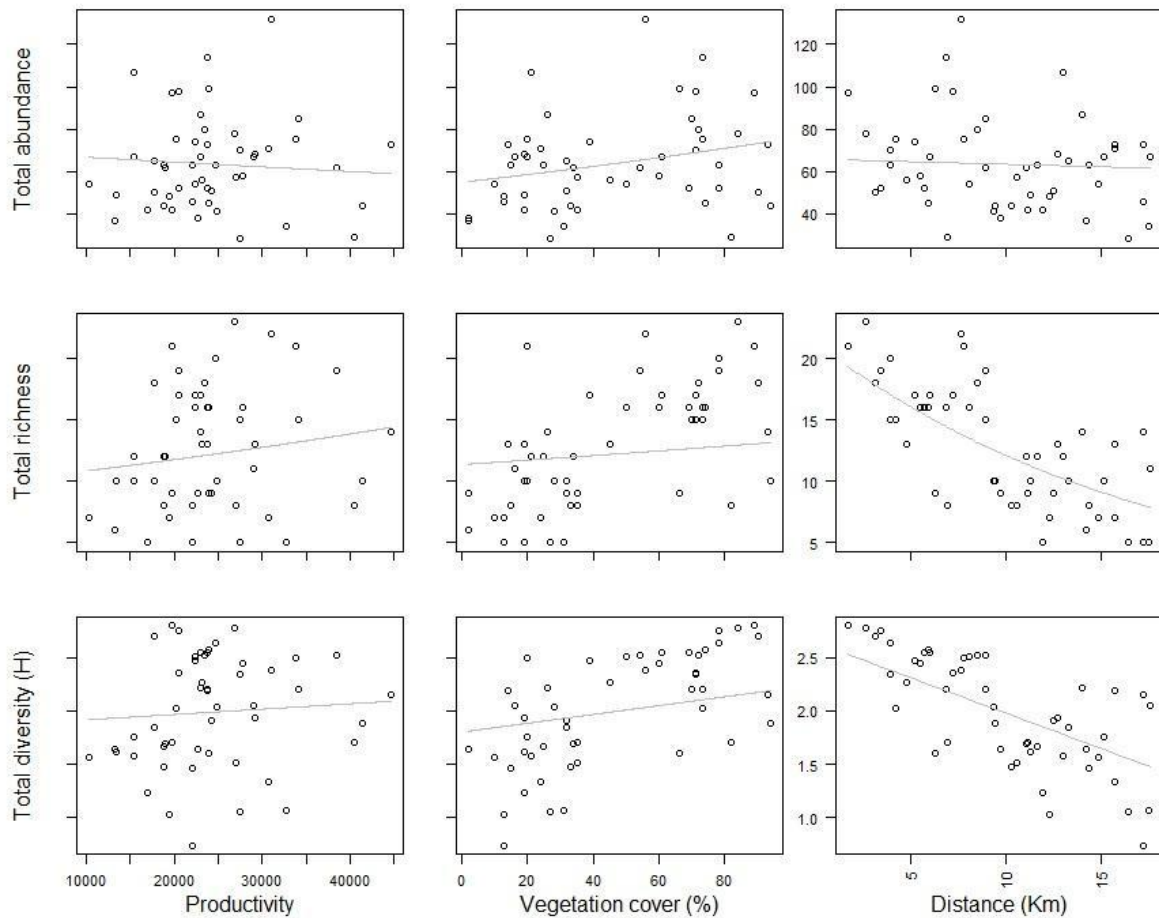
Fig. 2. Responses of total abundance, richness and diversity index of bird assemblages to different environmental variables in a subtropical city in northern Argentina (Great San Miguel de Tucumán). The lines represent the contribution of each variable while controlling the other co-variables. The effects of environment on species richness and abundance were estimated using Poisson GLMs

250

251   The responses to environmental variables differed between bird groups (Table 3 and

252 see complementary material). Abundance of ML species related positively with productivity

253 and distance to SSJ, whereas richness associated negatively with distance and vegetation

254 cover. Abundance of ESF birds was positively related with vegetation cover and negatively

255 related with productivity and distance to SSJ; while richness was negatively related with

256 distance to SSJ. Richness and abundance of YMF species were both positively associated

257 to vegetation cover and negatively related with productivity and distance to SSJ.

Table 3
Response of three groups of birds to environments variables in cities of northern Argentina. Point parameter estimates and (standard deviation) of the contribution of explaining variables are presented. Estimates were taken from Poisson models that fit the abundance and species richness of each bird group to the three explaining variables. Explaining variables were normalized to avoid huge differences in the magnitude of the estimates. Bird groups (ML: modified landscapes species, ESF: edges and secondary forests species, YMF: Yungas mature forests species; modified from Blendinger and Alvarez, 2009). Values in bold indicate statistical significance $p<0.05$.

Attribute	Group	productivity	Vegetation cover	Distance to forest
Abundance	ML	0.044 (0.027)	-0.022 (0.037)	0.059 (0.033)
	ESF	**-0.113** (0.043)	**0.170** (0.061)	-0.091 (0.057)
	YMF	-0.083 (0.095)	**0.564** (0.145)	**-0.854** (0.156)
Species richness	ML	0.107 (0.064)	-0.004 (0.088)	-0.133 (0.081)
	ESF	0.033 (0.088)	-0.057 (0.124)	**-0.399** (0.122)
	YMF	0.002 (0.140)	**0.431** (0.203)	**-0.549** (0.208)

Discussion

Diversity and composition of bird assemblages

The heterogeneous composition and abundance of bird groups found in our study suggests that despite their negative effects (Marzluff & Ewing 2001; Morelli et al. 2016), cities constitute novel ecosystems, with particular characteristics, new spaces and availability of certain resources for birds and for biodiversity in general. This, in turn, might explain the different responses of bird species inhabiting urban environments found in our study (Table 3), and furthermore, it highlights the importance of assessing these effects, at the level of sensitive ecological groups, whose variety of responses could be masked at the assemblage level. Most of the individuals registered in this study belong to the modified landscape (ML) group (Table 1), mostly due to the inclusion of House Sparrow (*Passer*

280   *domesticus*), and Rock Pigeon (*Columba livia*), two exotic species which are abundant in

281   urban areas (Shochat et al., 2010a). These species are highly associated with human

282   presence, and represented 50% of the abundance within this group. These results are

283   consistent with patterns observed in other urban landscapes around the world (Leveau and

284   Leveau, 2004 and 2012; Juri and Chani, 2005; Brandán et al. 2006; Alberti et al., 2008a;

285   Sodhi et al., 2008; Vitousek et al., 2008; Shochat et al. 2010a; MacGregor-Fors and Ortega-

286   Álvarez, 2011; Morelli et al., 2016) where bird communities tend to be dominated by one or a

287   few cosmopolitan species. On the other hand, the edge and secondary forest (ESF) and

288   Yungas mature forest groups (YMF) presented fewer individuals than the ML species group.

289   This result suggests that those species tend to be more associated with natural forest

290   habitats, and are thus less tolerant to urban disturbances (Donnelly and Marzluff, 2006). The

291   Yungas mature forest group presented a remarkable lower number of individuals than the

292   other groups (Table 1), but exhibited a high number of species (see Appendix), which may

293   be due to a source-sink effect produced by the natural forests located at Sierra de San

294   Javier, close to San Miguel de Tucumán and Yerba Buena cities.

295   *Bird assemblages and environmental variables*

296   We found a general pattern of increasing richness and diversity of bird assemblages

297   with increasing urban productivity. This reinforces the concept that primary productivity, as

298   an indicator of resource availability, constitutes an important supporting factor for bird

299   species in urban areas. Although similar patterns were reported by different authors

300   (Mittelbach et al 2001; Bailey et al., 2004; Phillips et al., 2010; Apellaniz et al., 2011), few of

301   them focused in urban ecosystems (Shochat et al., 2004 and 2006, Chao-Nien et al. 2006,

302   Alberti 2015). It has been observed that cities may offer different resources that can maintain

303   and attract different species, increasing local diversity. Reis and colleagues (2012) found

304   that native species, such as humming birds, take advantage of urban resources, like native

305   or exotic flowers in urban parks and house gardens in Brazil. Contrary to our expectation,

306   the weak negative correlation of bird abundance with productivity and the strong positive

307   correlation with vegetation cover we found (Fig. 2) may suggest that some resources are

308   more space dependent than others. Vegetation productivity is an indicator of the natural

309   resources availability (e.g. food) that can be spatially concentrated while vegetation cover is

310   a better indicator of some space dependent resources (e.g. habitat for nesting and

311   hiding). This pattern suggest that in cities the abundance of birds could be related not only to

312   the feed resources provided by plants, but that urban environments could be offering

313   alternative resources such as anthropogenic refuse and bird-feeders that could be

314   supporting them. Shochat and colleagues (2010) suggest that the availability of food,

315   although they are of low quality as refuse, function as "bottom up" control increasing the

316   density of birds in cities. The positive relation with vegetation cover founded proves that

317   green spaces are needed in urban settlements, to provide suitable habitats with the capacity

318   to maintain urban communities, not only for bird assemblages but also for other taxa such as

319   arthropods and mammals (McKinney et al., 2006; Cavia et al., 2008; Croci et al., 2008;

320   Sattler et al., 2010; Hostetler et al, 2011; MacGregor-Fors and Ortega-Álvarez 2011). We

321   also observed a negative association between species richness and diversity with increasing

322   distance to Sierra de San Javier, probably due to a source-sink process (Fig. 2). Natural

323   surroundings, usually with higher density of native species, act as a source of species

324   promoting their dispersion towards other sites as cities (Sol et al., 2013). This will be

325   influenced by the distance and quality of the matrix (i.e. proportion of urban trees) that act

326   connecting or isolating sites (Fernández-Juricic 2000, Jokimaki 2001, MacGregor-Fors and

327   Ortega-Álvarez 2011; Tremblay y St. Clair 2011).

328   At the group level, the responses to environmental variables were diverse (Table 3).

329   The abundance of modified landscape species increased with productivity and with higher

330   distance to Sierra de San Javier, showing a great dependence on resource availability in

331   cities and an avoidance of natural environments, where they may be less competitive. These

332   species probably do not establish in native forests or in sites with higher proportion of native

333   resources and vegetation cover because their niche (life story strategies, diet, habitat,

334   breeding) and opportunistic behaviour might be incompatible with the complex vegetation

335   structure of mature forests. Furthermore, the fact that these species are well adapted to

336   anthropogenic disturbances may enable them to use niches which are less exploited by

337   native species in urban settlements. On the other hand, the species richness of this group

338   decreases with distance to natural areas, which may be due to the presence of few dominant

339   species in highly urban sites, far away from natural environment. These species could be

340   exerting a strong control over other species. For example, related to behavioural aspects,

341   House Sparrow (Passer domesticus) is aggressive and exhibits a gregarious behaviour

342   feeding in groups, which may scare off other solitary species (Shochat et al., 2010a).

343   The abundance of ESF and YMF birds decreased with increasing productivity. In

344   agreement with Faeth and colleagues (2005) and Shochat and colleagues (2010a)

345   competition among species might explain this negative association with highly productive

346   sites. Species of edges and secondary forests related positively to vegetation cover, and

347   negatively with distance. This is probably due to the fact that these species depend on a

348   greater vegetation structural complexity, provided by native forests and by nearby habitats.

349   Finally and in agreement with our expectations, richness and abundance of Yungas mature

350   forest species were negatively associated to distance and positively associated with

351   percentage of vegetation cover. This could be the result of a strong dependence of these

352   species to the environmental characteristics of sites similar to forests, such as vegetation

353   species composition, weather conditions, humidity or a higher proportion of places for hiding.

354   Although we did not evaluate the vegetal composition, it has been demonstrated that a

355   greater diversity in the composition of species of trees and shrubs is positively related to the

356   richness of birds in urban environments (Fernandez-Juricic, 2004; Evans et al., 2009). The

357   presence of Yungas mature forest individuals at mid-distance, highly-productive and

358   vegetated sites suggests that the presence of parks and gardens might facilitate their

359   dispersion, increasing habitat connectivity, even for these specific groups.

360   Given that urban ecosystems harbour a great diversity of species, we believe that

361   obtaining continuous data (more frequency) as such provided by recorders, could be helpful

362   to detect the presence of infrequently encountered species that are not being detected with

363 usual sampling design. This could be complemented with occupancy models proposed by

364 MacKenzie and colleagues (2002, 2006), that allow differentiate between true-absence and

365 non-detection species (MacIvor & Packer 2016).

366 **Conclusions**

367 Urbanization is a rapidly growing phenomenon in Latin America, for which the

368 understanding of the underlying processes that shape biodiversity patterns in cities is key for

369 future scenarios assessing and planning. We consider that our findings could be

370 extrapolated to other areas since Gran San Miguel de Tucumán (GSMT) is probably

371 representative of many cities in South America, which are undergoing urban growth-

372 expansion processes. Our results show that productivity plays an important role in predicting

373 the richness and abundance of bird assemblages in urban environments. The different

374 responses of birds (at the assemblages and group levels) to productivity found in this study

375 shows that resources availability differentially affects bird species, and derived in a greater

376 understanding of the internal variability of bird assemblages to urban environmental

377 changes. It has largely been shown that biodiversity is important for ecosystems functioning,

378 for maintaining the capacity of providing goods and services, and for strengthening the

379 relationship of people with the natural environment, improving well-being and life quality

380 (Grimm et al., 2008, Alberti et al 2008). Therefore, ensuring a higher availability of resources

381 is important for the functioning of cities and for their integration with the surrounding natural

382 environments. Therefore, it is necessary to develop urban planning strategies for improving

383 vegetation structure and species tree composition on sidewalks and public areas, which

384 would increase both the amount of resource available (food, habitat) and connectivity

385 between the urban matrix and native forests. This will improve and allow the flow and

386 maintenance of native species and biodiversity in cities.

387

397 **References**

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399 Auer, S.K., Bassar, R.D., Fontaine, J.J., Martin. T.E., 2007. Breeding biology of passerines
400   in a subtropical montane forest in northwestern Argentina. Condor 109:321–333.
401 Alberti, M. 2008a. Advances in Urban Ecology: Integrating Humans and Ecological
402   Processes in Urban Ecosystems. Springer. New York
403 Alberti, M., Marzluff, J.M., Shulenberger, E., Bradley, G., Ryan, C., Zumbrunnen, C., 2008b.
404   Integrating humans into ecology: opportunities and challenges for studying urban
405   ecosystems. In: Marzluff JM, Endlicher W, Bradley G, Simon U, Shulenberger E, Alberti
406   M, Ryan C, ZumBrunnen C (eds) Urban Ecology: An international perspective on the
407   interaction between humans and nature pp. 143-158. Springer Science+Business
408   Media, LLC, New York, USA.
409 Alberti, M., 2010. Maintaining ecological integrity and sustaining ecosystem function in urban
410   areas. Current Opinion in Environmental Sustainability 2:178–184.
411 Alberti, M., 2015. Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology
412   &Evolution* 30 (2): 114-126.
413 Apellaniz, M., Bellocq, I., Filloy, J., 2012. Bird diversity patterns in Neotropical temperate
414   farmlands: The role of environmental factors and trophic groups in the spring and
415   autumn. *Austral Ecology* 37: 547–555.
416 Bailey, S.A., Horner-Devine, G.L., Moor, L.A., Carney, K.M., Anderson, S., Betrus, C.,
417   Fleishman, E., 2004. Primary productivity and species richness: relationships among
418   functional guilds, residency groups and vagility classes at multiple spatial scales.
419   *Ecography* 27: 207-217.
420 Belaire, J.A., Westphal, L.M., Whelan, C.J., Minor, E.S., 2015. Urban residents' perceptions
421   of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices.
422   *The Condor*: Ornithological Applications 117:192–202.
423 Bellocq, M.I., Filloy, J., Zurita, G.A., Apellaniz, M.F., 2011. Responses in the abundance of
424   generalist birds to environmental gradients: the rufous-collared sparrow (*Zonotrichia
425   capensis*) in the southern. *Neotropics. Ecoscience* 18: 354-362.
426 Blair, R.B., Johnson, E.M., 2008. Suburban habitats and their role for birds in the urban-rural
427   habitat network: points of local invasion and extinction? *Landscape Ecolgy* 23:1157-
428   1169.
429 Blendinger, P.G., Álvarez, M.E., 2009. Aves de la Selva Pedemontana de las Yungas
430   australes In: Brown AD, Blendinger PG, Lomáscolo T, García-Bes P (eds) Ecología,
431   historia natural y conservación de la Selva Pedemontana de las Yungas australes pp.
432   233–272. Ediciones del Subtrópico, Tucumán, Argentina
433 Blendinger, P. G., Jiménez, J., Macchi, L., Martín, E., Sánchez, M. S., Ayup, M. M., 2015.
434   Scale-dependent spatial match between fruits and fruit-eating birds in Andean mountain
435   forests. Biotropica 47:702–711.
436 Brandán, Z.J., Marigliano, N.L., Navarro, C.I., Antelo, C., 2006. Estructura y composición

específica de la comunidad de aves en un área suburbana de la provincia de Tucumán, Argentina. *Acta Zoológica Lilloana*. 50: 47-53.

Brown, A. D., Pacheco, S., Lomáscolo, T., Malizia, L., 2005. Situación ambiental en los Bosques Andinos Yungueños. En: La situación ambiental Argentina 2005. 53-72p.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol 65: 23–35

Buyantuyev, A., Wu, J., 2009. Urbanization alters spatiotemporal patterns of ecosystem primary production: A case study of the Phoenix metropolitan region, USA. *Journal of Arid Environments* 73: 512–520.

Cabrera, A., 1976. Regiones fitogeográficas argentinas. In: Enciclopedia Argentina de agricultura, jardinería y fruticultura pp. 1-85. Acme, Buenos Aires, Argentina.

Cavia, R., Cueto, G., Suárez, O., 2008. Changes in rodent communities according to the landscape structure in an urban ecosystem. *Landscape and Urban Planning* 90: 11–19.

Chao-Nien, K., Pei-Fen, L., Ruey-Shing, L., 2006. Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. *Diversity and Distributions* 12: 546–554.

Croci, S., Butet, A., Georges, A., Aguejdad, R., Clergeau, P., 2008. Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. *Landscape Ecology* 23: 1171-1186.

Donnelly, R., Marzluff, J.M., 2006. Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. *Urban Ecosystem* 9: 99-117.

Dearborn, D.C., Kark, S., 2009. Motivations for Conserving Urban Biodiversity. *Conservation Biology* 24 (2):432–440.

Evans, K.L., Newson, S.E., Gaston, K.J., 2009. Habitat influences on urban avian assemblages *Ibis* 151, 19–39.

Faeth, S.H., Warren, P.S., Shochat, E., Marussich, W.A., 2005. Trophic dynamics in urban communities. *BioScience* 55: 399-407.

Faggi, A., Perepelizin, P., 2006. Riqueza de aves a lo largo de un gradiente de urbanización en la ciudad de Buenos Aires. Rev *Museo Argentino de Ciencias Naturales* 8: 289-297

Fengsong, P., Xia, L., Xiaoping, L., Shujie, W., Zhijian, H., 2013. Assessing the differences in net primary productivity between pre- and post-urban land development in China. *Agricultural and Forest Meteorology* 171–172 pp 174–186.

Fernández-Juricic, E., 2004. Spatial and temporal analysis of the distribution of forest specialists in an urban-fragmented landscape (Madrid, Spain) implications for local and regional bird conservation. *Landscape Urban Plan*. 69: 17– 32.

Figueirola, P.I., Mazzeo, N.A., 1998. Urban-rural temperature differences in Buenos Aires. Int J Climatol 18: 1709-1723

Gallo, K.P., McNAB, A.L., Karl, T.R., Brown, J.F., Hood, J.J., Tarpley, J.D., 1993. The use of a vegetation index for assessment of the urban heat island effect.*Journal Remote Sensing* 14: 2223-2230

Gelman, A., Hill, J., 2007. Generalized linear model. In: Alvarez RM, Beck NL, Wu LL (eds) Analytical Methods for Social Research. Data analysis using regression and multilevel hierarchical models. pp. 109 -136. Cambridge University Press, Cambridge, USA.

Gioia, A., Paolini, P., Malizia, A., Oltra-Carrió, R., Sobrino, J.A., 2014. Size matters: vegetation patch size and surface temperature relationship in foothills cities of Northwestern Argentina. *Urban Ecosystem* 4: 1161-1174

Grau, H.R., 2010. Ecología de la interfase natural-urbana. San Javier-Tucumán como modelo de estudio. In: Grau HR (ed) Ecología de la interfase natural – urbana: Bases para el estudio y la planificación de las interacciones entre la Sierra de San Javier y el Gran San Miguel de Tucumán. pp. 11-18. EDUNT, Tucumán, Argentina.

Grau, H.R., Paolini, L., Malizia, A., Carilla, J., 2010. Distribución, estructura y dinámica de los bosques de la sierra de San Javier. In: Grau HR (ed) Ecología de la interfase natural – urbana: Bases para el estudio y la planificación de las interacciones entre la Sierra de San Javier y el Gran San Miguel de Tucumán. pp. 33-50. EDUNT, Tucumán, Argentina.

Grimm, N.B, Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J.G., Bai, X.M., Briggs, J.M., 2008. Global change and the ecology of cities. *Science* 319:756-760

Gutiérrez Angonese, J., 2010. Dinámica espacio-temporal de crecimiento urbano en el pedemonte oriental de la sierra de San Javier (1986-2045) In: Grau HR (ed) Ecología de la interfase natural – urbana: Bases para el estudio y la planificación de las interacciones entre la Sierra de San Javier y el Gran San Miguel de Tucumán. pp. 137-151. EDUNT, Tucumán, Argentina.

Gutiérrez Angonese, J., Grau, H.R., 2014. Assessment of swaps and persistence in land cover changes in a subtropical periurban region, NW Argentina. *Landscape Urban Planning* 127: 83–93.

Haedo, J., Gasparri, N.I., Blendinger, P.G., 2010. Estructura espacial del ensamble de aves en el gradiente de urbanización de Yerba Buena – San de Tucumán, noroeste de Argentina. In: Grau HR (ed) Ecología de la interfase natural – urbana: Bases para el estudio y la planificación de las interacciones entre la Sierra de San Javier y el Gran San Miguel de Tucumán. pp. 153-166. EDUNT, Tucumán, Argentina.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O´Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water and broad-scale geographic patterns of species richness. *Ecology* 84: 3015–3117

Hepinstall, J.A., Alberti, M., Marzluff, J.M., 2008. Predicting land cover change and avian community responses in rapidly urbanizing environments. *Landscape Ecology* 23: 1257-1276

Hostetler, M., Allen, W., Meurk, C., 2011. Conserving urban biodiversity? Creating green infrastructure is only the first step*. Landsape Urban Planning*100 (4):369-371

Imhoff, M.L., Bounoua, L., DeFries, R., Lawrence, W.T., Stutzer, D., Tucker, C.J., Ricketts, T., 2004. The consequences of urban land transformation on net primary productivity in the United States. *Remote Sens Environ* 89: 434-443

Jokimaki, J., Fernández – Juricic, E., 2001. A habitat island approach to conserving birds in urban landscape: case studies from southern and northern Europe. *Biodiversity and Conservation* 10: 2023-2043

Jönsson, P., Eklundh, L., 2004. TIMESAT - a program for analyzing time-series of satellite sensor data. <u>*Computers and Geosciences*</u> 30: 833-845

Juri, M.D., Chani, J.M., 2005. Variación en la composición de comunidades de aves a lo largo de una gradiente urbano (Tucumán, Argentina). *Acta zoológica Lilloana* 49: 49-52

Leveau, L.M., Leveau, C.M., 2004. Comunidades de aves en un gradiente urbano de la ciudad de Mar del Plata, Argentina. *Hornero* 19: 13-21

Leveau, L.M., Leveau, C.M., 2012. The role of urbanization and seasonality on the temporal variability of bird communities. *Landsc Urban Plann*106: 271- 276

Lynch, J.F., 1995. Effects of point count duration, time-of-day, and aural stimuli on detectability of migratory and resident bird species in Quintana Roo, Mexico. USDA Forest Service Gen Tech. Rep. PSW-GTR-149.

Lomáscolo, S.B., Monmany, A.C., Malizia, A., Martin T.E.. 2010. Flexibility in nest-site choice and nesting success of *Turdus rufiventris* (Turdidae) in a montane forest in northwestern Argentina. Wilson Journal of Ornithology 122:674–680.

Loreau, M., Naeem, S., Inchausti P., Bengtsson J., Grime J.P., Hector A., Hooper D.U., Huston M.A., Raffaelli D., Schmid B., Tilman D. Wardle, D.A., 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges Review. SCIENCE (294), 804-808.

MacGregor-Fors, I., Ortega-Álvarez, R., 2011. Fading from the forest: Bird community shifts related to urban park site-specific and landscape traits. *Urban Forestry & Urban Greening* 10: 239–246.

Mangeaud, A, Videla, M., 2005. En busca de la independencia perdida: la utilización de Modelos Lineales Generalizados Mixtos en pruebas de preferencia. *Ecología Austral* 15: 199-206

MacKenzie, D.I., Nichols, J.D., Lachman, G. B., Droege, S., Royle, J. A., Langtimm, C. A.,

2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D.I, Nichols, J.D, Royle, J.A, Pollock, K.H, Bailey, L.L, Hines, J.E., 2006. Occupancy, estimation and modeling. Inferring patterns and dynamics of species occurrence. Nancy Maragioglio (Ed.) ELSEVIER, California, USA

MacIvor, J.S., Packer, L., 2016. The bees among Us: Modelling Occupancy of Solitary Bees. PLoS ONE 11(12): e0164764. doi:10.1371/journal. pone.0164764

Marzluff, J.M., Ewing, K., 2001. Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. *Restor Ecol* 9:280–292.

Marzluff, J.M., 2008. Island biogeography for an urbanizing world: How extinction and colonization may determine biological diversity in human-dominated landscapes. In: Marzluff JM, Endlicher W, Bradley G, Simon U, Shulenberger E, Alberti M, Ryan C, ZumBrunnen C (Eds) Urban Ecology: An international perspective on the interaction between humans and nature. pp. 355-372. Springer. New York, USA.

McKinney, M.L., 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystem* 11:161–176.

Melles, S., Glen, S., Martin, K., 2003. Urban bird diversity and landscape complexity: species-environment associations along a multiscale habitat gradient. Conser Ecol 7, 5 (online). http://www.ecologyandsociety.org/vol7/iss1/art5/

Minor, E., Urban, D., 2010. Forest bird communities across a gradient of urban development. *Urban Ecosyst* 13: 51-71.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396

Morales-Castilla, I., Rodríguez, M.A., Hawkins, B.A., 2012. Deep phylogeny, net primary productivity, and global body size gradient in birds. *Biological Journal of the Linnean Society* 106: 880–892

Morelli, F., Benedetti, Y., Ibanez Alamo, J.D., Jokimaki, J., Mand, R., Tryjanowski, P., Pape Møller, A., 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Global Ecology and Biogeography* http://wileyonlinelibrary.com/journal/geb

Niemela, J., Saarela, S.R., Soderman, T., Kopperoinen, L., Yli-Pelkonen, V., Vare, S., Kotze D.J**.,** 2010. Using the ecosystem services approach for better planning and conservation of urban green space: a Finland case study. *Biodiversity Conservation* 19:3225–3243.

Ortega – Álvarez, R., MacGregor – Fors, I., 2011. Dusting-off the file: A review of knowledge on urban ornithology in Latin America. *Landsc Urban Plann* 101: 1-10

Phillips, L.B., Hansen, A.J., Flather, C.H., Robison-Cox, J., 2010. Applying species–energy theory to conservation: a case study for North American birds. *Ecol Appl* 20: 2007–2023.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Boone, C.G., Groffman, P.M., Irwin E. Kaushal, S. S., Marshall, V., McGrath, B.P., Nilon, C.H., Pouyat, R.V., Szlavecz, K., Troy A., Warren, P., 2011. Urban ecological systems: Scientific foundations and a decade of progress. Review. *Journal of Environmental Management* 92: 331-362.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ralph, C.J., Sauer, J.R., Droege, R., 1995. Monitoring bird populations by point counts. U.S. Department of Agriculture, Forest Service General Technical Report PSW-149, Albany.

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

Running, S.W., Nemani, R.R., Heinsch, F.A., Zhao, M., Reeves, M., Hashimoto, H., 2004. A continuous satellite-derived measure of global terrestrial primary production. *BioScience*, *54*(6), 547. http://doi.org/10.1641/0006-68(2004)054[0547:acsmog]2.0.co;2

Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist M.K., Moretti, M., 2011. Spider, bee, and bird communities in cities are shaped by environmental control

602   and high stochasticity. *Ecology* 91(11), pp. 3343–3353.
603 Sekercioglu, C.H., 2006. Increasing awareness of avian ecological functions. *Trends in*
604   *Ecology and Evolution.* 21:464-471
605 Shochat, E., Stefanov, W.L., Whitehouse, M.E.A., Faeth, S.H., 2004. Urbanization and
606   spider diversity: influences of human modification of habitat structure and productivity.
607   *Ecol Appl* 14(1): 268–280
608 Shochat, E., Warren, P.S., Faeths, S.H., Mclntyre, N.E., Hope, D., 2006. From patterns to
609   emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution* 21:
610   186-191.
611 Shochat, E., Lerman, S.B., Anderies, J.M., Warren, P.S., Faeth, S.H., Nilon, C.H., 2010a.
612   Invasion, competition, and biodiversity loss in urban ecosystems. *Bioscience* 60(3):199-
613   208.
614 Shochat, E., Lerman, S., Fernández-Juricic, E., 2010b. Birds in urban ecosystems:
615   population dynamics, community structure, biodiversity, and conservation. In: Urban
616   Ecosystem Ecology. J. Aitkenhead-Peterson and A. Volder (ed.) Pp: 75-86. Agronomy
617   monographs 55 ISBN: 978-0-89118-181-1
618 Sodhi, N.S., Posa, M.R.C., Lee, T.M., Warkentin, I.G., 2008. Effects of disturbance or loss of
619   tropical rainforest on birds. *Auk* 125: 511–519.
620 Tryjanowski, P., Skorka, P., Sparks, T.H. et al., 2015. Urban and rural habitats differ in
621   number and type of bird feeders and in bird species consuming supplementary food.
622   *Environmental Science and Pollution Research International*, 22, 15097–15103.
623 Villegas, M., Garitano-Zavala, A., 2010. Bird community responses to different urban
624   conditions in La Paz, Bolivia. *Urban Ecosyst* 13: 375-391
625 Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 2008. Human Domination of
626   Earth's Ecosystems. In: Marzluff JM, Endlicher W, Bradley G, Simon U, Shulenberger E,
627   Alberti M, Ryan C, ZumBrunnen C (Eds) Urban Ecology: An international perspective
628   on the interaction between humans and nature, pp. 3-14. Springer Science+Business
629   Media, LLC, New York, USA.
630 White, M.A., Nemani, R.R., Thornton, P.E., Running, S.W., 2002. Satellite Evidence of
631   Phenological Differences between urbanized and rural areas of the Eastern United
632   States deciduous broadleaf forest. *Ecosystems* 5: 260–277.
633 Williams, N.S.G., Schwartz, M.W., Vesk, P.A. et al., 2009. A conceptual framework for
634   predicting the effects of urban environments on floras. *Journal of Ecology* 97:4–9.
635 Whelan, C.J., Wenny, D.G., Marquis, R.J., 2008. Ecosystem services provided by birds.
636   Annals of the New York Academy of Sciences 1134: 25–60.
637 Wu, J., 2013. Landscape sustainability science: ecosystem services and human well-being
638   in changing landscapes. *Landscape Ecol* 28:999–1023.
639 Wu, J., 2014. Urban ecology and sustainability: The state-of-the-science and future
640   directions. *Landscape and Urban Planning* 125: 209–221.
641 Zhang, X., Friedl, M.A., Schaaf, C.B., Strahler, A.H., Schneider, A., 2004. The footprint of
642   urban climates on vegetation phenology. Geophysical Research Letters 31, L12209, doi:
643   10.1029/2004GL020137