UNIVERSITÀ DEGLI STUDI DI TORINO

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This is an author version of the contribution published on:
Questa è la versione dell'autore dell'opera:
[Global Change Biology, 24: 1046-54, 2018, DOI: 10.1111/gcb.13964]

The definitive version is available at:
La versione definitiva è disponibile alla URL:
https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.13964

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14   **Non-linearities in bird responses across urbanisation gradients: a meta-analysis**
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16   **Running head:** Effects of urbanisation on birds
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18   Péter Batáry[1,2,*], Kornélia Kurucz[3], Marcela Suarez-Rubio[4] and Dan E. Chamberlain[5]
19
20   [1]Agroecology, University of Goettingen, Grisebachstr. 6, 37077 Göttingen, Germany,
21   pbatary@gmail.com
22   [2]GINOP Sustainable Ecosystems Group, MTA Centre for Ecological Research, Klebelsberg
23   Kuno u. 3, 8237 Tihany, Hungary
24   [3]Szentágothai Research Centre, University of Pécs, Ifjúság útja 20, 7624 Pécs, Hungary
25   kornelia.kurucz@gmail.com
26   [4]Institute of Zoology, University of Natural Resources and Life Sciences, Gregor-Mendel-
27   Straße 33, 1180 Vienna, Austria, marcela.suarezrubio@boku.ac.at
28   [5]Dipartimento di Scienze della Vita e Biologia dei Sistemi, University of Turin, Via
29   Accademia Albertina 13, 10123 Torino, Italy, dan.chamberlain99@googlemail.com
30
31   **Corresponding author:** Péter Batáry, Agroecology, University of Goettingen, Grisebachstr.
32   6, D-37077 Göttingen, Germany, Tel.: +49-551-3922358; Fax: +49-551-398806. E-mail:
33   pbatary@gmail.com
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35   **Keywords:** abundance, biodiversity, city size, gradient length, species richness, suburban,
36   systematic review, rural.
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38   **Type of paper:** Primary Research Article
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43

44   **Abstract**

45   Urbanisation is one of the most extreme forms of environmental alteration, posing a major

46   threat to biodiversity. We studied the effects of urbanisation on avian communities via a

47   systematic review using hierarchical and categorical meta-analyses. Altogether, we found 42

48   observations from 37 case studies for species richness and 23 observations from 20 case

49   studies for abundance. Urbanisation had an overall strong negative effect on bird species

50   richness, whereas abundance increased marginally with urbanisation. There was no evidence

51   that city size played a role in influencing the relationship between urbanisation and either

52   species richness or abundance. Studies that examined long gradients (i.e. from urban to rural)

53   were more likely to detect negative urbanisation effects on species richness than studies that

54   considered short gradients (i.e. urban vs. suburban or urban vs. rural areas). In contrast, we

55   found little evidence that the effect of urbanisation on abundance was influenced by gradient

56   length. Effects of urbanization on species richness were more negative for studies including

57   public green spaces (parks and other amenity areas) in the sampled landscapes. In contrast,

58   studies performed solely in the urban matrix (i.e., no green spaces) revealed a strong positive

59   effect on bird abundance. When performing subset analyses on urban-suburban, suburban-

60   rural and suburban-natural comparisons, species richness decreased from natural to urban

61   areas, but with a stronger decrease at the urban–suburban interface, whereas bird abundance

62   showed a clear intermediate peak along the urban-rural gradient, although abundance in

63   natural areas was comparable to that in suburban areas. This suggests that species loss

64   happens especially at the urban-suburban interface, and that the highest abundances occur in

65   suburban areas compared to urban or rural areas. Thus, our study shows the importance of

66   suburban areas, where the majority of birds occur with fairly high species richness.

Introduction

Urbanisation is one of the most extreme forms of environmental alteration, posing a major threat to biodiversity and altering fundamental ecosystem services upon which human civilisation depends (Aronson et al., 2014; Sol et al., 2014). The problems caused by urbanisation are diverse. As environmental conditions are significantly altered, natural habitats of many plant and animal species are rapidly reduced and transformed (Grimm et al., 2008). Cities are novel ecosystems, characterised by fragmented environments with a higher level of disturbance than natural habitats and with a strongly altered pattern of resources (Rebele, 1994; Alberti, 2015). However, with the rapid expansion of urban development (Cohen et al., 2006; Seto et al., 2013) and the associated modification of habitats, it is crucial to understand the relationship between biodiversity and urban habitats (Clergeau et al., 1998).

Bird abundance and community composition in urban areas have been well described, with the main conclusion that bird community composition becomes increasingly impoverished with urban development, leading to the dominance of a few abundant species (Kelcey & Rheinwald, 2005), and hence resulting in long-term reduction in diversity (Chace & Walsh, 2006; Sol et al., 2014). Researchers have commonly observed lower species richness in urban areas relative to that of the surrounding rural landscapes (Clergeau et al., 2006; Sandström et al., 2006). However, these patterns are by no means universal, and other studies have found a non-linear response, in which areas with intermediate levels of urbanisation exhibit the highest richness (Blair, 1996; Marzluff, 2001; McKinney, 2002; Tratalos et al., 2007), whilst overall bird abundance often increases from rural to urban areas (Chase & Walsh, 2006; Faeth et al., 2011; Njorge et al. 2014), although other studies have found no trend (Chamberlain et al., 2017) or inconsistent responses across different cities (Garaffa et al., 2009; Jokimäki et al., 2002).

The variety of responses of bird communities to urbanisation gradients may arise for a number of reasons. First, there is no generally accepted definition of what is an 'urban'

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93 landscape, and considerable differences in classification of urban, suburban and rural habitats

94 exist among countries and continents (McIntyre et al., 2000; Seto et al., 2013). Thus,

95 behavioural responses of animals to urban gradients may differ between individual studies, in

96 part due to variations in gradient composition. Second, gradient length and resolution may

97 affect the conclusions of studies. In particular, many studies often reduce the urban-rural

98 gradient to a simple dichotomy, which may obscure important non-linear effects in terms of

99 urban-suburban and suburban-rural transitions (Alberti, 2015). Third, the characteristics of

100 individual cities may affect responses along the urban-rural gradient. Whilst this may be

101 underpinned by a large number of interacting factors (e.g. pollution levels, socioeconomic

102 conditions, habitat management, availability of green space), human population size in cities

103 can be a general indicator of key characteristics (Bettencourt & West, 2010), such as habitat

104 loss, fragmentation and disturbance. Thus human population size has been shown to be

105 important in affecting patterns of bird species richness within cities (Gagné et al., 2016) and

106 of bird abundance responses to urban-rural gradients (Garaffa et al., 2009), although Clergeau

107 et al. (2001) found no effect of human population size on species richness.

108   The main objective of this study was to perform a set of meta-analyses based on a

109 comprehensive and systematic literature review, thereby synthesising the relative impact of

110 urbanisation on bird assemblages. Importantly, we also assessed factors that may have

111 underpinned the wide variation in responses detected in previous studies. In particular: (1) we

112 adopted an objective definition of urban, suburban and rural areas (e.g. Clergeau et al., 2001

113 and Saari et al., 2016) in order that different gradients can be broadly comparable; (2) we

114 assessed bird responses across a simple urban-rural contrast, but also assessed intermediate

115 levels of urbanisation, thus allowing detection of non-linear responses; and, (3) we assessed

116 the responses of bird communities in relation to city size, which is assumed to be a good

117 indicator of city-level characteristics (as per Bettencourt & West, 2010). This type of analysis

118 provides a statistical framework for integrating results of previous studies, and aids our

5

119 understanding of both the ecological implications of increasing urbanisation and how to

120 mitigate its threat to biodiversity.

121

122 **Methods**

123 We studied the effects of urbanisation on bird communities within a systematic review

124 framework using meta-analysis. In ecology, there is a growing need for quantitative research

125 syntheses to generate higher order conclusions (Gurevitch et al., 2001; Stewart, 2010). In

126 contrast to qualitative and descriptive traditional reviews, meta-analysis allows the

127 quantification and summary of results of several independent studies examining the same

128 question (Gurevitch et al., 1992; Cooper et al., 2009). In meta-analysis, the magnitude of

129 standardised effects (effect size) is quantified from each individual study, and these are then

130 used to calculate the combined (overall) magnitude and significance of the effect under the

131 meta-analytical study (Hedges & Olkin, 1985).

132

133 *Literature search and study selection*

134 We conducted a systematic literature survey using Web of Science and Scopus databases

135 (until 15th June 2015) for topics including the following so called PICO (Population,

136 Intervention, Comparator and Outcome) combination of search terms (Higgins & Green

137 2008): (bird OR avian) AND (urban* OR rural OR suburban) AND ("species richness" OR

138 diversity OR abundance OR density). We refined the searches by excluding (editorial material

139 OR review OR meeting abstract OR book chapter) document types in Web of Science Core

140 Collection, and (book series OR book OR conference proceedings OR review) source types in

141 Scopus. This resulted in a total of 2351 potential publications.

142   Only studies published in peer-reviewed journals were included in the meta-analysis,

143 relying on the peer-review process as a first step of quality control. After a duplicate filtering

144 for hits located by both databases with Mendeley reference manager software (Mendeley

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145   2015), we performed a filtering through the title and abstracts of each article, then through the

146   full text of each potentially relevant article to decide whether the article matched our selection

147   criteria (for the detailed selection process see the PRISMA flow diagram in supplementary

148   Fig. S1). We applied the following inclusion criteria for study selection: (1) studies that

149   investigated the changes in bird species richness and/or abundance along an urbanisation

150   gradient (urban vs. suburban vs. rural areas or urban-rural gradient); (2) studies that were

151   carried out in cities and included at least four spatial replicates per urbanisation gradient

152   category; and (3) studies that reported mean, standard deviation, standard errors of mean or

153   confidence interval (CI), and sample size for urbanisation gradient categories, or studies that

154   reported statistics (F, t or Chi-square values and sample size) on urbanisation gradient effect

155   on birds. Studies that investigated a single group of birds or a single functional guild, which

156   did not represent the whole community, were excluded. Altogether, we found 39 relevant

157   papers, comprising 42 observations of 37 case studies for species richness (Table S1), and 23

158   observations of 20 case studies for abundance (Table S2). A list of articles excluded during

159   full text filtering and reasons for exclusion is presented in Table S3. In cases where an article

160   was excluded due to under-reported statistics, we contacted the authors for further

161   information (15 articles), but the response rate was low (40%).

162

163   *Data extraction*

164   To test the dependence of the urbanisation effect on city size, we used the human population

165   data provided in the articles or checked the population size of a city for the year when the

166   study was carried out using online databases and websites (Tables S1-2). Given the

167   inconsistent and often subjective classifications of urban land use types (Seto et al., 2013), we

168   standardised definitions based on descriptions provided in the articles used in the meta-

169   analysis and re-categorised the data according to the following classification to provide more

170   homogenous comparison across studies: "Natural" – natural or semi-natural habitats with

171   little or no human habitation; "Rural" – very low density of housing in a modified, usually

172   farmland matrix; "Suburban" – residential areas, consisting of low-rise houses with lawns

173   and/or private gardens, and relatively high vegetation cover (*ca.* 50% or more, where

174   quantified); and, "Urban" – dominated by artificial, sealed surfaces (>50% where quantified),

175   and characterized by commercial/industrial buildings or high-rise residential areas. In cases

176   where only qualitative descriptions were given, we accepted, or re-classified as necessary,

177   categories which were stated to be predominated by the land uses described above (i.e. we

178   assumed the 50% thresholds, as above). However, in some cases, it was still not possible to

179   separate categories, in particular urban and suburban classes.

180   Of the 39 studies used in the meta-analyses, we accepted the classification of 22 studies

181   (Tables S1-2). We changed the original classification of urban land use types according to our

182   categorization for eleven studies, either in terms of changing the definition (e.g. from

183   suburban to urban), amalgamating groups used in a given study into one of our four

184   categories, or changing the terminology to fit in with our classification. Among them, there

185   were six studies where urban and suburban classifications could not be clearly separated, and

186   so were classified as "Urban + Suburban". Additionally, there were six further studies that

187   investigated a gradient of settlement size or a grid-based urbanisation gradient, where such a

188   classification was not possible. The latter were included in the summary analyses and

189   calculation of overall mean effect size, but not in the categorical or subset analyses (see

190   below).

191   Based on this re-classification, the species richness and abundance datasets were

192   divided into two groups according to which part of the urbanisation gradient was studied.

193   Thus we defined a "short gradient", if the comparison was urban vs. suburban or suburban vs.

194   rural habitats, and a "long gradient", if the whole urban to rural gradient was analysed (Fig.

195   S2). Importantly, urban public green spaces, including parks, public gardens and other

196   amenity areas, can be significant contributors to overall biodiversity (e.g. Fernández-Juricic &

197   Jokimäki, 2001), but may occur across the urban-rural gradient, and yet themselves form

198   rather separate habitats within a given land use category. To account for this (11 studies), we

199   incorporated green spaces (referred to in the analysis as parks for simplicity, but

200   encompassing a range of urban green spaces) as a factorial moderator in the meta-analyses

201   (i.e. presence or absence of parks included within the sampled landscapes for a given land use

202   type). There were nine studies that did not specify whether green spaces were included and

203   which were omitted from this analysis.

204

205   *Effect size calculation*

206   For an effect size measure, we used Pearson's correlation coefficient (*r*). The effect sizes and

207   their variances were calculated for all observations in different ways depending on the type of

208   source data: (1) from two-level categorical data (e.g. urban vs. rural classes), Hedges' *g* (i.e.

209   the unbiased standardised mean difference) was calculated based on the mean, standard

210   deviation and sample size (number of study sites) of species richness and abundance of urban

211   and rural areas. This was then transformed to Pearson's correlation coefficient; (2) from

212   continuous urbanisation gradients, Pearson's *r* was calculated from *t*, *F* or χ^2 data; (3) from

213   three-level categorical data (e.g. urban-suburban-rural classes), Hedges' *g* was calculated for

214   urban-suburban and suburban-rural data separately, then these were transformed to Pearson's

215   *r* (Lajeunesse, 2013). Then we computed the combined urban-suburban and suburban-rural

216   effect sizes considering multiple comparisons within a study (Borenstein et al., 2009); (4) if

217   studies did not provide data for the whole community (e.g. overall abundance), but they

218   provided data separately for traits (e.g. abundance presented only for feeding groups and not

219   for all species), we first calculated effect sizes for the separate traits, then combined them in

220   one Pearson's *r* considering multiple outcomes within a study (Borenstein et al., 2009), and

221   finally we corrected these effect sizes by weighting them based on the relative abundance of

222   the feeding groups. All Pearson's *r* values were transformed to Fisher's *z* for all analyses, but

223　were back-transformed for data visualization, since the interpretation of Pearson's r is more

224　straightforward. A negative effect size indicated a decrease in species richness or abundance

225　from rural to urban areas.

226

227　*Meta-analysis*

228　We performed hierarchical meta-analyses separately for species richness and abundance,

229　which allowed the specification of nesting factors. Then we performed mixed effects models

230　with fixed effects (see moderators, i.e. predictor variables, below) and random effects to

231　account for differences across studies, assuming that they do not share a common mean effect,

232　but that there is random variation among studies, in addition to within-study sampling

233　variation (Borenstein et al., 2009; Harrison, 2011). The models also took into account the

234　hierarchical dependence in our data due to cases where multiple observations (i.e. effect sizes)

235　were obtained from the same study. Having several effect sizes from the same publication

236　violates the assumption that effect sizes are independent (Rossetti et al., 2017). Therefore, we

237　included a publication-level random effect as a nesting factor to incorporate this dependency

238　of multiple outcomes within study observations (see Appendix S2 for model codes).

239　Additionally, we also considered the geographic dependencies of the studies by including

240　continent as the first nesting factor in all models.

241　　First, we performed random effects summary meta-analyses to calculate the overall

242　mean effect size for all species richness data and all abundance data separately (Appendix

243　S2). This provided a general measure of the overall effect of urbanisation, which implicitly

244　assumes a linear relationship. Given that more than 80% of papers reported a simple measure

245　of species richness (number of species observed), rather than using richness estimates

246　adjusted for sampling effort or abundance (e.g. rarefaction), we used this metric in the

247　analysis. When type of index (simple or adjusted richness) was included as a factorial

248　moderator, there was no significant moderation effect (Q_m= 2.875; p= 0.090). The output of

10

249   each statistical test consisted of the mean effect size for the analysis with accompanying 95%

250   Cis, and a total heterogeneity statistic (Q). The heterogeneity statistic is a weighted sum of

251   squares and is tested against a χ^2 distribution with d.f. = n-1. Estimates of the effect size were

252   considered to be significantly different from zero if their 95% CIs did not include zero

253   (Borenstein et al., 2009).

254   Second, we performed categorical meta-analyses using gradient length (short or long)

255   and inclusion of urban green spaces in the sample for a given study (referred to as park or

256   non-park) as moderators (Appendix S2). The total heterogeneity in categorical meta-analysis

257   can be partitioned into variance explained by the categorical factor in the model (between-

258   group heterogeneity) and residual error variance (within-group heterogeneity) with χ^2 tests

259   indicating their significance. A significant between-group heterogeneity indicated that species

260   richness or abundance responses to urbanisation differed based on gradient length or inclusion

261   of green spaces. Additionally, we performed meta-regressions using city size as a continuous

262   moderator (city size was measured as population size and was log-transformed to achieve a

263   normal distribution and hence a better model fit). There was no relationship between city size

264   and gradient length (two sample t-test for species richness: t = -1.42, df =26, p = 0.167; for

265   abundance: t = 1.38, df =15, p = 0.187). We did not include season in which species richness

266   was measured as moderator as the majority of studies were carried out in the breeding season.

267   Third, to assess potential non-linear responses in species richness and abundance along

268   the urbanisation gradient, we performed subset analyses for urban-suburban, suburban-rural

269   and suburban-natural comparisons using studies that considered the four categories: urban,

270   suburban, rural and natural, and provided data for at least one of the comparisons. This

271   enabled us to calculate effect sizes (Fisher's z transformed to Pearson's correlation

272   coefficient) for urban-suburban, suburban-rural and suburban-natural comparisons. Here, we

273   often analysed dyads of urban-suburban, suburban-rural and suburban-natural comparisons

274   together, which meant that suburban categories were included in many studies twice. To

275 account for the non-independence of multiple treatments with a common control (Borenstein

276 et al., 2009), we included the dyad containing the corresponding urban-suburban and

277 suburban-rural, or urban-suburban and suburban-natural, comparisons as a nesting factor

278 (Tables S4-5; Appendix S2).

279

280 *Publication bias*

281 Studies finding a significant effect may be more likely to be published than studies finding no

282 effects, which can bias the outcome of meta-analyses. We therefore explored the possibility of

283 publication bias graphically (funnel plots) and statistically (regression test; Rothstein *et al*.,

284 2005). The regression test for funnel plot asymmetry examines the relationship between the

285 standardised effect size and sample size across the studies. A significant *P* value may indicate

286 publication bias, whereby studies with small sample size are only published if they show large

287 effect sizes. All analyses were performed with the metafor package (Viechtbauer, 2010) in R

288 (R Development Core Team, 2015).

289

290 **Results**

291 In the summary meta-analysis of all data, we found a significant overall negative effect of

292 urbanisation on bird species richness, showing that in general species richness was

293 consistently lower towards more urbanised landscapes (Table 1, Fig. 1a). Bird abundance

294 increased with urbanisation with a small, marginally significant effect (Fig. 1b).

295 **Table 1.** Summary table of meta-analyses showing total heterogeneity ('all', only effects of
296 urbanisation without moderators), and heterogeneities explained by moderators (city size
297 [continuous gradient on log scale], gradient length [short vs. long] and green space ['park',
298 yes vs. no]) with corresponding residual heterogeneities.

	d.f.	Q	P
Species richness			
all	41	1901.95	<0.001
city size	1	1.92	0.166
residual	26	298.88	<0.001
gradient length	1	1.10	0.295
residual	39	1899.58	<0.001
park	1	0.80	0.371
residual	26	317.07	<0.001
Abundance			
all	22	308.62	<0.001
city size	1	<0.01	0.994
residual	15	133.18	<0.001
gradient length	1	0.15	0.697
residual	20	307.68	<0.001
park	1	12.88	<0.001
residual	17	208.83	<0.001

299
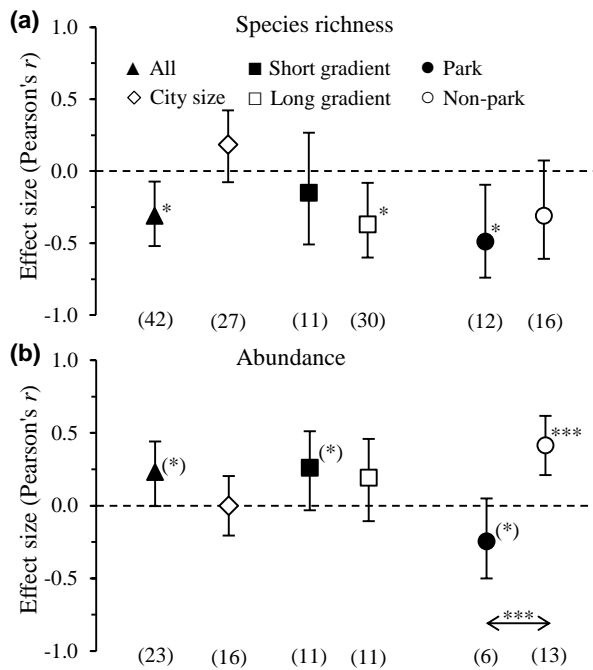
300 **Figure 1.** The effects of urbanisation on (a) species richness and (b) abundance of birds
301 depending on city size (continuous gradient on log scale), gradient length (short vs. long) and
302 green spaces ('Park', yes vs. no). Mean effect sizes and 95% CIs are shown. Numbers under
303 symbols indicate sample size. Asterisks ((*)$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)
304 above effect size symbols denote a significant difference from zero (within-group
305 heterogeneity), whereas one above a horizontal arrow indicates a significant difference
306 between park and non-park studies (Table 1).

307

308   Including city size as a moderator, we found only a small, positive, non-significant

309 moderation effect of urbanisation on bird richness (Table 1, Fig. 1a). For abundance, there

13

310   was no marked moderation effect of city size at all (Fig. 1b). When we analysed the potential

311   effect of gradient length, we found stronger negative effects in long than in short gradients on

312   species richness (although this between-group heterogeneity was not significant as shown in

313   Table 1). Additionally, for the short gradient, the effect was not significantly different from

314   zero (Fig. 1a). For bird abundance, there was a small, marginally significant, positive effect in

315   short gradients and no effect in long gradients, but there was no significant difference

316   between the two gradient lengths (Table 1, Fig. 1b). Finally, studies including green spaces

317   showed a large and significantly negative urbanisation effect on species richness in contrast to

318   studies not including them, but their effect sizes did not differ from each other (Table 1, Fig.

319   1a). However, in the case of abundance, the urbanisation effects in 'parks vs. non-parks'

320   showed a strong contrast, with significant positive effects in the absence of green spaces and

321   marginal negative effects when green spaces were present (Fig. 1b).

322   When considering urban-suburban vs. suburban-rural or suburban-natural contrasts, bird

323   species richness showed that urbanisation had a large negative effect from suburban to urban

324   areas, a less strong, but still significant decrease from natural to suburban areas, but no change

325   from rural to suburban areas (Table 2, Fig. 2a,b). Additionally, effect sizes of urban-suburban

326   vs. suburban-rural comparisons, and also urban-suburban vs. suburban-natural comparisons,

327   differed from each other significantly. For abundance, we found that bird numbers increased

328   with a small effect from natural to suburban areas, and with a large effect from rural to

329   suburban areas, but then decreased with a small effect from suburban to urban areas (Fig. 2

330   c,d). Finally, these two pairs of effect sizes (urban-suburban vs. suburban-rural and urban-

331   suburban vs. suburban-natural) also differed from each other significantly. These results

332   therefore demonstrate a non-linear, intensifying decrease in species richness along the

333   gradient from natural to urban areas, with a steady state from rural to suburban areas followed

334   by a strong decrease toward urban areas (Fig. 2b). Finally, we observed a non-linear, hump-

335   shaped pattern in abundance along the gradient with the highest values being in suburban

336   areas, and a marked increase from rural to suburban areas (Fig. 2d). Natural areas had similar,

337   though slightly lower, abundance compared to suburban areas.

338   **Table 2.** Summary table of subset meta-analyses showing tests of moderators (between-group
339   heterogeneities; groups: urban-suburban, suburban-rural and suburban-natural comparisons)
340   with residual heterogeneities.

	d.f.	Q	P
Species richness			
between-group	2	66.67	<0.001
residual	26	188.43	<0.001
Abundance			
between-group	2	59.25	<0.001
residual	18	173.49	<0.001

341
342   None of the funnel plots of effect size vs. standard error of mean showed strong

343   skewness (Fig. S3), indicating no initial evidence of publication bias in our dataset.

344   Regression tests did not show significant relationships between effect sizes and sample sizes

345   (species richness: $z = 1.76$, $P = 0.078$; abundance: $z = 0.16$, $P = 0.866$). Therefore, there was

346   no evidence of publication bias.
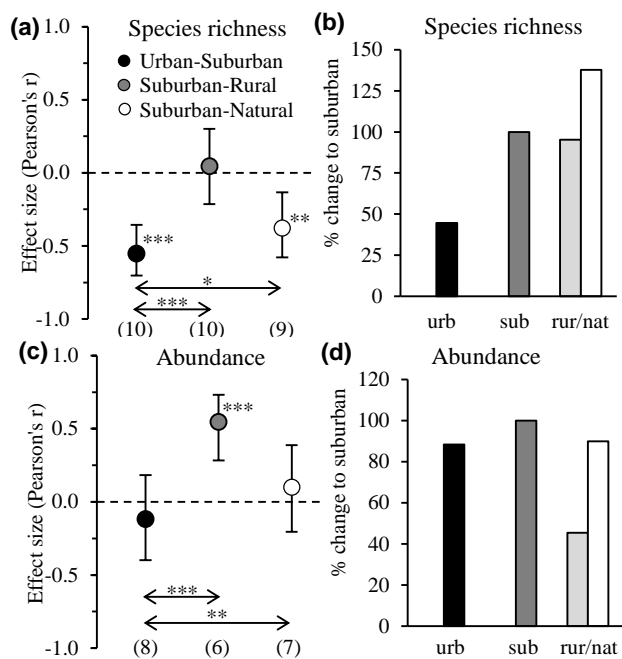
347   **Figure 2.** Effects of urbanisation on (a) species richness and (c) abundance of birds for urban-
348   suburban vs. suburban-rural and urban-suburban vs. suburban-natural comparisons and
349   barplots (b, d) presenting relative change compared to suburban areas set to 100 %. For
350   figures a and c, values shown represent effect size estimates and 95% CIs, and numbers under
351   symbols represent sample size. Asterisks ((*)$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)
352   above effect size symbols denote a significant difference from zero (within-group
353   heterogeneity), whereas those above a horizontal arrow indicate a significant difference
354   between urban-suburban and suburban-rural and urban-suburban vs. suburban-natural

355 comparisons (Table 2). Barplots are based on individual effects (Pearson's *r*) corresponding
356 to the slope of simple regressions. urb: urban, sub: suburban, rur: rural and nat: natural areas.
357

Discussion

359 Our meta-analysis of urbanisation effects showed opposing general trends between bird

360 species richness and abundance, richness decreasing and abundance increasing with

361 increasing urbanisation, although effect size and significance level were lower for the latter.

362 When considering urban-suburban-rural/natural contrasts, the overall richness trend was

363 confirmed in that there was an increasing trend from urban to natural landscapes. However,

364 abundance showed a clear intermediate peak along the urban-rural gradient, although

365 abundance in natural areas was markedly higher than that in rural areas.

366
367   The overall effect sizes indicated that urbanisation affects species diversity (as

368 measured by species richness) negatively, but has a positive effect on bird abundance, which

369 confirms the general finding that overall abundance and biomass of birds typically increases

370 with increasing urbanisation as the number of species declines, with just a few species

371 contributing to the majority of individuals (e.g. Blair, 2004; Cam et al., 2000, Chace & Walsh,

372 2006; Clergeau et al., 2006), although these effects were relatively weak. When accounting

373 for potential non-linearities by assessing urban-suburban, suburban-rural and suburban-

374 natural contrasts, the pattern of decline in species richness with increasing urbanisation was

375 still evident and stronger when natural landscapes were considered. These results therefore

376 support a more-or-less constant negative impact of urbanisation on bird diversity (as per, for

377 example, Clergeau et al., 2001, 2006; Sandström et al., 2006), rather than a peak at

378 intermediate levels of the gradient, which has been commonly assumed (e.g. Marzluff, 2017).

379   In contrast to other studies, however, there was evidence of an intermediate peak in

380 abundance in relation to the urban-rural gradient. This suggests that suburban habitats as

381 defined in this study, whilst supporting fewer species than natural areas and similar number of

species as rural areas, can support a greater abundance of individuals of those species that can

exploit this habitat. There are a number of reasons that may underpin this pattern, which could

include greater energy availability (e.g. through bird feeding – Robb et al., 2008) or reduced

competition or predation (Alberti, 2015). However, considering the whole gradient from

urban to natural habitats (rather than being restricted to the typical urban-rural gradient), it is

evident that abundance in suburban areas is similar to that in natural areas, whereas it is

markedly lower in rural areas (Fig. 2). Given that most rural areas comprise low density

housing within an agricultural matrix, this pattern may also be related to negative impacts of

farming practices on bird communities (e.g. Chamberlain et al. 2000).

Whilst there have been several reviews of bird community composition along

urbanisation gradients, there are very few which have taken a quantitative meta-analytical

approach (Saari et al., 2015), and assumptions about consistent patterns seem to be based

more on qualitative assessments (e.g. Chace & Walsh, 2006; Grimm et al., 2008). Indeed,

Saari et al. (2015), in a multi-taxa meta-analysis of terrestrial animals based on 26 studies,

found weak evidence of negative effects of urbanisation on species richness, and no evidence

of consistent responses of abundance. Clergeau et al. (2001) did find evidence of negative

effects of urbanisation on bird species richness in a meta-analysis of 18 studies, but they did

not consider abundance. Our meta-analysis provides further support to the negative effects of

urbanisation on bird species richness with a much larger sample size (37 studies) using robust

statistical techniques, but it also is the first to provide evidence of a non-linear response of

bird abundance to an urbanisation gradient.

There was no evidence that city size played a role in influencing the relationship

between urbanisation and either species richness or abundance. Whilst other studies have

found relationships between city size and either species richness or abundance (Garaffa et al.,

2009; Gagné et al., 2016), Clergeau et al. (2001) also did not find any association between

bird species richness and human population size, nor urban extent or the bird diversity of

408 adjacent rural habitats. To some extent, these differences may have arisen due to the nature of

409 the sample of cities. Both Garaffa et al. (2009) and Gagné et al. (2016) considered a sample

410 from more restricted geographical areas than our study and that of Clergeau et al. (2001), thus

411 there may have been less influence of large scale biogeographic factors. However, Clergeau et

412 al. (2001) also found that more fine-scaled habitat variables were better determinants of bird

413 communities than landscape-level metrics. Similarly, Evans et al. (2009) concluded based on

414 a literature review that in general, local factors are more important than regional factors in

415 influencing bird communities. Further quantification of finer-scale, local habitat composition

416 would be useful in this respect, although such detailed information is currently available in

417 too few studies to undertake the meta-analysis carried out here.

418   The effect of urbanisation on species differed between different gradient types. The

419 overall negative effect on species richness was especially clear (i.e. strong, negative

420 significant effect) in studies that examined the whole urban to rural gradient, while there was

421 no significant effect in studies which compared two urbanisation categories only. In contrast,

422 there was little evidence that the effect of urbanisation on abundance was influenced by

423 gradient length.

424   There was a decrease in abundance with increasing urbanization in studies where green

425 spaces were included in the sampled landscapes, and an increase in abundance where they

426 were absent. It is possible that generalist and opportunistic species well adapted to urban

427 environments, and thus occurring in high numbers in several cities, could increase their

428 population numbers in heavily developed land-uses (e.g., residential, commercial, industrial)

429 more than in landscapes including green space (Carbó-Ramírez & Zuria, 2011). There was

430 evidence that bird species richness was more negatively impacted by urbanization when green

431 spaces were present. Given that parks have generally been assumed to be of benefit to urban

432 biodiversity (e.g. Nielsen et al., 2014), this result is unexpected. Urban parks are thought to

433 contain most species occurring in cities, but this in itself may be why they might experience a

434   more expressed negative effect of urbanisation in contrast to the urban matrix (Fernández-

435   Juricic & Jokimäki, 2001), i.e. urbanization effects in species rich areas which include green

436   spaces may be more evident than urbanization effects where species richness is already low.

437   Additionally, it should be stressed that these analyses did not test species richness in green

438   spaces *per se* against species richness in the urban matrix. Rather, the comparison was

439   between studies which included green spaces within the sampled landscape and those that did

440   not. Furthermore, a range of public green spaces were included (mostly parks, but also

441   'recreation areas', golf courses and urban woodlands), hence our analyses covers a wide range

442   of green space types. Given these factors, it is not really possible to draw firm conclusions on

443   the value of green space for bird diversity based on these results. Nevertheless, our findings

444   suggest that the value of green spaces to urban bird diversity may be influenced by landscape

445   context. Further dedicated studies are needed to assess the role of urban green spaces on wider

446   avian communities across urban-rural gradients.

447   The majority of the papers analysed did not consider separate groups of species (e.g.

448   defined on the basis of taxonomic relatedness or ecological requirements), but rather used

449   fairly simple measures of species richness and abundance of the whole community. However,

450   bird species vary greatly in the extent to which they exploit urban habitats (e.g. Evans et al.,

451   2010, Sol et al., 2014). In particular, urban habitats often have a higher species richness

452   and/or greater abundance of non-native species (e.g. Sol et al., 2012). The extent to which

453   native and non-native species may have responded differently to the gradients analysed here

454   is impossible to assess (only four papers considered native and exotic species separately), but

455   future gradient studies should invest more effort in measuring responses of different species,

456   especially non-native species.

457   Biodiversity studies on urban-rural gradients typically use land use classifications (i.e.

458   urban, suburban, rural) to assess responses to urbanization, as for the vast majority of studies

459   considered in this paper. This does, however, have some drawbacks. First, category

460   definitions may differ widely from study to study. We have attempted to account for these

461   differences by taking our own (admittedly broad) definitions of land use categories and re-

462   classifying where necessary. In most cases, descriptions were sufficient to achieve this, even

463   when no quantitative information was presented. Second, comparing categories, rather than

464   assessing responses to a continuous gradient, may restrict the ability to detect more subtle

465   non-linear patterns along the length of the gradient, and importantly may be limited in terms

466   of planning urban development where threshold effects of urbanization on bird communities

467   could be identified. Despite our relatively simple classification, it is nonetheless notable that

468   we did detect non-linear effects. Nevertheless, future studies should seek to measure

469   urbanization using clearly defined and continuous measures, or at the very least should

470   provide full quantitative descriptions of any defined land use categories.

471

472   **Conclusions**

473   Urbanisation affects bird species diversity. Though species loss is more marked from

474   suburban to urban than from rural to suburban areas, our results nonetheless suggest that

475   urbanisation exerts a consistent more-or-less negative linear effect on bird species richness.

476   Previous reviews have found that the universality of richness and abundance responses is

477   unclear (Saari et al. 2015). Here, in the most comprehensive quantitative review of birds yet,

478   we find linear responses for richness (which have been less commonly found in literature) and

479   non-linear responses for abundance (which are previously unreported). By examining the

480   whole urban to rural gradient (i.e. long gradients), patterns in species richness are likely to be

481   detected, although this is unclear for bird abundance. Non-linear response of bird

482   communities to urbanisation should be accounted for in the future, preferably by adopting a

483   universally accepted definition of urbanization measured along continuous axes, thus enabling

484   a more precise estimate of its effects, for example to identify threshold values where

485   communities change in order to improve conservation planning for urban development.

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620 **SUPPORTING INFORMATION**

621 **Appendix S1** References of studies included in meta-analyses

622 **Appendix S2** Details of meta-analysis models

623 **Figure S1** PRISMA flow diagram of the literature screening process

624 **Figure S2** Illustration of classification of short and long urbanisation gradients

625 **Figure S3** Funnel plots

626 **Table S1-S2** Lists of observations/studies included in meta-analyses

627 **Table S3** Excluded papers and reasons for exclusions

628 **Table S4-S5** Lists of observations/studies included in subset meta-analyses on non-linear

629 responses