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14 **Non-linearities in bird responses across urbanisation gradients: a meta-analysis**

15

16 **Running head:** Effects of urbanisation on birds

17

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34

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36 systematic review, rural.

37

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39

40 **Author contributions:**

41 PB and KK designed the study with support from MSR and DEC; KK collected and prepared
42 data; PB and KK analysed data; all authors contributed to the writing of the manuscript.

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.

67 **Introduction**

68 Urbanisation is one of the most extreme forms of environmental alteration, posing a major
69 threat to biodiversity and altering fundamental ecosystem services upon which human
70 civilisation depends (Aronson et al., 2014; Sol et al., 2014). The problems caused by
71 urbanisation are diverse. As environmental conditions are significantly altered, natural
72 habitats of many plant and animal species are rapidly reduced and transformed (Grimm et al.,
73 2008). Cities are novel ecosystems, characterised by fragmented environments with a higher
74 level of disturbance than natural habitats and with a strongly altered pattern of resources
75 (Rebele, 1994; Alberti, 2015). However, with the rapid expansion of urban development
76 (Cohen et al., 2006; Seto et al., 2013) and the associated modification of habitats, it is crucial
77 to understand the relationship between biodiversity and urban habitats (Clergeau et al., 1998).

78 Bird abundance and community composition in urban areas have been well described,
79 with the main conclusion that bird community composition becomes increasingly
80 impoverished with urban development, leading to the dominance of a few abundant species
81 (Kelcey & Rheinwald, 2005), and hence resulting in long-term reduction in diversity (Chace
82 & Walsh, 2006; Sol et al., 2014). Researchers have commonly observed lower species
83 richness in urban areas relative to that of the surrounding rural landscapes (Clergeau et al.,
84 2006; Sandström et al., 2006). However, these patterns are by no means universal, and other
85 studies have found a non-linear response, in which areas with intermediate levels of
86 urbanisation exhibit the highest richness (Blair, 1996; Marzluff, 2001; McKinney, 2002;
87 Tratalos et al., 2007), whilst overall bird abundance often increases from rural to urban areas
88 (Chase & Walsh, 2006; Faeth et al., 2011; Njorge et al. 2014), although other studies have
89 found no trend (Chamberlain et al., 2017) or inconsistent responses across different cities
90 (Garaffa et al., 2009; Jokimäki et al., 2002).

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

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

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

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

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

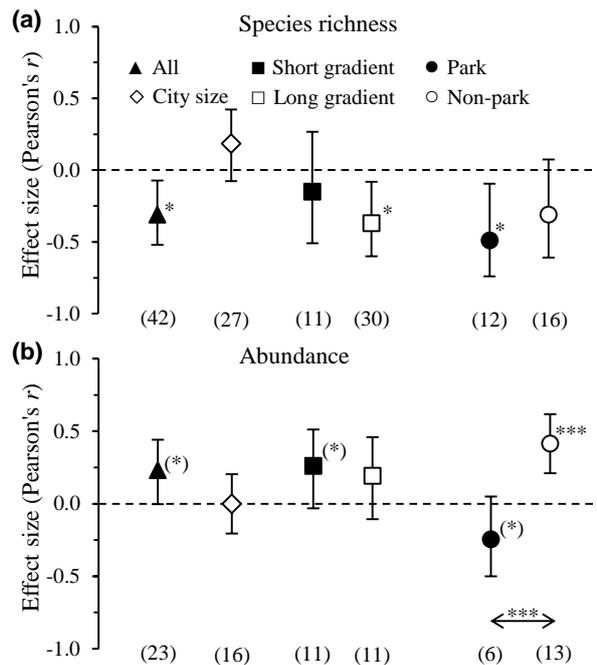
290 **Results**

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

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

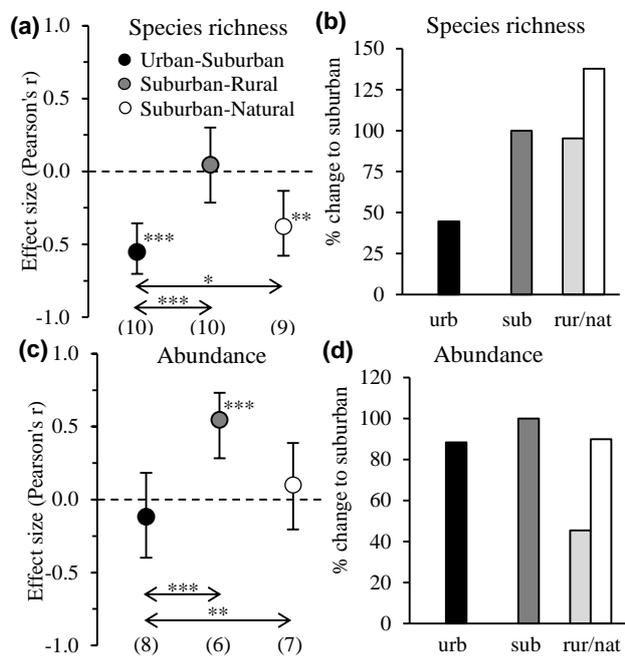
336 areas, and a marked increase from rural to suburban areas (Fig. 2d). Natural areas had similar,
 337 though slightly lower, abundance compared to suburban areas.

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

358 **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

382 species as rural areas, can support a greater abundance of individuals of those species that can
383 exploit this habitat. There are a number of reasons that may underpin this pattern, which could
384 include greater energy availability (e.g. through bird feeding – Robb et al., 2008) or reduced
385 competition or predation (Alberti, 2015). However, considering the whole gradient from
386 urban to natural habitats (rather than being restricted to the typical urban-rural gradient), it is
387 evident that abundance in suburban areas is similar to that in natural areas, whereas it is
388 markedly lower in rural areas (Fig. 2). Given that most rural areas comprise low density
389 housing within an agricultural matrix, this pattern may also be related to negative impacts of
390 farming practices on bird communities (e.g. Chamberlain et al. 2000).

391 Whilst there have been several reviews of bird community composition along
392 urbanisation gradients, there are very few which have taken a quantitative meta-analytical
393 approach (Saari et al., 2015), and assumptions about consistent patterns seem to be based
394 more on qualitative assessments (e.g. Chace & Walsh, 2006; Grimm et al., 2008). Indeed,
395 Saari et al. (2015), in a multi-taxa meta-analysis of terrestrial animals based on 26 studies,
396 found weak evidence of negative effects of urbanisation on species richness, and no evidence
397 of consistent responses of abundance. Clergeau et al. (2001) did find evidence of negative
398 effects of urbanisation on bird species richness in a meta-analysis of 18 studies, but they did
399 not consider abundance. Our meta-analysis provides further support to the negative effects of
400 urbanisation on bird species richness with a much larger sample size (37 studies) using robust
401 statistical techniques, but it also is the first to provide evidence of a non-linear response of
402 bird abundance to an urbanisation gradient.

403 There was no evidence that city size played a role in influencing the relationship
404 between urbanisation and either species richness or abundance. Whilst other studies have
405 found relationships between city size and either species richness or abundance (Garaffa et al.,
406 2009; Gagné et al., 2016), Clergeau et al. (2001) also did not find any association between
407 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.

486

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493

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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