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3 Running title: Urban colonization traits

4 **Urban colonization is driven by a mixture of evolutionarily conserved and**
5 **labile traits**

6 David A. Duchene^{1*}, Carolina Pardo-Diaz², Maider Iglesias-Carrasco¹

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8 ^a*Research School of Biology, Australian National University, ACT 2601, Australia*

9 ^b*Biology Program, Universidad del Rosario, Carrera 24 No.63C-69, Bogotá, 111221*

10 *Colombia*

11

12 *Corresponding author

13 David A. Duchêne

14 Research School of Biology

15 Robertson Building, 46

16 Australian National University

17 Canberra, ACT 2601

18 Australia

19 Telephone: +61 4 12026379

20 Email: david.duchene@anu.edu.au

21

22 **Abstract**

23

24 Urbanization is a fast and dramatic transformation of habitat that generally forces native
25 fauna into novel ecological challenges. The biological prerequisites necessary to establish in
26 urban areas have been widely studied, but the macroevolutionary characteristics of traits that
27 allow urban colonization remain poorly understood. Urban colonization might be facilitated
28 by traits that are evolutionarily conserved and which lead to a diversity of closely related
29 species. Alternatively, urban colonization might be associated with labile traits that
30 frequently arise and are lost. In a large data set from passerine birds, we find that urban
31 colonization has a signal of highly labile traits, despite many traits associated with
32 colonization being highly conserved. Urban colonization is associated with traits that allow
33 faster speciation than non-urban-colonizing counterparts, and more frequently transition to
34 non-urban trait states than in the opposite direction. Overall, the traits that facilitate urban
35 colonization are a mix of highly conserved and labile traits and appear to provide an
36 evolutionarily successful strategy.

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39 **Keywords:** body mass, brain size, anthropic habitats, evolutionary distinctiveness,
40 urbanization.

41 **Introduction**

42

43 Urbanization is one of the most rapid anthropogenic changes to the environment, and can
44 have a dramatic impact on local communities [1,2]. While urbanization is often associated
45 with a loss of biodiversity and of evolutionary distinctiveness [3], a broad range of species
46 have successfully established in these novel environments. Understanding the biological traits
47 that allow urban colonization can be important for predicting the impact of urbanization on
48 biodiversity. In birds, there are several biological predictors of successful urban colonization
49 including lack of plumage dichromatism, large body mass, large brain size, migration ability
50 and broad environmental tolerance [4–8]. Such a collection of traits might impact species
51 survival, leaving a mark across deep evolutionary timescales [9,10]. However, the
52 macroevolutionary trajectory of the complete set of traits in urban-colonizing species remains
53 poorly understood.

54 The macroevolution of traits that facilitate urban colonization is driven primarily by
55 three processes: speciation, extinction, and the transition among species that do not have such
56 traits and those that do. In consequence, the distribution of urban colonizing species in a
57 phylogeny will depend on the rate of each of these processes. One possible scenario is that
58 the transition between traits that do not allow urban colonization and those that do is
59 infrequent in either direction. In such cases, the traits that allow colonization might only
60 occur among closely related species and will be clustered across the phylogeny. Any
61 differences in the current diversity of the urban colonizers versus non-colonizers is then
62 driven by differences in rates of speciation and extinction, and not by the rate of appearance
63 and disappearance of traits. In birds, however, urban colonizers come from a broad range of
64 taxa, suggesting that the rate of transition between traits is actually high [3,11].

65 In another scenario, species might frequently transition between having traits that
66 facilitate urban colonization and those that do not. The speciation and extinction rates of
67 urban colonizers might be similar to those of non-colonizers, but the traits that allow
68 colonization might be frequently gained and lost. If urban colonization is driven by such
69 evolutionarily labile traits, colonizers and non-colonizers will be highly dispersed across their
70 phylogeny. However, there is also evidence against this hypothesis, since many of the traits
71 associated with urban colonization are conserved, such as brain size [11].

72 Alternatively, urban-colonizers and non-colonizers might differ in rates of both
73 diversification (speciation and extinction) and transition. In this case, colonizers and non-
74 colonizers might differ in their pattern of phylogenetic clustering, and several combinations
75 of rates of speciation, extinction and transition can lead to such an observation. One
76 interesting case occurs when transition is high in a single direction (e.g., non-urban colonizer
77 traits to urban-colonizer traits), and the frequently-emerging traits cause an increased rate of
78 extinction by benefitting individuals at the expense of the population. This phenomenon has
79 been termed “evolutionary suicide” [12,13]. Examples of traits that have been proposed to
80 emerge often but reduce the evolutionary success of species include self-compatibility in
81 plants [14] or some forms of specialization [15]. The traits that allow urban colonization
82 might be such an evolutionary “dead-end”, if urban colonization increases the already-high
83 chances of extinction in those species. This hypothesis might explain the loss of evolutionary
84 distinctiveness in urban areas [2] and the lack of phylogenetic clustering in urban colonizers

85 [3], and should appear as a highly dispersed or “tippy” pattern of urban colonizers in their
86 phylogeny [16].

87 Apart from the main three scenarios explained so far, there are other combinations of
88 rates of speciation, extinction, and transition that might govern the macroevolution of current
89 urban-colonizers and non-colonizers. Therefore, to test the pattern associated with urban
90 colonization and whether it is driven by traits that are evolutionarily successful or
91 detrimental, and either conserved or labile, we analyzed published data from passerine birds.
92 We first tested whether urban colonization and three traits previously associated with urban
93 colonization (brain size, body mass, and plumage dichromatism) are phylogenetically
94 dispersed within the passerines. We then used maximum likelihood and simulation
95 approaches to test whether the collection of traits that might have allowed colonization of
96 urban areas are either evolutionarily conserved, or tend to be either labile or even suicidal at a
97 macroevolutionary scale.

98

99 **Methods**

100

101 To gain insight into the types of traits that allow urban colonization, we examined the
102 macroevolutionary features of the species that have successfully colonized urban areas. We
103 gathered information about urban presence/absence [17] of passerine birds, and three traits of
104 species associated with the colonization and establishment of passerines in urban areas: brain
105 size ([4,18], but see [11,19]), body mass [5,8] and plumage dichromatism [8] (see
106 Supplementary Information for data collection).

107 We first tested whether brain size, body mass, plumage dichromatism and urban
108 colonization of the set of species for which the latter variable was available are either
109 taxonomically grouped or randomly dispersed across their phylogeny. Previous studies have
110 already explored the phylogenetic characteristics of brain size, body mass, plumage
111 dichromatism in datasets including large samples of the extant passerine species (e.g., [20]).
112 To explore whether similar patterns are seen only for the set of species for which there are
113 data on presence/absence in urban areas, we ran these analyses on the reduced data set for
114 which all variables were available (brain size, $n = 251$; body mass, $n = 506$; plumage
115 dichromatism, $n = 506$).

116 We first estimated the maximum clade credibility (MCC) phylogenetic tree of a
117 random sample of 1000 time-calibrated trees containing every species of birds [21]. The
118 complete MCC tree was pruned to contain the 506 species of passerine birds for which the
119 other data were available (or 251 species for the dataset in brain size), and was then used for
120 subsequent analyses. We tested whether urban habitat colonization is either significantly
121 phylogenetically clustered or over-dispersed by calculating Fritz and Purvis’ D statistic [22]
122 and comparing that value to 1000 simulations under each of the two null models, using the R
123 package *caper* [23]. Similarly, we tested the hypotheses that the variables of brain size, body
124 mass and plumage dichromatism have phylogenetic signal by testing the significance of
125 Pagel’s λ [24] as implemented in the R package *phytools* [25].

126 To assess whether traits that allow urban colonization are highly labile or even
127 suicidal, we performed two tests of the macroevolution of successfully colonizing species
128 (see [16] for full details on this method): (i) we tested whether colonizing species have had a

129 greater number of evolutionary origins (*NoTO*), and (ii) whether they have a lower number of
130 also-colonizing sister species (*SSCD*) than expected under a null process in which rates of
131 gain and loss of a trait are equal in both directions (as proposed in [16]), using the R package
132 *phylogenetics* [26]. Traits that are likely to be significantly labile or suicidal have values of
133 these metrics that are significantly different from the null, and also have a *D* statistic of
134 phylogenetic clustering indicating a significantly dispersed phylogenetic distribution [16].
135 We performed these analyses assuming that we have an incomplete sample from the
136 passerines ($506 / 5966 = 0.085$).

137 We examined whether the data contained a signal of significant differences in rates of
138 speciation, extinction, or transition between colonizing and non-colonizing species by testing
139 models of binary state-speciation and extinction (BiSSE; [27,28]). The diversification rates in
140 passerine birds are likely to be affected by many factors that are not considered in this study
141 (e.g., [29]). Therefore, we restricted our analyses to testing whether the distinction between
142 colonizers and non-colonizers is superior to more simple models where the distinction is not
143 present. If the primary drivers of diversification rates in passerines are entirely unrelated with
144 the traits associated with urban colonization, the distinction between colonizers and non-
145 colonizers will not be meaningful and lead to similar fit in models of diversification.

146 We tested whether a model in which colonizing and non-colonizing species have
147 different rates of speciation, extinction, and transition (hereafter “full model”), was superior
148 to four alternative models in which colonizing and non-colonizing species have (i) identical
149 speciation rates, (ii) identical extinction rates, (iii) identical transition rates, or (iv) equivalent
150 values for each of these traits across the two groups. The models were corrected for
151 incomplete taxon sampling and likelihood ratio tests were performed comparing the full
152 model and each of these alternative hypotheses. Results were corrected for multiple tests
153 using false discovery rates.

154

155 **Results**

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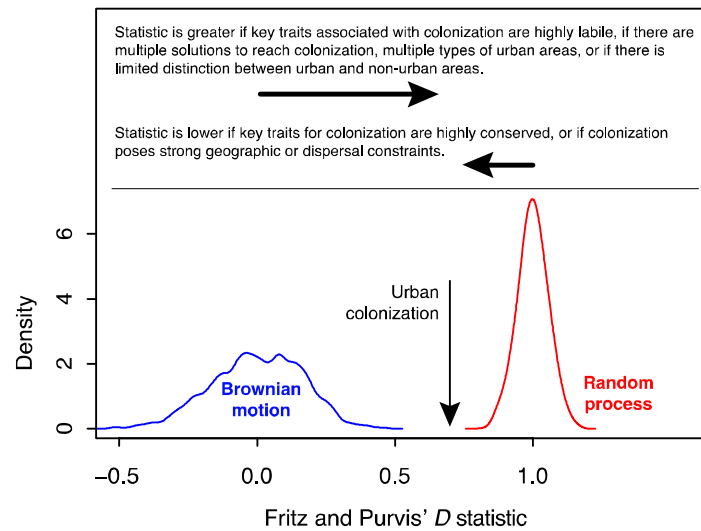
157 We found that in passerine birds there is significant phylogenetic signal in plumage
158 dichromatism ($\lambda = 0.78, p < 0.001$), brain size ($\lambda = 0.88, p < 0.001$), and body mass ($\lambda = 0.88,$
159 $p < 0.001$). Meanwhile, colonization of urban areas is significantly more phylogenetically
160 dispersed than a pattern emerging from Brownian motion. However, it is also significantly
161 more clustered than a random assortment of species across the phylogeny of passerine birds
162 ($D = 0.695, p < 0.001$; Fig. 1). Nonetheless, we find that evolutionary factors associated with
163 urban colonization lead to a greater number of evolutionary origins, and a smaller number of
164 also-colonizing sister taxa than expected under a Brownian motion evolutionary process
165 ($NoTO = 3.35, p < 0.001$; $SSCD = 193.21, p < 0.001$).

166 Tests of BiSSE models showed that the full model, which makes a distinction
167 between urban colonising species and non-colonizers, provided a significantly better fit than
168 models that did not make a distinction between the two groups in terms of their speciation
169 rates ($p < 0.001$), rates of transition ($p = 0.003$), or in all of speciation, extinction, and
170 transition rates ($p < 0.001$; Fig. 1; Table S1). However, the full model was not significantly
171 superior to a model in which the two groups share an identical extinction rate ($p = 0.099$; $\varepsilon =$
172 0.146). In the full model and the more simple model where extinction rates are identical,

173 speciation rates were estimated to be greater in urban colonizing species ($\lambda_U = 0.412$) than in
174 non-colonizing species ($\lambda_N = 0.149$), and the estimated rate of transitions between states was
175 estimated to be greater in the direction from colonizing species to non-colonizers ($q_{UN} =$
176 0.158) than the opposite ($q_{NU} = 0.023$).

177

178 **Figure 1.** Fritz and Purvis' D statistic of phylogenetic clustering for urban colonization
179 (black vertical arrow) as a proxy of the traits that allow this phenomenon. Expected
180 distributions shown are drawn from simulations of the data under an evolutionary processes
181 of Brownian motion (blue) and random change (red). We describe some of the factors that
182 might cause an increase in phylogenetic dispersal versus clustering of traits associated with
183 urban colonization.

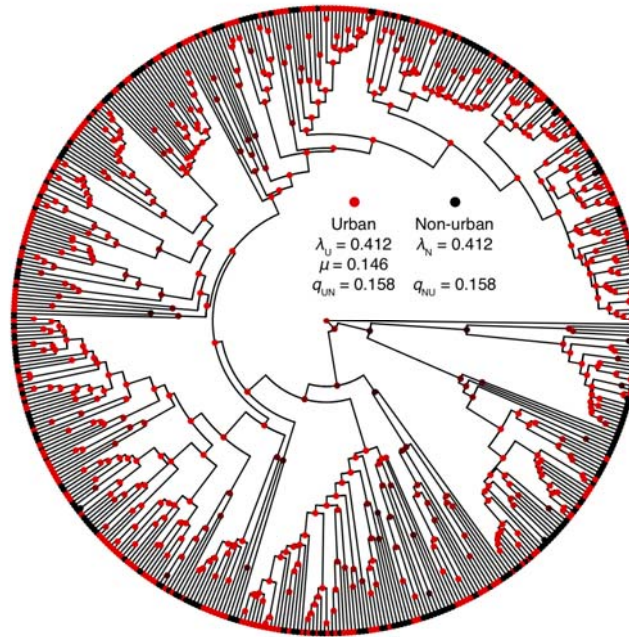


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187 **Figure 2.** Phylogenetic tree of the passerine species sampled showing the positioning of
188 urban colonizers (red) and non-urban colonizers (black). Internal nodels and the statistics
189 shown are drawn from the maximum likelihood estimate of the ancestral states under the
190 BiSSE model. The estimates shown are not intended to represent the model that best
191 describes the processes the drove the diversification of passerine birds.
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Discussion

197 Some collections of traits can influence the chances of species success or demise, so the
198 macroevolutionary history of different groups of traits have been a longstanding matter of
199 interest (e.g., [10,22]). Our data show that rates of transition and speciation might be uneven
200 while extinction rates are similar. This suggests that many of the traits that are associated
201 with urban colonization of species of passerine birds are evolutionarily conserved. However,
202 urban colonizers are not significantly grouped phylogenetically in passerine birds, suggesting
203 that urban colonization is not driven by purely conserved or labile traits. Some of the traits
204 that allow urban colonization are likely to be labile and have frequently been lost in the
205 evolution of passerines. Interestingly, the complete collection of traits has provided a
206 comparatively successful strategy over the traits that occur in non-urban species. Therefore,
207 our data suggest that urban areas are not a sink of biodiversity that accelerates the demise of
208 species with already unfortunate macroevolutionary trajectories.

209 Some of the traits explored here might have direct effects on the elevated rate of
210 speciation in urban-colonizing species. However, this effect occurs in the opposite direction
211 as might be expected, because urban species tend to have large body size and have lower
212 amounts of sexual selection [8], both of which are associated with slower rates of
213 diversification [20,30]. Instead, other features of urban colonizers might have been associated
214 with their relatively high speciation rates. One example is being a dietary generalist, which is

215 strongly associated with diversification rates in birds [20] and is a distinctive feature of urban
216 colonizers [11].

217 Urban colonizers are associated with relatively fast speciation rates and frequent
218 transition towards a different combination of traits. Some successful evolutionary strategies
219 can frequently breakdown and lead to novel diversity. Examples include the common switch
220 from self-incompatibility to the less-successful self-compatibility strategy in the plant family
221 Solanaceae [14], or the frequent switch from bisexuality to the less-successful unisexuality in
222 liverworts [31]. Similarly, generalist taxa sometimes have faster rates of diversification and
223 greater rates of transition to specialization than the opposite direction [15]. In addition to
224 being dietary generalists, urban-colonizing species have been proposed to have broad
225 environmental tolerances [7] and high behavioural flexibility ([4,32] but see [11,19]), which
226 are likely easily lost evolutionarily, yet might provide species with resilience and long term
227 evolutionary success.

228 Our results suggest that urban areas attract species with traits that are robust in
229 macroevolutionary terms, such that cities might serve as a reservoir of biodiversity [33,34].
230 This is consistent with the lack of evidence for poor health in urban taxa [35–37] and the fact
231 that urban species are often in the process of becoming reproductively isolated from non-
232 urban counterparts [33]. The high rate of transition out of the traits that allow urban
233 colonization means that novel diversity arising from urban areas might contain non-urban
234 traits (e.g., strong sexual selection, small body size, specialization). Understanding the
235 medium- and long-term evolutionary trajectories of urban species might aid urban planning
236 in the future, since the predicted increase in urbanization might impact species without
237 suitable traits (e.g., specialist species).

238 While urban areas are associated with the homogenization of biodiversity and the loss
239 of evolutionary distinctiveness, the traits that allow for colonization of these areas do not
240 appear to cause increased extinction rates at a macroevolutionary scale. Since urban
241 colonization is not phylogenetically clustered, it is also likely to be driven by highly labile
242 and common traits. Labile traits that are most likely to contribute to urban colonization might
243 include nesting location [5] or song type [38], while other conserved traits might include
244 feeding habits or brain size [4]. Exploring the macroevolution of traits further on species
245 colonization of novel habitats is likely to bring important insights into species sensitivity to
246 future urbanization.

247

248 **Author contributions**

249

250 DAD, MIC, and CPD conceived the idea, MIC and CPD collected the data, DAD analysed
251 the data, all the authors interpreted the results and helped drafting the manuscript.

252

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254

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257

258 **Conflict of interest**

259

260 The authors declare no conflict of interest

261

262 **Ethics**

263

264 Not applicable

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266 **Data accessibility**

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268 The data used in this project are available at github.com/duchene/urbanSexSel.

269

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