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1 Interspecific conflict structures urban avian assemblages

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7 Land cover change, of which urbanization is a major driver, remains the greatest threat to
8 terrestrial biodiversity. More than half of all people now live in cities spread across 3% of the
9 global terrestrial surface, and this population is predicted to rise to 68% by 2050 (1). Growth
10 in urban land area is concomitantly forecast to triple between 2000 and 2030 to 1.2M km² (2).
11 The growth of cities - anthropogenic biomes - provides particular challenges for biodiversity.
12 Conservation ecologists are now increasingly interested in uncovering the life history
13 attributes, ecological processes, and species-specific behaviors that dictate the structure of
14 these novel urban organismal assemblages (3). In PNAS, Martin & Bonier (4) employ a global
15 dataset of species interactions and proceed to erect and test three alternative hypotheses in
16 which behavioral dominance might directly, or indirectly, influence the occurrence and
17 distribution of urban species.

18 Cities represent a recent and dramatic shift from the historical habitats within which species
19 evolved. The constraints on resource availability, reduction in both habitat diversity and
20 structural complexity tends to lead to the simplification, homogenization and reorganization of
21 biotic communities in urban areas (5). Given their globally ubiquitous nature, relative ease of
22 field identification, and sampling cost-effectiveness, birds have been the taxon of choice for
23 many urban biodiversity studies. Most historical research has focused on patterns of species
24 occupancy in cities in biomes as diverse as the Arctic (6) and the Amazon (7), but such work
25 on patterns is now giving way to progress on understanding processes (8). We now know that
26 urban species tend to have broader environmental tolerance and increased behavioral
27 flexibility, often reflected in larger brain sizes and even altered endocrine responses, and that
28 these selection pressures drive further changes in animal phenotypes and genotypes (9).
29 Competition between species may also limit species occurrence in cities, but has historically
30 received less detailed examination given shortfalls in knowledge of the likely outcomes of
31 species interactions.

32 Constraints on coexistence among competing species may regulate community structure via
33 interspecific resource competition if resources are limited, as may often be the case within
34 Anthropogenic landscapes (10). Such competitive dominance exists when environmental
35 conditions favor one species over another, leading to higher fitness of competitively superior
36 species (11). This competitive dominance does not however always equate to social
37 dominance – dominance arising from consistent aggressive interspecific interactions, as more
38 aggressive species may still be outcompeted by their subordinates. However, social
39 dominance can lead to competitive exclusion and hence narrower realized niches for
40 subordinate species (12). Examining the role of competitive interactions in structuring
41 communities is complicated by the need to assemble a large database of individual aggressive
42 interactions and such behaviors are rarely observed under field conditions. However, it has
43 proven possible to assemble such databases, either by trawling through the academic
44 literature looking for documented interactions (13), and recently through massively crowd-
45 sourced protocol-driven data collection by citizen scientists (14) opening the door to more
46 nuanced studies of the effects of animal behavior on organismal assemblages.

47 In this issue, Martin & Bonier (4) propose three hypotheses in which to examine the impact of
48 species interactions on species co-distributions, considering that cities might represent either
49 an opportunity for some species, or, more frequently, a challenge. Their first hypothesis, the
50 'Subordinate Tolerance hypothesis' posits that subordinate species may be more successful

51 in cities given their exclusion from preferred resources and habitats by dominant species, in
52 effect predisposing them to success in such highly disturbed environments often characterized
53 by low resource availability and high predation pressure. Contrarily, their 'Competitive
54 Interference Hypothesis' (Fig. 1a) expects the monopolization of urban habitats by
55 behaviorally dominant species. These are expected to suppress the abundance of, or entirely
56 exclude co-occurring subordinate species with similar ecologies in sympatry that might
57 otherwise thrive in cities. These subordinate species might occupy urban niches in the
58 absence of their competitors, although the authors also note that such ecological filtering might
59 also lead to a failure of subordinate species to accrue adaptations to urban environments at
60 all. Finally, the 'Dominant Advantage Hypothesis' recognizes that the aggression associated
61 with behavioral dominance may be linked to other traits such as disturbance tolerance,
62 neophilia and boldness – signaling phenotypic plasticity (12) which may predispose dominant
63 species to urban adaptation and hence success in occupying cities.

64 Martin & Bonier (4) set out to test these alternative hypotheses by determining how behavioral
65 dominance might either directly or indirectly influence species occurrence in a global sample
66 of breeding birds in 492 large cities for which inferred dominance relationships among closely
67 related species have been published (Fig. 1b). City level breeding bird status was solicited by
68 regional expert elicitation, with respondents assigning scores of species status in cities from
69 'absent' to 'widespread', giving the authors an index of the degree to which cities represent
70 either an 'opportunity' or a 'challenge' for bird species. In recognizing the urban-rural
71 continuum and that many cities may include substantial areas of 'natural' habitat, they
72 informed their multiple respondents per city to assign urban bird species status away from
73 such natural habitat enclaves. Their species interaction data came from a survey of the
74 literature, with the caveats that some relationships are better established than others.

75 The authors initially uncovered evidence supporting their Competitive Interference Hypothesis
76 (Fig. 1a), with urban-adapted, subordinate species proving to be less widespread in cities than
77 closely-related dominant species in sympatry. This indicating that direct competitive
78 interactions may preclude subordinate species occupancy of cities. However, they also found
79 that this relationship belied substantial geographic variation in responses, with support for the
80 Competitive Interference Hypothesis in Europe, North America and Australia but not in Africa,
81 South America and Asia. To understand why this might be the case, they used Bayesian
82 generalized linear mixed models to explore the role of variation in latitude, climate, economic
83 development, human population size, phylogeny, and sampling biases in agreement with their
84 hypotheses. Of these potential predictors, only the level of economic development proved
85 significant, suggesting that economic development may intensify the impacts of competition
86 on subordinate species, leading to a reduction in avian biodiversity in cities.

87 The Martin & Bonier (4) study does not stretch to unpacking how a rather crude metric such
88 as economic development acts in favor of dominant species by exacerbating the
89 consequences of competition among closely-related species of birds in developed countries.
90 However, they do speculate about three possible pathways. The first is the potential for more
91 marked spatiotemporal clumping of resources in developed countries, especially human
92 handouts at waste treatment facilities. Secondly, there may be reduced control of resources
93 (including habitat) in cities in developing countries leading to higher habitat structural
94 complexity and greater resource availability. Finally, all species in developing countries may
95 exhibit higher mortality rates leading to a reduction in population sizes of dominant species
96 and diminishing opportunities for their competitive exclusion of subordinates species from
97 urban habitats. These are of course not mutually exclusive, and given the broad functional
98 and phylogenetic diversity of the species in the study, then drivers of community collapse in
99 different groups may be highly idiosyncratic. These patterns are amenable to more detailed
100 future analyses that look at species trait distributions which may influence urban persistence
101 (15) and differ between developed and developing countries and co-vary with latitude.
102 Understanding these relationships might also shine a light on another important caveat of the
103 results of (4) in that the authors are unable rule out the potential effect of dominant species

104 restricting subordinates from preferred habitats outside of cities, leading to secondary effects
105 on their distribution within cities.

106 Martin & Bonier (4) focus only on dyadic interactions between congeners, a comparative
107 analysis that permits phylogenetic and spatial breadth, yet interactions between species
108 extend beyond species pairs and interspecific competitive dominance research now seeks to
109 quantify more complex patterns such as dominance hierarchies (14). Network theory analyses
110 may reveal mathematical intransitivities such as the 'rock-paper-scissors relationship' in
111 behavioral ecology (11). In this instance, despite pairwise competitive advantages, no single
112 species can dominate and exclude all others in speciose communities. However,
113 environmental filters operating in urban areas may break these complex relationships - as
114 some species become locally extinct due to a loss of critical resources. Their local extinction
115 may enable others to monopolize resources and exclude remaining functionally similar
116 heterospecifics. Such impacts might be most pronounced in the tropics, where species
117 packing is highest (16) and act to reduce species richness in future as these cities develop.
118 Tropical bird communities are also characterized by a high prevalence of obligate and
119 facultative mixed flock foraging species for which interspecific interactions are characterized
120 by social mutualisms (17). Understanding how this co-dependence may act to dampen the
121 impacts of competition would be a novel research priority. Not also to be ignored is the
122 seasonal influx of migrant species into tropical and subtropical cities; the ranges of 92% of
123 bird species intersect the tropics at some part of their life cycle (16). This intense seasonal
124 pulse of disruptive competition from non-breeding species might also account for geographical
125 differences in the relationships between breeding dominant and subordinate species. Detailed
126 field experiments are needed to provide direct evidence for the causal role of competition in
127 such circumstances (8, 9), including the role of invasive species (18) which could be
128 uncovered through a combination of manipulative and space-for-time swap studies.

129 The models of Martin & Bonier (4) provide insights into the effects of competition in structuring
130 avian assemblages and pose a challenge for policy makers in such complex socio-ecological
131 systems as cities (3). The loss of avian biodiversity services mediated by competitive
132 interactions among species has potentially far-reaching implications for key ecosystem
133 processes, including control of phytophagous and/or disease vectoring insects and for seed
134 dispersal and these losses mirror those seen in the simplification of rural landscapes (10).
135 There is an urgent need to improve urban wildlife habitat in the interstitial spaces between
136 human infrastructure to ameliorate biodiversity loss driven by changes in species interactions
137 which are apparently even more problematic in developed than developing countries (Fig. 1c).
138 Bolder targets (19) and cost-effective strategies (3, 20) are required to drive this restoration
139 forward in urban areas.

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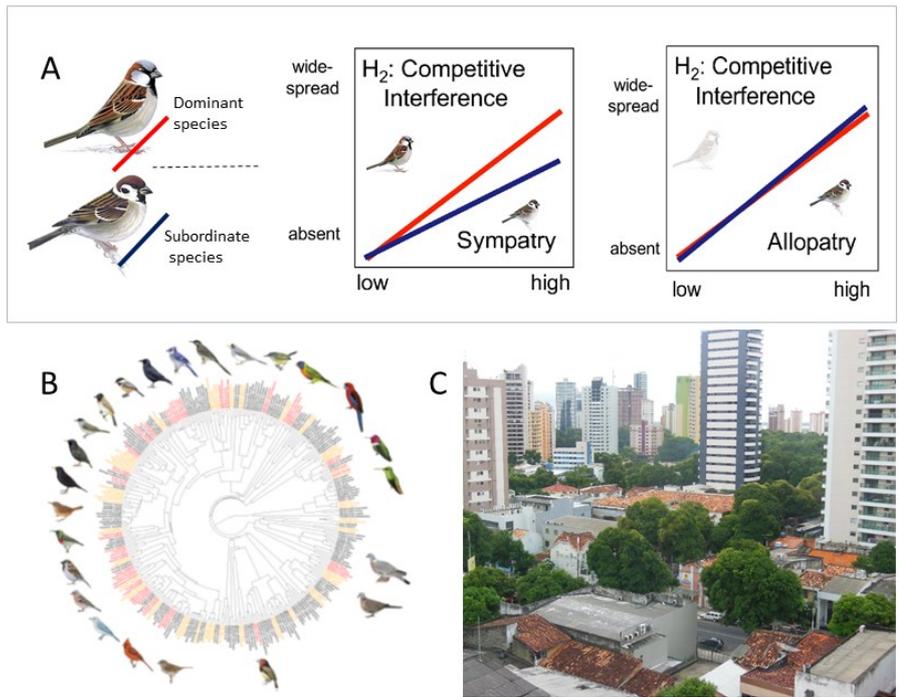
186 Fig. 1. Understanding interspecific dominance competition in urban landscapes a) the
 187 Competitive Interference Hypothesis of Martin & Bonier (4) posits that behaviorally dominant
 188 species e.g. here House Sparrow *Passer domesticus* will suppress the abundance of, or
 189 entirely exclude co-occurring subordinate species such as here Tree Sparrow *Passer*
 190 *montanus* in sympatry that might otherwise thrive in cities. Species pairs included in the study
 191 represented a broad swathe of the avian tree of life (b). Belém an example of a city in a
 192 developing country which still retains wildlife habitat potentially facilitating species co-
 193 existence. A and B are adapted with permission from ref. 5, sparrow vignettes reprinted with
 194 permission from RSPB images; C author's own image.

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200 Figure 1.