

1 **Urbanization alters ecological and evolutionary interactions between Darwin’s finches and**  
2 ***Tribulus cistoides* on the Galápagos Islands**

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RH: Ecology and evolution of urban species interactions

Total word count: Abstract: ; Introduction:; Materials and methods: ; Results: ; Discussion: ;

Acknowledgements: ; Number of tables: ; Number of figures: ; Number of supplements: .

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5 **Abstract**

6 Emerging evidence suggests that urbanization shapes the ecology and evolution of species  
7 interactions. Islands are particularly susceptible to urbanization due to the fragility of their  
8 ecosystems; however, few studies have examined the effects of urbanization on species  
9 interactions on islands. To address this gap, we studied the effects of urbanization on interactions  
10 between Darwin's finches and its key food resource, *Tribulus cistoides*, in three towns on the  
11 Galápagos Islands. We assessed the effects of urbanization on seed and mericarp removal,  
12 mericarp morphology, and finch community composition using natural population surveys,  
13 experimental manipulations, and finch observations. We found that both seed and fruit removal  
14 rates were higher in urban compared to non-urban populations in the natural and experimental  
15 populations, and that urbanization modified selection on mericarp size and defense. Urban  
16 environments supported smaller and less diverse finch communities than non-urban  
17 environments. Together, our results suggest that urbanization can dramatically alter ecological  
18 interactions between Darwin's finches and *T. cistoides*, leading to modified selection on *T.*  
19 *cistoides* populations. Our study demonstrates that urban development on islands can have  
20 profound effects on the ecology and evolution of trophic interactions.

21

22 **Keywords:**

23 Anthropocene; herbivory; Jamaican feverplant, pinzon; plant defense; plant-herbivore, puncture  
24 vine, seed predation; urban evolution

## 25 **1. Introduction**

26 Urbanization results in substantial changes to the environment. Urban habitats are typically  
27 warmer, more polluted, and more fragmented than nearby non-urban habitats, which can lead to  
28 changes in the abundance and persistence of populations, and altered diversity and community  
29 [1–3]. Emerging evidence suggests that ecological changes associated with urbanization may  
30 alter natural selection and drive the evolution of novel adaptations [4,5]. Most examples of  
31 contemporary urban evolution occur in well-established cities, especially in Europe and North  
32 America [4,6]. However, we still have limited knowledge of how urbanization in tropical regions  
33 and particularly on islands can influence the ecology and evolution of species. Islands may be  
34 particularly sensitive to urbanization because of the unique and often fragile ecosystems they  
35 support, and even small human settlements may have large-scale effects on the ecosystem [7].  
36 Our study addresses these gaps using the iconic Darwin’s finch-*Tribulus* interaction of the  
37 Galápagos archipelago.

38 Urbanization can affect both the ecology and evolution of species interactions [8].  
39 Predictions about how interactions will respond to urbanization are complex, especially for  
40 antagonistic interactions [9,10]. Antagonistic (e.g. predator-prey) interactions are inherently  
41 interconnected, and may be susceptible to urbanization through effects on one or both trophic  
42 levels. For instance, urbanization may decouple predator-prey interactions through the addition  
43 of food subsidies from anthropogenic resources [11], or may be intensify interactions when  
44 urban habitat fragmentation reduces available niche space, increasing the frequency of  
45 interactions [12,13]. These changes may lead to novel selection pressures on one or both  
46 interacting species [10]. Despite increasing work on species interactions in urban environments,

47 it remains unclear how urbanization simultaneously shapes both the ecology and evolution of  
48 these interactions.

49 The Galápagos Islands of Ecuador provide an ideal system to test questions about how  
50 urbanization affects the ecology and evolution of species interactions on islands. Ground finches  
51 and *Tribulus cistoides* L. (Zygophyllaceae, common names puncture vine or Jamaican  
52 feverplant)) on the Galápagos have a long history of study [19–21], and it is clear that these  
53 species are experiencing a dynamic and ongoing co-evolutionary arms-race [17]. When resources  
54 are scarce during the dry season, *T. cistoides* is an important food resource for three medium and  
55 large beaked ground finch species: *Geospiza fortis*, *G. magnirostris*, and *G. conirostris* [18–20].  
56 Predation on *T. cistoides* has led niche segregation and evolutionary changes in beak morphology  
57 in these finch species [21–23]. In turn, finches influence mericarp survival, and select for  
58 smaller, harder, and more defended mericarps [17]. Urbanization on the Galápagos Islands  
59 influences both finches and *T. cistoides* populations [24–28]. Humans are one of the primary  
60 dispersers of *T. cistoides* on the Galápagos [27], and urbanization reduces resource partitioning  
61 through selection on beak morphology in *G. fortis* [25,29], likely due to the increased availability  
62 of human food [25] and urban-induced behaviour modifications [30].

63 Despite clear evidence of the impacts of urbanization on ground finches and *T. cistoides*  
64 individually, no work has examined the effects of urbanization on interactions between these  
65 species. Our objective was to understand the effects of urbanization on the ecology and evolution  
66 of interactions between ground finches and *T. cistoides*. We studied seed removal rates, selection  
67 on mericarp morphology, and ground finch community composition on three islands on the  
68 Galápagos archipelagos (figure 1). We used this system to ask three questions: 1) Does seed  
69 removal by finches differ between urban and non-urban populations of *T. cistoides*? 2) Does

70 urbanization alter selection imposed by seed removal on mericarp size and defense? 3) Does the  
71 abundance and community structure of Galápagos finch populations differ between urban and  
72 non-urban sites, and how might this relate to patterns of seed removal and selection? Here, we  
73 aim to identify the joint effects of how urbanization affects the ecology and evolution of  
74 antagonistic species interactions in a fragile island ecosystem.

## 75 **2. Methods**

### 76 **a) Study site and system**

77 We studied seed and fruit removal rates, selection on mericarp morphology, and finch  
78 community composition on three islands on the Galápagos archipelagos: Floreana, Isabela, and  
79 Santa Cruz. We selected these locations because both large beaked ground finches and *T.*  
80 *cistoides* are common in and around the towns. We have described our study site and study  
81 system in detail in the supplemental methods.

### 82 **b) Study design**

83 This study was comprised of three components: a survey of natural populations of *T. cistoides* to  
84 estimate seed removal rates; an experiment with mericarp defense traits artificially manipulated  
85 to measure mericarp removal; and ground finch community observations. We studied each of  
86 these components at the end of the dry season from January-March 2018 in urban and non-urban  
87 locations on each of the three islands. For each component described below, we considered a  
88 population to be urban if it occurred within a town's borders.

#### 89 *Natural population survey*

90 To test for differences in seed removal rates and selection among urban and non-urban  
91 populations, we conducted a survey of seed removal in natural *T. cistoides* populations in  
92 February 2018. Natural populations provided us with a picture of natural variation in seed

93 removal between urban and non-urban habitats across islands over 8-12 months because  
94 mericarps are produced in the wet season, and typically persist for many months until  
95 germinating or decaying the following wet season [31]. We sampled 16 populations on Floreana  
96 ( $N = 9$  urban and 7 non-urban), 28 populations on Isabela ( $N = 15$  urban and 13 non-urban), and  
97 41 populations on Santa Cruz ( $N = 22$  urban and 19 non-urban). We collected 20 mericarps from  
98 each population (except for one population where we only found 19 mericarps), for a total of  
99 1,699 mericarps. We counted the number of seeds eaten from each mericarp to estimate seed  
100 removal rate. Following a modified protocol outlined in Carvajal et al. [17], we measured six  
101 size and defense traits on each mericarp: mericarp length, width, depth, the length of the longest  
102 spine, presence or absence of lower spines, and spine position (figure 1d).

### 103 *Fruit removal experiment*

104 At the same time as the natural population surveys, we conducted a six week-long experiment to  
105 test for variation in fruit removal rates and selection in *T. cistoides*. This experiment  
106 complemented our natural population surveys by allowing us to causally determine how  
107 morphology affects removal and natural selection on mericarps by finches. However, the shorter-  
108 term nature of the experiment meant that mericarp removal rates provided a shorter window of  
109 predation pressure. We collected 800-900 intact mericarps (i.e. not attacked by finches) from  
110 non-urban populations on each island. We weighed the mericarps and measured the same six  
111 morphological traits measured in the natural population survey (figure 1d). We selected 20 urban  
112 and 20 non-urban populations per island ( $N = 40$  populations per island) and placed a petri dish  
113 (100 mm diameter) in each population. Each dish contained 20 mericarps placed on top of  
114 locally collected substrate (i.e. volcanic sand and gravel) for a total of 2,120 mericarps. We  
115 randomly selected half of the mericarps and used wire cutters to clip off all of their spines to

116 create an “undefended” mericarp, while the other half were left with their spines intact as  
117 “defended” mericarps. Although *T. cistoides* exhibits natural variation in spine number [17,18],  
118 we selected mericarps that had four spines so that our manipulation simulated mericarps with  
119 four (defended) versus zero (undefended) spines. We marked each mericarp with a unique  
120 identifier on its dorsal surface using a black sharpie marker so that we could identify each  
121 individual mericarp at the conclusion of the experiment.

122 We left the mericarps in the field for six weeks, and then collected them to score removal.  
123 Using the identifying marks placed on the mericarps, we determined which mericarps had been  
124 removed and which remained in the tray. If a mericarp was removed, we counted it as “eaten”  
125 because ground finches often carry mericarps away from the location where they collect them to  
126 crack them on a hard surface. We also counted the number of seeds removed from each mericarp  
127 that was recovered, but the number of recovered mericarps with seeds was too small for analysis  
128 (< 1% of the total sample), so our analyses focused on the removal rate. We carefully placed  
129 petri dishes in locations where humans would not walk, thus we are confident that mericarp  
130 removal was due to finch consumption and not human dispersal [27]. Some petri dishes were  
131 disturbed during the experiment (three on Floreana, six on Isabela, eight on Santa Cruz), and  
132 these petri dishes were excluded from the analyses.

### 133 *Finch community observations*

134 To determine how ground finch community composition varies with urban development, we  
135 conducted surveys at urban and non-urban *T. cistoides* natural populations on each island. We  
136 selected six sites per island ( $N = 3$  urban and 3 non-urban) ensuring that each site had clear lines  
137 of sight within 50 m of the center of the population. We surveyed each location for five minutes  
138 and recorded finch sightings within 50 m during that time. Although *G. fortis* and *G.*

139 *magnirostris* are the only vertebrate seed predators of *T. cistoides* seeds on the islands we studied  
140 [17], we recorded all finch species that frequently interact with *G. fortis* and *G. magnirostris* and  
141 thus could influence their distribution, abundance, or behavior. We repeated the surveys four  
142 times on Santa Cruz and three times on Floreana and Isabela.

### 143 c) Statistical analyses

144 We used R v 3.6.2 [32] for all analyses, details about the statistical analyses can be found in the  
145 supplemental materials and methods. The R code and data files can be found in the supplemental  
146 materials.

## 147 3. Results

### 148 a) Natural population survey

149 There were effects of urbanization, mericarp size, and defense on seed removal rate in *T.*  
150 *cistoides* populations (Table S2). The number of seeds eaten per mericarp was 1.25% higher in  
151 urban populations than in non-urban (*Urbanization*:  $\chi^2_1 = 3.91$ ,  $p = 0.048$ ). More seeds were  
152 eaten from small mericarps (*Size*:  $\chi^2_1 = 10.74$ ,  $p < 0.001$ ), but on average seed removal was  
153 greater in urban populations than from non-urban population (*Urbanization*  $\times$  *Size*:  $\chi^2_1 = 4.51$ ,  $p$   
154  $= 0.034$ ; figure 2a), suggesting seed removal imposed stronger selection for large mericarps in  
155 urban populations. There was no main effects of island or mericarp defense, however the effect  
156 of both size and defense differed among islands (*Island*  $\times$  *Size*:  $\chi^2_2 = 8.89$ ,  $p = 0.012$ ; *Island*  $\times$   
157 *Defense*:  $\chi^2_2 = 6.69$ ,  $p = 0.035$ ), consistent with selection on these traits varying among islands.

### 158 b) Fruit removal experiment

159 Mericarp removal during our experiment was influenced by urbanization and defense traits  
160 (Table S2). Mericarp removal rate was 43% higher in urban populations (*Urbanization*:  $\chi^2_1 =$



161 4.98,  $p = 0.026$ ), and 39% higher on clipped (undefended) mericarps (*Clipped*:  $\chi^2_1 = 8.44$ ,  $p =$   
162 0.004), although this effect did not vary with urbanization (*Urbanization*  $\times$  *Clipped*:  $\chi^2_1 = 0.05$ ,  
163  $p = 0.823$ ).

164 However, urbanization interacted with natural variation in mericarp defenses  
165 (*Urbanization*  $\times$  *Defense*:  $\chi^2_1 = 4.24$ ,  $p = 0.039$ ). Well-defended mericarps were removed more  
166 often from urban populations compared to non-urban populations (figure 2b), suggesting that  
167 fruit removal by finches imposes selection for poorly defended mericarps in urban populations.  
168 In contrast, mericarps that were poorly defended experienced a higher removal rate in non-urban  
169 populations than in urban populations, indicating that the defensive function of spines switched  
170 between urban and non-urban habitats (figure 2b). To better understand which traits were  
171 causing this effect, we ran additional analyses that included individual defense traits as  
172 covariates, instead of the composite defense trait (supplemental methods). We found that  
173 mericarps with longer spines were more likely to be removed in urban populations than non-  
174 urban populations (*Urbanization*  $\times$  *Spine length*:  $\chi^2_1 = 4.95$ ,  $p = 0.027$ ; Table S2), but no effect  
175 of lower spine or spine position.

### 176 c) **Finch community composition**

177 We observed five species of ground finches across sites: two *G. magnirostris*, 171 *G. fortis*, 268  
178 *G. fuliginosa*, 54 *G. scandens*, and 11 *Platyspiza crassirostris*. We found no change in the total  
179 or relative abundances of *G. fortis* in the finch communities among urban and non-urban sites  
180 (*Urbanization*:  $\chi^2_1 = 1.10$ ,  $p = 0.294$ ) or among islands (*Islands*:  $\chi^2_2 = 1.22$ ,  $p = 0.544$ ). We were  
181 unable to evaluate differences in abundance of *G. magnirostris* among populations because only  
182 two individuals were observed.

183           The effect of urbanization on the abundance and diversity of the finch community  
184 differed among islands (abundance: *Urbanization* × *Island*:  $\chi^2_1 = 6.94$ ,  $p = 0.031$ ; diversity:  
185 *Urbanization* × *Island*:  $\chi^2_1 = 8.591$ ,  $p = 0.001$ ; Table S3). Finches were 55% and 18% more  
186 abundant in non-urban locations relative to urban populations on Isabela and Santa Cruz,  
187 respectively, whereas there was no difference in abundance between urban and non-urban  
188 locations on Floreana. We observed a similar trend for diversity (Table S3).

#### 189 **4. Discussion**

190 We found that urban environments modify the ecology and evolution of interactions between  
191 Darwin's finches and *T. cistoides*. We measured the effect of urbanization on these interactions  
192 using a combination of natural population surveys, field experiments, and finch community  
193 observations. Seed and fruit removal rates were higher in urban populations in both natural and  
194 experimental populations (Q1), and urbanization modified selection on mericarp morphology  
195 (Q2). In natural populations, seed removal imposed stronger selection for large mericarps in  
196 urban populations than in non-urban populations, while in experimental populations, fruit  
197 removal imposed selection for poorly defended mericarps in urban populations. Lastly, while we  
198 found no difference in the abundance of *G. fortis* and *G. magnirostris*, urban environments  
199 supported smaller and less diverse ground finch communities than non-urban environments (Q3).  
200 Together, our results suggest urbanization can dramatically alter ecological interactions between  
201 finches and *T. cistoides*, leading to modified selection on *T. cistoides* populations.

##### 202 **a) Mericarp predation in urban environments**

203 We observed direct effects of urbanization on seed and mericarp removal. We found that  
204 removal was higher in urban populations than in non-urban populations in both the natural and  
205 experimental populations. Increased mericarp removal in urban habitats is consistent with the

206 hypothesis that urbanization intensifies interactions between finches and *T. cistoides*. These  
207 interactions may have been intensified because *T. cistoides* is more abundant in urban areas on  
208 the Galápagos islands (MTJJ and RAJ, personal observation). Humans are the primary dispersers  
209 of *T. cistoides* on the Galápagos [27] and *T. cistoides* populations are most likely to be  
210 established in and around towns. If ground finches exhibit a functional response to *T. cistoides*,  
211 then their consumption of *T. cistoides* seeds may be correlated with the plant's abundance in a  
212 habitat [33]. Such a functional response would explain why urban *T. cistoides* populations  
213 experienced greater predation pressure from foraging finches, despite lower finch abundances in  
214 these environments.

#### 215 **b) Selection on mericarp morphology**

216 We found that urbanization alters selection on mericarp morphology. In urban environments,  
217 consumption by finches imposed selection for large but poorly defended mericarps. In the natural  
218 populations, we observed higher seed removal from small mericarps in urban and non-urban  
219 habitats, but this effect was strongest in urban populations. Small mericarps may be more  
220 energetically efficient to open [22,34], leading finches to choose small mericarps over large ones.  
221 Combined with greater abundances of *T. cistoides* in urban areas, preferential consumption of  
222 small mericarps may intensify selection for large mericarps in urban areas. Our results contrast  
223 with a previous study which found that finches impose selection for smaller mericarps in natural  
224 populations of *T. cistoides* [17]. The differences in findings may be the result of yearly variation  
225 in climate that contributes to differences in resource availability. We conducted our study at the  
226 end of the dry season following a relatively dry year, but annual variation in precipitation can  
227 lead to differences in resource availability [35], and thus differences in the intensity of mericarp  
228 consumption by finches. Repeating this study across wet and dry years would help separate out

229 the effects of urbanization from those of climate on the evolutionary ecology of interactions  
230 between Darwin's finches and *T. cistoides*.

231 In the experimental populations, we observed increased removal of well-defended  
232 mericarps from urban populations, whereas in non-urban populations we observed greater  
233 removal of mericarps with fewer defences. This result suggests the surprising result that  
234 urbanization is associated with finches preferring better defended mericarps. It is presently  
235 unclear why urbanization modifies the direction of selection on mericarp defense. Mericarp  
236 spines are expected to deter predators from accessing the seeds, an expectation that is consistent  
237 with our findings from the non-urban populations and those from Carvajal et al. [17]. However,  
238 we found that finches preferred mericarps with longer spines in urban populations. Finches may  
239 prefer mericarps with longer spines because they were easier to pick up and manipulate.  
240 Alternatively, longer spines can facilitate dispersal by humans [27], but we deliberately placed  
241 the dishes in locations where humans were unlikely to disturb them so that mericarp removal  
242 would be the result of finch consumption. Further experiments that include finch observations at  
243 each experimental site are needed to distinguish between these possibilities.

244 While our study of natural populations was complementary to our experiments, these two  
245 components of our study also differed in several important ways. First, natural populations were  
246 available to finches for a longer period of time than the experimental populations, leading to  
247 variation in seed removal unrelated to mericarp morphology. Natural populations may have been  
248 more likely to experience seed removal because the finches would already have known where to  
249 find them. In contrast, finches had to first locate the novel experimental populations before  
250 removing the mericarps. Second, because they were exposed longer, the natural populations  
251 experienced a greater range of climatic variation, potentially affecting the strength of selection

252 they experienced [35]. Lastly, we were able to track how many seeds were removed from each  
253 mericarp in the natural populations, but not from the experimental populations. Seed removal  
254 gives a more precise estimate of the fitness effects experienced by the plants and could have  
255 resulted in different patterns of selection than mericarp removal.

#### 256 **c) Urban finch communities**

257 Differences in the urban and non-urban ground finch communities may have contributed to  
258 patterns of predation and selection on *T. cistoides*. Finch abundance differed between urban and  
259 non-urban sites, although the direction of this difference varied among islands. We observed  
260 lower abundance and diversity in urban sites than in non-urban sites on Santa Cruz and Isabela,  
261 the largest two islands. This result is consistent with many other studies that find that bird  
262 communities are often negatively affected by urbanization (reviewed in [8]). In contrast, there  
263 were no significant differences in abundance or diversity between urban and non-urban sites on  
264 Floreana, the smallest island, suggesting that town size might play a role in shaping finch  
265 communities. Our study tracked how consumption by finches affects the ecology and evolution  
266 of *T. cistoides*. To determine if an evolutionary response of *T. cistoides* populations feeds back to  
267 affect the ecology or evolution of finches, studies that combine yearly resampling to track  
268 changes in mericarp morphology, beak shape and finch behaviour through time would be  
269 necessary.

#### 270 **d) Conclusion**

271 Together, our results suggest that urbanization modifies the ecology and evolution of interactions  
272 between finches and *T. cistoides*. Our study examined the effects of urbanization in an island  
273 ecosystem, which are predicted to be particularly sensitive to disturbance. Because of this  
274 fragility, perturbations to the landscape through human development and the introduction of

275 invasive species may have large-scale effects on the ecology and evolution of native island  
276 species [7]. Our study suggests that urbanization alters the evolutionary ecology of species on  
277 islands and identifies trophic interactions as a key mediator of species interactions in the urban  
278 island ecosystem.  
279

280 **Data accessibility.** Data and code are included in the supplementary material and will be  
281 submitted to the Dryad Digital Repository once accepted for publication.

282 **Authors' Contribution.** MTJJ and RAJ designed the study and questions, MTJJ, RAJ, and JAC  
283 set up the experiment and/or applied for permits, and MTJJ and RAJ collected the data. LRR  
284 conducted the analyses and wrote the manuscript, with input from all authors.

285 **Competing interests.** We declare we have no competing interests

286 **Funding.** L.R.R. was funded by a Queen Elizabeth II Graduate Scholarship in Science and  
287 Technology, M.T.J.J. was funded by a NSERC Discovery Grant, CRC Tier II and Steacie  
288 Fellowship, and J.A.C. was funded by the Galapagos Science Center POA Grant and COCIBA  
289 Grant Universidad San Francisco de Quito.

290 **Acknowledgements.** We thank the Galapagos National Park for permission and facilitation of  
291 our research, and the Charles Darwin Foundation for accommodation and for permitting us to  
292 conduct research on their property. C. Richter, M. Johnson, and O. Johnson for help with  
293 collecting mericarps and recording data, and D. Reyes and S. Carvajal-Endara for donating data  
294 from six natural non-urban populations on Isabela. We thank D. Reyes, and members of the  
295 EvoEco Lab for feedback on the manuscript.

296

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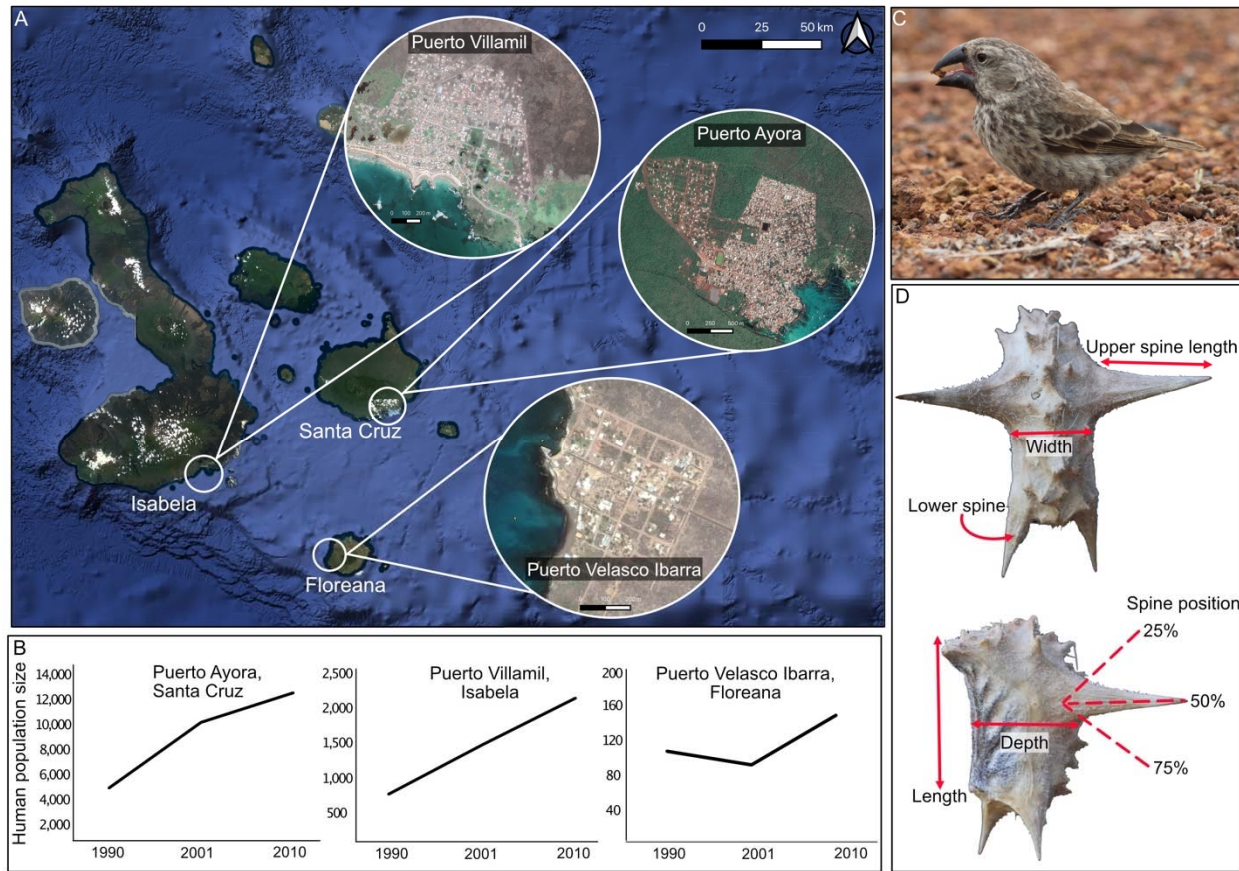
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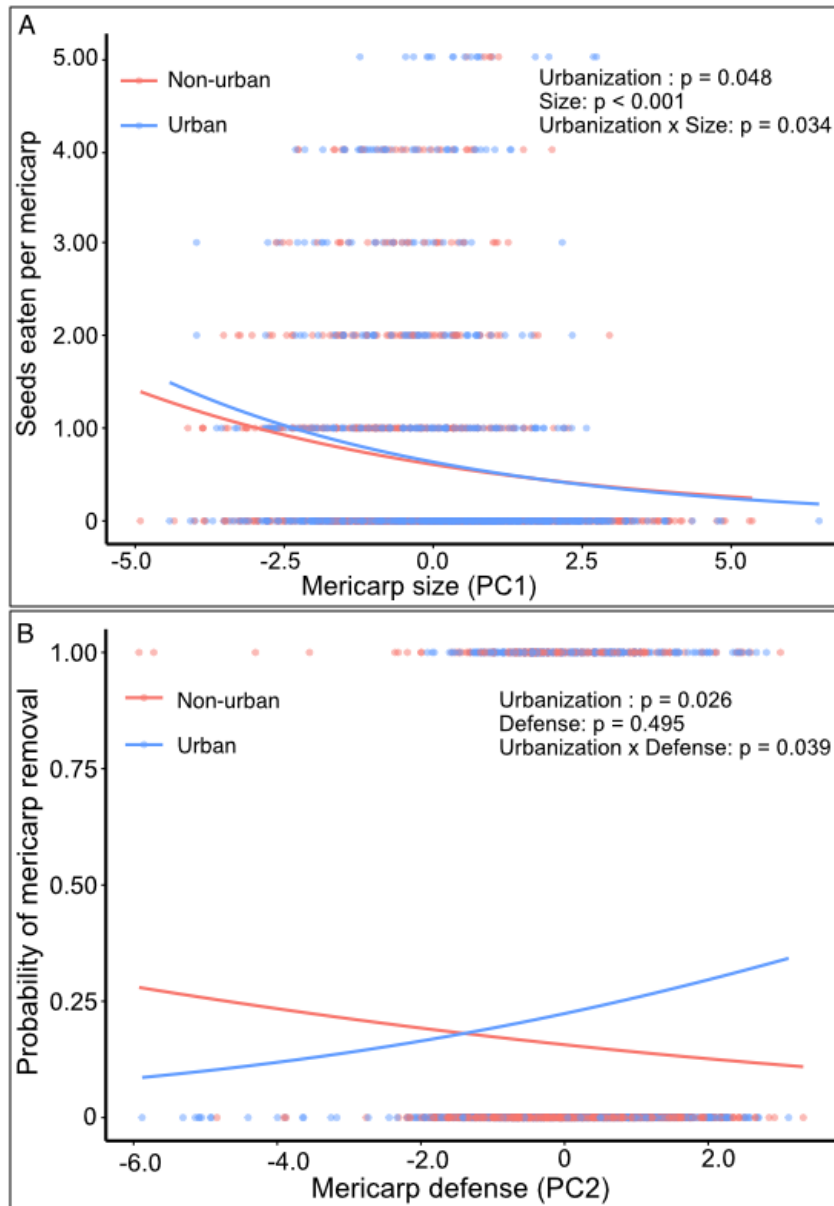
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386 **Figures**



387  
388 Figure 1. a) Map of the Galápagos Islands, with the three islands sampled and their principle  
389 towns. Maps were taken from Google Satellite dating from 2018. B) Change in population size  
390 in each town from 1990-2010 [41], ordered from largest (Santa Cruz) to smallest (Floreana);  
391 note, the human population has continued to grow rapidly but censuses are carried out only every  
392 10 years. c) A female medium ground finch (*Geospiza fortis*) holding a *Tribulus cistoides*  
393 mericarp in its beak. d) Dorsal and lateral images of a *T. cistoides* mericarp, with each of the six  
394 morphological traits measured. All images taken by MTJJ.



395

396 Figure 2. Seed and fruit removal by finches in natural and experimental populations of *Tribulus*  
397 *cistoides*. a) The number of seeds eaten per mericarp declined with cumulative mericarp size  
398 (PC1) in natural populations of *T. cistoides*, with small mericarps being eaten more in urban  
399 areas than in non-urban areas. b) The probability of mericarp removal from experimental  
400 populations increased with mericarp defense (PC2) in urban populations but declined in non-  
401 urban populations.