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1 **Eco-evolutionary dynamics of interference competition**

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37 **Abstract**

38 Theorists have identified several mechanisms through which species that compete exploitatively  
39 for resources could coexist. By contrast, under current theory, interference competitors could  
40 coexist only in rare circumstances. Yet, some types of interference competition, such as  
41 interspecific territoriality, are common. This mismatch between theory and nature inspired us to  
42 model interference competition in an eco-evolutionary framework. We based the model on the  
43 life cycle of territorial birds, and ran simulations to examine whether natural selection could  
44 rescue a superior interference competitor from extinction without driving a superior exploitative  
45 competitor extinct. We found that coexistence between interference competitors can occur over a  
46 wide range of ecological plausible scenarios, and up to the highest levels of resource overlap. An  
47 important caveat is that coexistence requires the species to coevolve. Reductions in population  
48 size and levels of genetic variation could destabilize coexistence between interference  
49 competitors, and thereby increase extinction rates over current estimates.

50 **Introduction**

51 The term “competition” encompasses two rather distinct categories of ecological interactions.  
52 Exploitative competition occurs indirectly through depletion of a shared, limiting resource  
53 (Krebs 2001). Interference competition is any costly interaction between individuals over access  
54 to a resource, aside from resource depletion itself, regardless of whether the resource is shared or  
55 limiting (Krebs 2001). Aggression and allelopathy are probably the most common types of  
56 interference competition in animals and plants, respectively (Inderjit *et al.* 2011; Meiners *et al.*  
57 2012; Grether *et al.* 2013). Interference competition occurs in microbes as well, through stabbing  
58 or poisoning of neighboring cells (Cordero & Datta 2016; Ghoul & Mitri 2016; García-Bayona  
59 & Comstock 2018). Competition of any kind could prevent species from coexisting, but the  
60 ecological literature is replete with models showing, collectively, that species that compete  
61 exploitatively can coexist under a variety of circumstances (Chesson 2000; HilleRisLambers *et*  
62 *al.* 2012). A consistent theme emerging from these models is the central role of trade-offs  
63 facilitating coexistence. By contrast, there have been very few attempts to incorporate  
64 interference competition into coexistence theory. Case & Gilpin (1974) added interference  
65 competition parameters to Lotka-Volterra competition equations and showed that coexistence  
66 between interference competitors is theoretically possible, but they did not clarify the  
67 circumstances under which this might occur. Using a mechanistic model, Vance (1984) showed  
68 that a superior interference competitor can drive a superior exploitative competitor extinct, and  
69 that the starting population densities can determine which species prevails. For coexistence to  
70 occur, interference competition has to be strong enough to override the superior exploitative  
71 competitor’s advantage, and yet each species has to reduce its own resource encounter rate much  
72 more than the other species’ (Vance 1984), which seems rather improbable (there appear to be no

73 documented empirical examples). Based on a two-consumer model with explicit resource  
74 dynamics, Amarasekare (2002) concluded that coexistence cannot occur under interference  
75 competition, even when one species is a superior exploitative competitor and the other is a  
76 superior interference competitor, unless the superior interference competitor also consumes or  
77 parasitizes the other species. Thus, species engaging only in costly forms of interference  
78 competition, such as interspecific territoriality and allelopathy, were predicted to not be able to  
79 coexist (Amarasekare 2002).

80        Yet, costly forms of interference competition are common in nature, as ecologists have long  
81 been aware (Darwin 1859; Case & Gilpin 1974; Diamond 1978; Schoener 1983; Dobson 1985).  
82 For example, nearly a third of all 322 species of passerine birds that breed in North America  
83 defend territories against one or more other species (Drury *et al.* 2020), and roughly half of the  
84 sympatric sister species in this clade are interspecifically territorial (Cowen *et al.* 2020; Drury *et*  
85 *al.* 2020). Ordinarily, mismatches between theory and nature would inspire theorists to question  
86 the assumptions of their models and seek ways to bring them more closely in line with reality,  
87 but that has yet to occur for interference competition. Empirical research on this subject has  
88 continued advancing, largely in a vacuum of formal theory (Grether *et al.* 2009, 2013, 2017;  
89 Peiman & Robinson 2010; Freshwater *et al.* 2014; Martin & Ghalambor 2014; Tobias *et al.*  
90 2014). For example, interspecific aggression appears to cause some species of rodents to  
91 partition resources in ways that enable them to coexist (Ziv & Kotler 2003; Levy *et al.* 2011;  
92 Pasch *et al.* 2013). As another example, interspecifically territorial birds and damselflies show  
93 clear evidence of having evolved in response to each other (Tobias *et al.* 2014; Drury *et al.* 2020;  
94 Grether *et al.* 2020; McEachin *et al.* 2021), which indicates that they have been in contact for  
95 many generations.

96 Different types of interference competition probably have different effects on coexistence.  
97 Recent theoretical and empirical advances have established that allelopathy might actually  
98 promote coexistence in plants (Hierro & Callaway 2021). Here we focus on interspecific  
99 territoriality between phenotypically similar species. This effectively narrows the scope to  
100 animals, but within animals, territoriality is common in many taxonomic groups, including  
101 insects, crustaceans, gastropods, fishes, amphibians, reptiles, birds, and mammals. Territoriality  
102 is a form of social dominance in which the resident individual has priority of access to resources  
103 or mates at a particular location. One important but often overlooked feature of interspecific  
104 territoriality is that it reduces interspecific exploitative competition by reducing spatial overlap.  
105 It is a mutually costly interaction only in the sense that the population mean fitness of both  
106 species would be higher in the other species' absence (Grether *et al.* 2017). At the individual  
107 level, territoriality has winners and losers, with the interaction rarely being symmetrical between  
108 species (Martin *et al.* 2017).

109 Asymmetries in interference competition should be able to mediate trade-offs that promote  
110 coexistence between resource competitors. For example, if species 1 can profitably exclude  
111 species 2 from high-suitability habitat patches, but species 2 is a superior exploitative competitor  
112 that can persist in habitat patches too low in suitability to support species 1, it follows that there  
113 must be a region of parameter space within which the species can coexist indefinitely. This is  
114 essentially the situation hypothesized to enable pied flycatchers and collared flycatchers to  
115 coexist in a mosaic of deciduous and coniferous forest (Qvarnström *et al.* 2009; Veen *et al.*  
116 2010). However, our goal was not to evaluate whether interspecifically territorial species could  
117 coexist in some static region of parameter space, but instead to determine whether species could  
118 evolve into that parameter space, under realistic conditions, and remain there indefinitely. More

119 specifically, we sought to determine whether a superior interference competitor could be rescued  
120 from extinction by agonistic character displacement, without driving a superior exploitative  
121 competitor extinct. Agonistic character displacement (ACD) can be defined as phenotypic  
122 evolution caused by interspecific interference competition (Grether *et al.* 2009). ACD can cause  
123 species to diverge or converge in competitor recognition and the traits used to recognize  
124 competitors, depending on whether recognizing individuals of other species as competitors is  
125 adaptive (i.e., increases an individual's fitness) (Grether *et al.* 2009). If our hypothetical species  
126 came into secondary contact and were similar enough phenotypically to recognize each other as  
127 competitors but were not actually in competition for limiting resources, they would be expected  
128 to diverge in competitor recognition until interference competition was eliminated. If instead the  
129 species overlapped substantially in resource use, interspecific territoriality might be adaptive for  
130 species 1 (the superior interference competitor) but not for species 2 (the superior exploitative  
131 competitor), in which case species 1 would be under selection to converge while species 2 was  
132 under selection to diverge, potentially resulting in species 1 chasing species 2 through  
133 evolutionary time. Could species 1 converge rapidly enough to avoid extinction, and if so, would  
134 species 2 go extinct, or would the species' population sizes stabilize in a type of coevolutionary  
135 stalemate or zero-sum game?

136 To determine what is theoretically possible while staying within the bounds of biological  
137 realism, we constructed an individual-based eco-evolutionary model based on the life cycle of  
138 territorial passerine birds, with survivorship and reproductive parameters from the published  
139 literature on pied and collared flycatchers (Qvarnström *et al.* 2009; Veen *et al.* 2010). In  
140 secondary contact simulations, we varied the level of dietary overlap, the proportions of high-  
141 and low-suitability habitat, the mean difference between the species in territorial fighting ability,

142 and the initial level of phenotypic divergence, to examine how these factors influence  
143 community composition over evolutionary timescales. The results show that ACD can indeed  
144 rescue a superior interference competitor from extinction without driving the other species  
145 extinct, but also that other outcomes are possible, depending on the parameter settings and  
146 chance events (e.g., mutation and genetic drift).

147

## 148 **Material and methods**

149 **The model.** Here we provide a conceptual overview; a detailed mathematical description of the  
150 model is provided in the Supporting Information. Interference competition is mechanistically  
151 explicit in the model, but exploitative competition is modeled implicitly. The exploited resources  
152 could represent any entity, the depletion of which reduces recruitment to the next generation. For  
153 *Ficedula* flycatchers, there is evidence that nest cavities are the key limiting resource (von  
154 Haartman 1956; Vallin *et al.* 2012), but for generality we consider the limiting resource to be  
155 food. Territory competition and reproduction occur during an annual breeding season. The  
156 breeding habitat is divided into discrete territories. If more than one breeding pair of the same  
157 species occupies a territory, the pairs compete exploitatively for food to feed their nestlings,  
158 which reduces nestling survival. If breeding pairs of different species occupy the same territory,  
159 they compete exploitatively in proportion to the level of dietary overlap between the species. To  
160 represent ecologically relevant trade-offs, baseline nestling survival is higher in species 2 than in  
161 species 1. We assume a spatially heterogeneous habitat in which territories vary in suitability.  
162 Due to selection on habitat preferences in the evolutionary past (not modeled), individuals only  
163 accept territories that exceed a suitability threshold, with species 1's suitability threshold higher



164 than species 2's. Thus, some territories serve as refuge for species 2, free from interspecific  
165 competition.

166 Territoriality is governed by four polygenic male traits: a phenotypic cue ( $z$ ) that is visible  
167 or audible from a distance (e.g., a prominent color patch), the central location ( $\mu$ ) and width ( $\sigma$ )  
168 of a Gaussian recognition function (Okamoto & Grether 2013), and a fighting ability state  
169 variable. As the sender's value of  $z$  approaches the receiver's value of  $\mu$ , the probability that the  
170 receiver recognizes the sender as a competitor increases. The width of the function ( $\sigma$ )  
171 determines how close the sender's value of  $z$  must be to the receiver's value of  $\mu$  for a given  
172 probability of recognition.

173 Territory settlement occurs at the start of each annual breeding season. Males of both  
174 species preferentially settle in unoccupied, high-suitability territories. Once the high-suitability  
175 territories are occupied, males of species 2 settle in unoccupied refuge territories. Any males still  
176 without territories enter occupied territories and encounter residents. If neither male recognizes  
177 the other as a competitor, they both stay. If one male recognizes the other as a competitor, they  
178 fight, one male wins, the other male leaves, and the fighting ability of both males is reduced by  
179 the same absolute amount. Residents have no inherent advantage over intruders. The probability  
180 of the male with higher fighting ability winning increases asymptotically with the difference  
181 between them in fighting ability. Males without a territory keep trying to acquire one until the  
182 territory settlement period ends. Then females arrive and pair up (monogamously) with  
183 conspecific territory holders. Individuals that fail to secure breeding territories remain unmated  
184 and do not compete with breeders. The fighting ability of surviving males is replenished between  
185 breeding seasons.

186 By setting the baseline nestling survival of species 2 higher than that of species 1, we made  
187 species 2 the superior exploitative competitor. In the absence of interference territoriality, species  
188 2 would out-reproduce species 1. If the species overlapped much in diet, species 2's population  
189 would grow at the expense of species 1's population, and thus species 1 would be driven to  
190 extinction.

191 To make species 1 the superior interference competitor, we set its baseline fighting ability  
192 higher than that of species 2. With large differences between the species in fighting ability,  
193 species 1 is always favored to win interspecific fights, but with smaller differences, a male of  
194 species 1 that declined in fighting ability due to prior fights could be favored to lose.

195 The model captures key trade-offs that have been hypothesized to enable pied and collared  
196 flycatchers to coexist (Qvarnström *et al.* 2009; Veen *et al.* 2010). Species 1 represents collared  
197 flycatchers, species 2 represents pied flycatchers, and the habitat suitability threshold represents  
198 the ratio of deciduous to coniferous trees (which is related to food availability). However, our  
199 model is not meant to match the flycatcher system in every detail. Also, we varied parameters  
200 that are not known to vary in that system, for the purposes of reaching general conclusions about  
201 systems in which similar trade-offs might occur.

202

203 **Model implementation.** We built the model on the sPEGG (simulating Phenotypic Evolution on  
204 General Purpose Graphics Processing Units) modeling framework (Okamoto & Amarasekare  
205 2018). sPEGG is a library of open-source code for explicitly tracking the survival, reproduction  
206 and genotypes of individuals, with customizable modules for mutation, recombination,  
207 migration, gene flow, etc. Individual-level processes (birth, death, behaviour, inheritance,  
208 development) were characterized as realizations of stochastic processes. We customized sPEGG

209 for the life cycle and reproductive biology of passerine birds and added modules simulating  
210 habitat selection and territoriality.

211

212 **Allopatric period and secondary contact.** For the first 1000 generations (years) of each  
213 simulation, populations of the two species breed in different communities with identical habitats.  
214 Initially, both species are genetically homogeneous. As genetic variation builds gradually  
215 through mutation and recombination, the species evolve to their respective optima for  $\sigma$  and  
216 degrees of separation between  $z$  and  $\mu$ , and population sizes stabilize. The first generation is  
217 highly territorial because  $z$  equals  $\mu$  within species, but if territoriality proved maladaptive, traits  
218  $z$  and  $\mu$  would diverge from each other until the probability of males recognizing conspecific  
219 males as competitors was negligible. Thus, intraspecific territoriality is not assumed by the  
220 model, and would be lost if selection opposed it. It is even possible to have interspecific  
221 territoriality without intraspecific territoriality, if one species' mean value of  $\mu$  diverged from its  
222 mean value of  $z$  and in doing so converged on the other species' mean value of  $z$ , although it is  
223 difficult to imagine a scenario in which selection would favor that outcome.

224 With the model parameterized with estimates of clutch size, nestling survival, and adult  
225 survival from the published literature on pied and collared flycatchers (Table S1), intraspecific  
226 territoriality is adaptive for both species, albeit more strongly so for species 1 than species 2,  
227 because species 1's baseline nestling survival is lower, and thus the fitness consequences of not  
228 being territorial are more severe for species 1. Starting in the 1001<sup>st</sup> year, individuals move from  
229 one community to the other between breeding seasons, with a probability of 0.5, which brings  
230 the species into contact. Simulations ran for 10001 years in total.

231

232 **Parameter sets, model output, and outcome classifications.** We varied dietary overlap (27  
233 levels), the fraction of refuge territories (14 levels), the species difference in fighting ability (6  
234 levels), and the initial phenotypic difference between the species in traits  $z$  and  $\mu$  (2 levels), in a  
235 fully factorial design, for a total of 4536 parameter sets. Each parameter set was run multiple  
236 times (mean  $\pm$  s.d. =  $13.5 \pm 1.6$ ) with different random seeds (61386 simulations in total).  
237 Parameter settings remained constant for the duration of a simulation. The model recorded the  
238 species, sex, age, phenotypes, and nestling survival of all individuals in selected years.

239 We considered the ecological outcome to be “coexistence” if both species persisted until the  
240 end of the simulation (9000 years). R scripts were used to classify the evolutionary outcome  
241 based on changes in the population means of  $z$  and  $\mu$  (see Figs. S1-S7). We restricted the  
242 evolutionary outcome classifications to simulations in which both species persisted  $> 999$  years  
243 because distinguishing between some alternative outcomes (e.g., unilateral divergence versus  
244 chasing) can be difficult over shorter time periods, especially in regions of parameter space  
245 where both outcomes are possible. Further information on the evolutionary outcome  
246 classifications is provided in the Supporting Information.

247 Forking, defined as one species’ mean values of  $z$  and  $\mu$  being on opposite sides of the other  
248 species’ mean values of  $z$  and  $\mu$ , occurred in 1584 (2.6%) of the simulations. The usual cause  
249 was that  $z_2$  and  $\mu_2$  separated somewhat during the allopatric period and were on opposite sides of  
250  $z_1$  and  $\mu_1$  when contact occurred (Fig. S8). We do not consider forking to be a plausible outcome  
251 in nature and therefore re-ran simulations in which forking occurred, using different random  
252 seeds.

253

254 **Results**

255 When the species were evenly matched in fighting ability, coexistence occurred only at relatively  
256 low levels of dietary overlap, and if one species prevailed, it was always the superior exploitative  
257 competitor (Fig. 1). Coexistence became progressively less likely as the fraction of the habitat  
258 where the superior exploitative competitor could breed without interference from the other  
259 species (henceforth, refuge habitat) increased (Fig. 1, upper left). In the region of parameter  
260 space where coexistence occurred, one or both species diverged from the other in competitor  
261 recognition until interspecific interference competition was eliminated (Fig. 1, lower left; Figs.  
262 S1-S3).

263 The eco-evolutionary picture changed rather dramatically when the inferior exploitative  
264 competitor was a superior interference competitor. The zone in parameter space where the  
265 species coexisted was substantially larger, but also, at the lowest fractions of refuge habitat, the  
266 superior exploitative competitor was likely to go extinct, especially when dietary overlap was  
267 high (Fig. 1, upper right). This was true even when the species difference in fighting ability was  
268 quite small (Fig. S9, upper right). As the species difference in fighting ability increased,  
269 coexistence became possible even with 100% dietary overlap and up to a refuge habitat fraction  
270 of 0.85 (Fig. 1, upper right). When dietary overlap was high, the superior interference competitor  
271 evaded competitive exclusion by chasing the superior exploitative competitor through  
272 evolutionary time (Fig. 1, lower right; Figs. S4, S11, S12). As the difference between the species  
273 in fighting ability increased, the level of dietary overlap at which the evolutionary dynamics  
274 switched from divergence to chasing progressively decreased (Figs. S11 and S12).

275 Unexpectedly, the relationship between the probability of coexistence and dietary overlap  
276 was U-shaped when the species differed in fighting ability (Figs. 2, Fig. S15). The rarity of  
277 coexistence at intermediate levels of dietary overlap arose from the high rate of extinction of the

278 superior interference competitor (Fig. S17), except at the lowest fractions of refuge habitat,  
279 where the superior exploitative competitor was at greater risk of extinction (Fig. S19). To clarify  
280 why coexistence occurred more often at high than intermediate levels of dietary overlap, we  
281 examined all cases in which both species persisted for at least 1000 years after contact. This  
282 revealed that extinction at intermediate levels of dietary overlap usually occurred while the  
283 superior interference competitor was chasing the superior exploitative competitor (Fig. S13; for  
284 examples, see Figs. S5 and S6). Evidently, selection on the superior interference competitor to  
285 recognize the superior exploitative competitor was not strong enough at intermediate levels of  
286 dietary overlap to maintain interspecific territoriality and forestall competitive exclusion.

287       The phenotypic similarity of the species at the time of secondary contact influenced the  
288 outcome in predictable ways. In the simulations summarized in Figs. 1 and 2, the species were  
289 initially 1 s.d. apart in the trait used for competitor recognition ( $z$ ), which corresponds to a  
290 heterospecific recognition probability of 0.85. Comparable results with an initial phenotypic  
291 difference of 2 s.d. and heterospecific recognition probability of 0.25 are shown in Figs. S10,  
292 S12 and S16. The lower probability of heterospecific recognition resulted in a broader zone in  
293 which the species always coexisted when they were evenly matched in fighting ability (Figs. S10  
294 and S16, upper left), but coexistence was less likely to occur at high levels of dietary overlap  
295 when the species differed in fighting ability (Figs. S10 and S16). Intuitively, it makes sense that  
296 the superior interference competitor would be at a disadvantage if it has to close a larger  
297 phenotypic gap to recognize heterospecifics consistently.

298       Indeed, when dietary overlap was high, the probability of coexistence was strongly,  
299 positively affected by whether heterospecifics recognized each other as competitors in the last  
300 years of contact during the simulations (Fig. 3). When the superior interference competitor failed

301 to converge rapidly enough to maintain a high probability of heterospecific recognition, it  
302 usually went extinct. The heterospecific recognition probability required to prevent competitive  
303 exclusion of the superior interference competitor decreased as the fraction of refuge habitat  
304 decreased and as the species difference in fighting ability increased (Fig. 3). However, at the  
305 lowest fraction of refuge habitat, the positive effect of heterospecific recognition on coexistence  
306 disappeared when the species differed greatly in fighting ability, because in this situation the  
307 superior exploitative competitor was at risk of extinction (Fig. 3, bottom panels).

308

### 309 **Discussion**

310 Our overall conclusion is that species that engage in costly forms of interference competition can  
311 coexist (or at least co-occur for thousands of generations) under biologically realistic conditions.  
312 Furthermore, coevolution allows interference competition to actually stabilize coexistence. An  
313 important corollary is that factors that impede natural selection could destabilize coexistence,  
314 resulting in extinction. Many species today have declining population sizes, increasing levels of  
315 inbreeding, and decreasing heterozygosity due to habitat loss and fragmentation (Andersen *et al.*  
316 2004; Keyghobadi 2007; Aguilar *et al.* 2008; Allentoft & O'Brien 2010). While it is generally  
317 understood that genetically depauperate species might fail to adapt when the environment  
318 changes (Feiner *et al.* 2021), our model shows that species engaging in interference competition  
319 could especially be in peril, even if the abiotic environment stays the same. Taking both  
320 interference competition and selection into account would likely to lead to better predictions  
321 about the effects of climate change and other anthropogenic disturbances on species ranges and  
322 biodiversity.

323 Our eco-evolutionary model also validates the original, interspecific Red Queen hypothesis,  
324 proposed nearly 50 years ago to explain a striking pattern in the fossil record. In most groups of  
325 organisms, the probability of extinction is independent of a taxon's age and effectively constant  
326 for millions of years (with the exception of mass extinction events) (Van Valen 1973). Van  
327 Valen (1973) deduced that the most plausible explanation for this pattern is that competing  
328 species can only increase in fitness by evolving at each other's expense, resulting in a zero-sum  
329 game in which none of the coevolving species increases in fitness in the long term. In other  
330 words, species have to keep evolving just to stay in the same "place" with their competitors. Van  
331 Valen formulated the Red Queen as a group selection hypothesis, but our simulations show the  
332 zero-sum game emerging from selection at the individual level, which puts the hypothesis on a  
333 solid theoretical foundation.

334 Our modeling approach applies to most, but not all, forms of interspecific territoriality. In our  
335 model, individuals have a single competitor recognition function that determines how they  
336 respond to both species. This is realistic for closely related species like *Ficedula* flycatchers  
337 (Nadachowska-Brzyska *et al.* 2013), because interspecific territorial aggression at the time of  
338 secondary contact would almost certainly result from homology in the phenotypic traits and  
339 neural templates used to recognize conspecifics (Grether 2011). Most cases of interspecific  
340 territoriality in birds do involve phenotypically and genetically similar species, but there are  
341 some well-documented cases involving phenotypically distinct species from different families  
342 (Drury *et al.* 2020). Modeling heterospecific recognition between such distantly related species  
343 would probably require two separate competitor recognition functions (i.e., one for conspecifics  
344 and the other for heterospecifics). It would be unrealistic, however, to assume species possess  
345 recognition functions for other species they have yet to encounter. Innate recognition of



346 phenotypically dissimilar species likely evolves in sympatry. Modeling the *de novo* evolution of  
347 heterospecific recognition may require integrating neural network models with explicitly genetic  
348 models of selection (Strand, E., Huse, G., & Giske 2002; Watson & Szathmáry 2016).

349 We refer to the resource that individuals compete for exploitatively in our model as food, but  
350 the results likely hold for any depletable limiting resources to which territory holders have  
351 priority of access. In *Ficedula* flycatchers, nest sites may be the key limiting resource (Slagsvold  
352 1978; Gustafsson 1987). Interspecific competition for food occurs during the nestling period in  
353 other cavity nesting birds (reviewed by Dhondt 2012), but *Ficedula* flycatchers have relatively  
354 small territories and frequently forage elsewhere (von Haartman 1956; Rybinski *et al.* 2016).  
355 While the most intensively studied *Ficedula* populations are provided with nest boxes, natural  
356 tree cavities vary in size and other characteristics that affect their suitability and accessibility to  
357 nest predators (Walankiewicz *et al.* 2007). Males with larger territories and more nest sites may  
358 have a higher probability of attracting a mate (or multiple mates; Alatalo *et al.* 1986; Dale &  
359 Slagsvold 1996), and with more nest sites to choose from, a lower probability of nest failure.  
360 Thus, for this study system, the model parameter that determines the relative strength of  
361 interspecific exploitative competition could be called “similarity in nest site requirements”  
362 instead of “dietary overlap”. Pied and collared flycatchers evidently have very similar nest site  
363 requirements, and collared flycatchers are dominant over pied flycatchers (Qvarnström *et al.*  
364 2010; Vallin *et al.* 2012), which suggests this species pair’s position in parameter space is the  
365 far-right side of the right-hand panels in figure 1, where coexistence is precarious, which species  
366 is at risk of extinction depends on the availability of refuge habitat for pied flycatchers, and when  
367 the species do coexist, they are locked in a coevolutionary stalemate.

368 We have shown that agonistic character displacement (ACD) can rescue a superior  
369 interference competitor from extinction, without driving a superior exploitative competitor  
370 extinct, in theory. Whether ACD enables interference competitors to coexist in nature is a  
371 different question. An alternative hypothesis is that learned competitor recognition somehow  
372 enables coexistence. Competitor recognition often involves learning (Grether 2011), as the  
373 following examples illustrate. There is experimental evidence that territorial damselfish learn to  
374 distinguish between competitors and non-competitors by observing feeding habits (Losey 1982).  
375 After Daphne Major was colonized by the large ground finch, the territorial songs of two smaller  
376 Darwin's finches shifted away from that of the larger competitor, apparently due to an imprinting  
377 bias (Grant & Grant 2010). Imprinting also appears to be how ants distinguish colony mates from  
378 intruders based on cuticular hydrocarbon profiles (reviewed in Grether 2011). However, in many  
379 situations, learning would be an inefficient and error-prone way to develop the ability to  
380 distinguish competitors from non-competitors (Grether *et al.* 2013, 2017). Many species overlap  
381 in resource use, but compete weakly. Individuals that innately distinguished competitors from  
382 non-competitors would have a selective advantage over those that had to learn which species to  
383 challenge or ignore. Whether damselfish have to learn which species to attack by watching them  
384 forage has not been established; the learning experiment was performed with a species  
385 damselfish do not encounter in the wild (Losey 1982). The song shift in Darwin's finches was  
386 also in response to a novel species, and whether it was effective in reducing aggression from that  
387 species is unknown (Grant & Grant 2010). In ants, innate recognition would not work because  
388 cuticular hydrocarbon profiles depend on a colony's diet, which changes over time (Leonhardt *et*  
389 *al.* 2007).

390 If learned competitor recognition and innate competitor recognition were different strategies  
391 in an evolutionary model based on territorial birds, we think innate competitor recognition would  
392 prevail. To be sure, how an individual responds to other species is probably a product of both  
393 innate biases and learning. For example, the territorial calls of crested and Thekla larks converge  
394 in syntopy, presumably because of learning, and this may facilitate defense of interspecific  
395 territories, but the birds also recognize each other's allopatric calls (Laiolo 2012, 2013). Learning  
396 could facilitate coexistence if it allowed a superior interference competitor's recognition function  
397 to track changes in a superior exploitative competitor's phenotype. But learning could also  
398 increase the probability of competitive exclusion if it enabled a superior exploitative competitor  
399 to avoid interspecific encounters. Thus, while we have shown in this paper that learning is not  
400 required for interspecific territoriality to stabilize coexistence, learning likely affects the outcome  
401 in nature. Incorporating learning into individual-based eco-evolutionary models is an important  
402 challenge for future research (Romero-Mujalli *et al.* 2019).

403

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410

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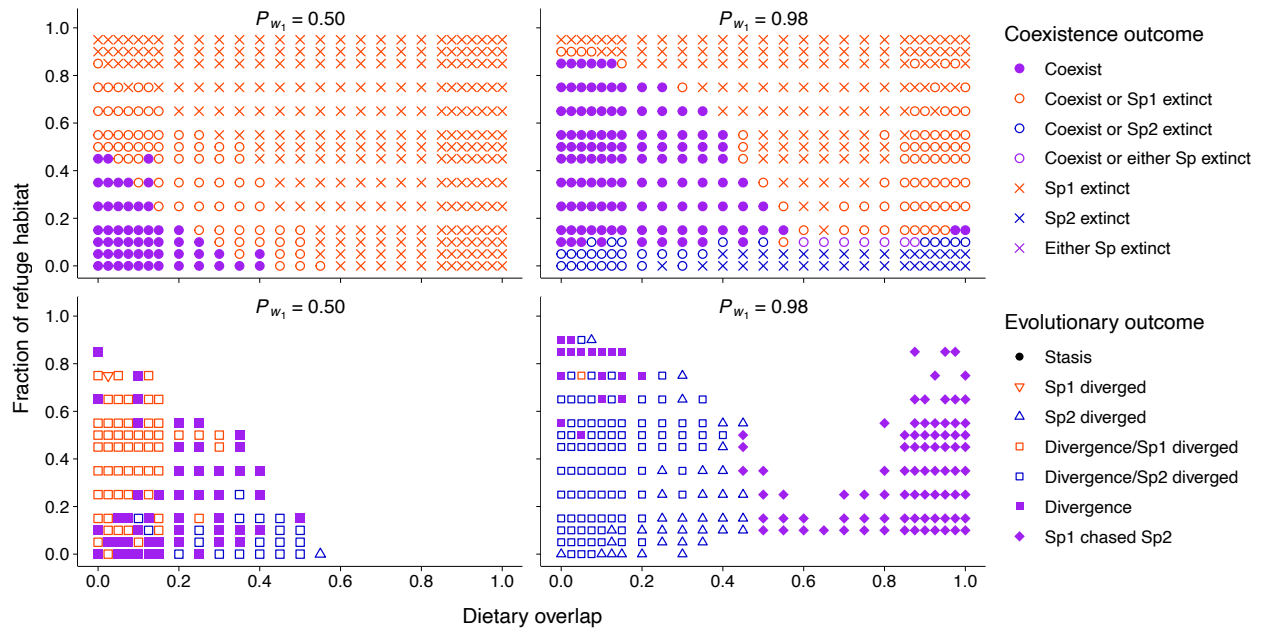
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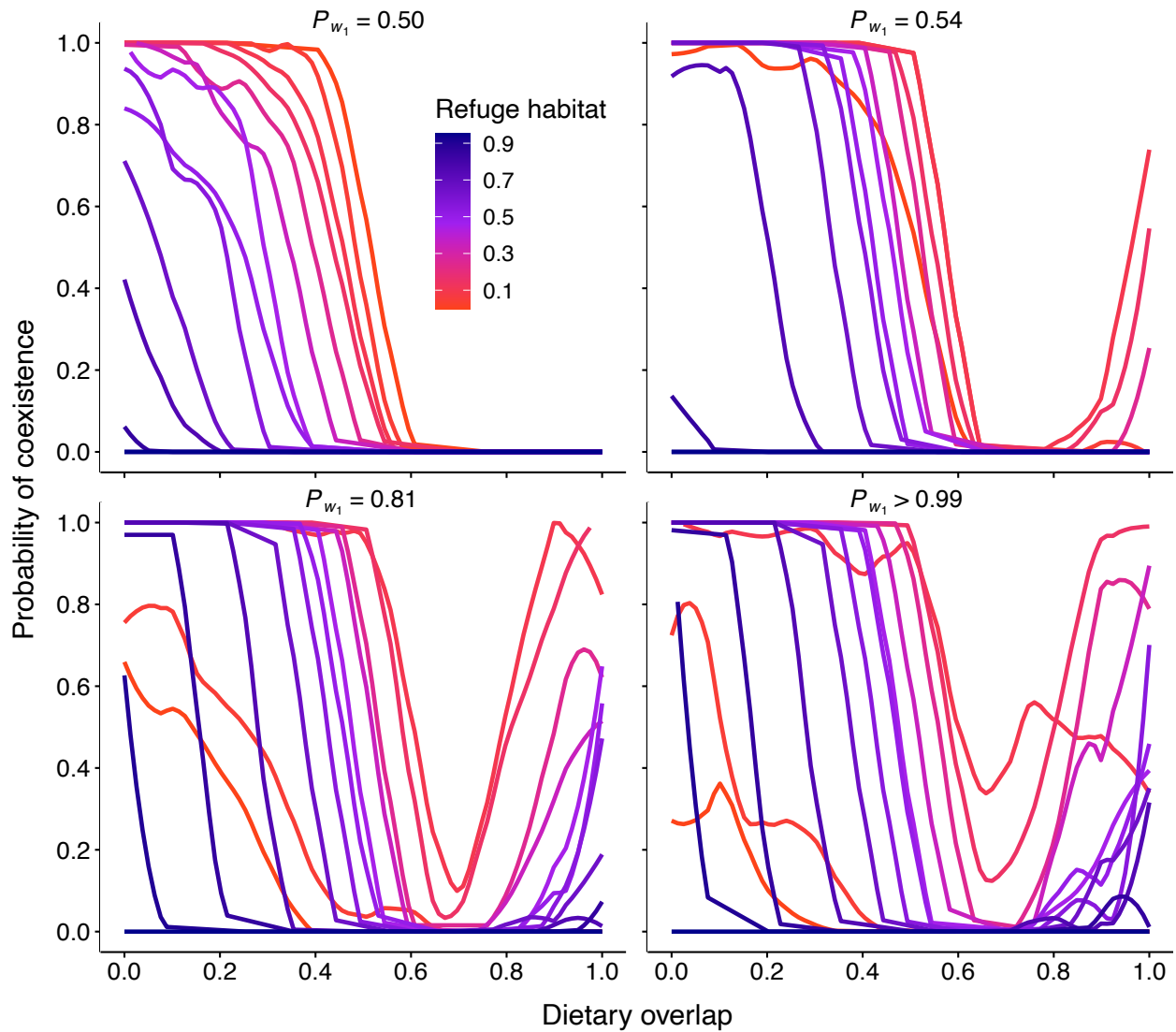
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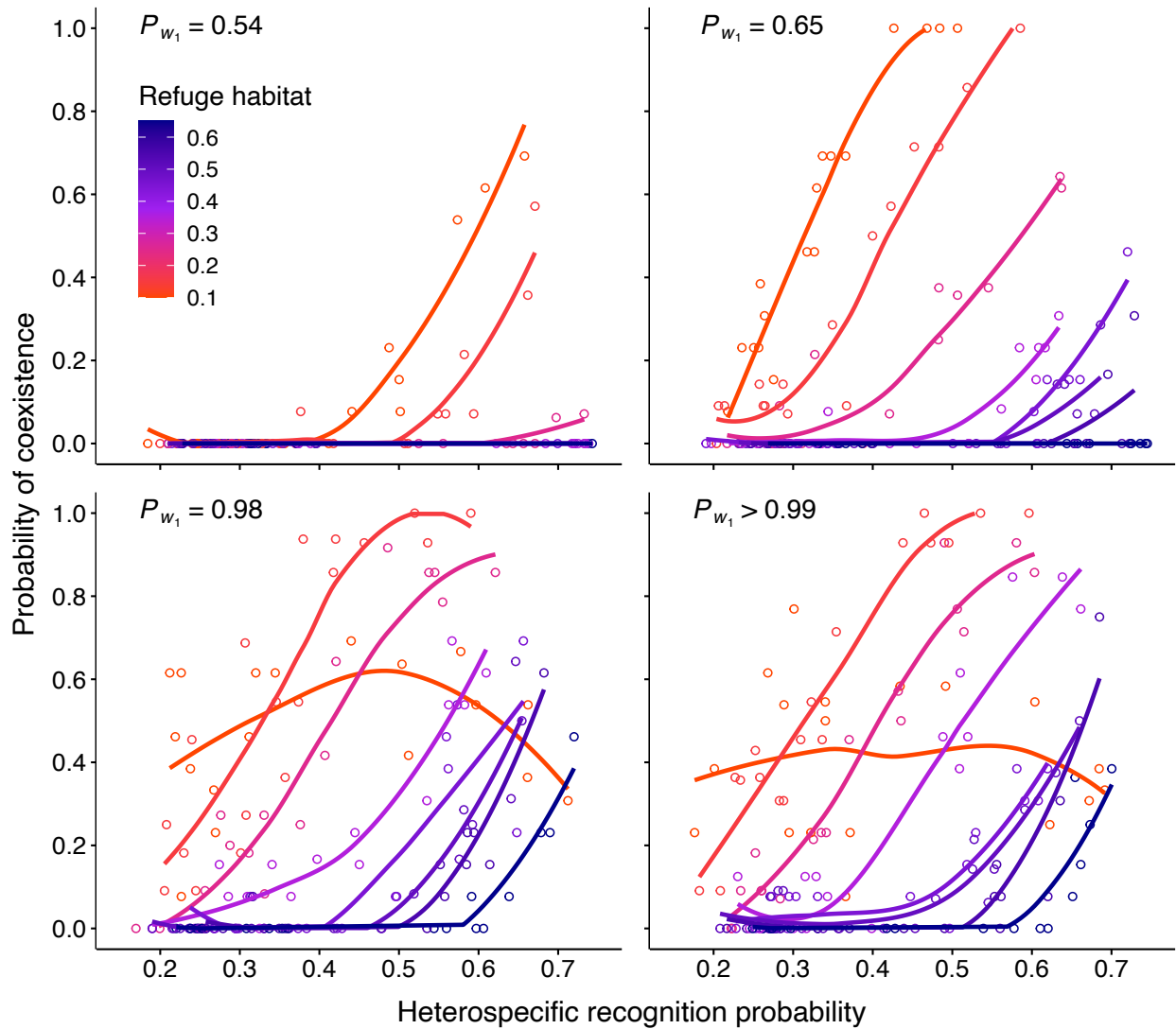
548

549 **Fig. 1.** Coexistence and evolutionary outcomes in relation to dietary overlap, the fraction of the  
550 habitat where species 2 could breed without interference from species 1, and the probability of  
551 species 1 winning interspecific fights ( $P_{w1}$ , based on the species difference in fighting ability).  
552 Each point represents a unique parameter set. In the top panels, symbols correspond to the  
553 observed coexistence outcomes (see legend). For example, “Coexist or Sp1 extinct” means that  
554 the species coexisted to the end or species 1 went extinct, in different simulation runs. In the  
555 lower panels, symbols correspond to the evolutionary outcomes when both species persisted to  
556 the end (see legend): “Stasis”, neither species’ mean values of  $z$  and  $\mu$  changed significantly;  
557 “Sp2 diverged”, species 2 shifted away from species 1 and species 1 exhibited stasis;  
558 “Divergence”, both species shifted away from the other; “Sp1 chased Sp2”, species 1 converged  
559 and species 2 diverged; “Divergence/Sp2 diverged”, both outcomes occurred in different  
560 simulation runs; etc. This figure summarizes a subset of the simulations in which the initial mean  
561 difference between the species in traits  $z$  and  $\mu$  was 1. Figs. S9 – S12 summarize all of the  
562 simulations.



563

564 **Fig. 2.** Probability of coexistence in relation to dietary overlap, the fraction of the habitat where  
 565 species 2 could breed without interference from species 1 (color scale), and the probability of  
 566 species 1 winning interspecific fights ( $P_{w1}$ ). The lines were generated by a non-parametric  
 567 smoothing function bounded by 0 and 1 (geom\_smooth in the R package ggplot2). Here, the  
 568 initial mean difference between the species in traits  $z$  and  $\mu$  was 1. Fig. S15 shows results for two  
 569 additional levels of  $P_{w1}$ , and Fig. S16 shows the probability of coexistence for simulations in  
 570 which the initial mean difference was 2.



571

572 **Fig. 3.** Probability of coexistence under high dietary overlap ( $\geq 0.75$ ) in relation to the average  
 573 probability of heterospecific males recognizing each other as competitors in the final years of  
 574 contact (i.e., just before one species went extinct or the simulation ended). Each point represents  
 575 a unique parameter set. The color scale indicates the fraction of the habitat where species 2 could  
 576 breed without interference from species 1 (limited to the range shown in the legend). The lines  
 577 were generated as in Fig. 2. The initial mean difference between the species in traits  $z$  and  $\mu$  was  
 578 1 or 2 in these simulations.