

1 **Interspecific behavioural interference and range dynamics: current insights and future**  
2 **directions**

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## 7 **Abstract**

8 Novel biotic interactions in shifting communities play a key role in determining the ability of  
9 species' ranges to track suitable habitat. To date, the impact of biotic interactions on range  
10 dynamics have predominantly been studied in the context of interactions between different  
11 trophic levels or, to a lesser extent, exploitative competition between species of the same  
12 trophic level. Yet, both theory and a growing number of empirical studies show that  
13 interspecific behavioural interference, such as interspecific territorial and mating interactions,  
14 can slow down range expansions, preclude coexistence, or drive local extinction, even in the  
15 absence of resource competition. We conducted a systematic review of the current empirical  
16 research into the consequences of interspecific behavioural interference on range dynamics.  
17 Our findings demonstrate there is abundant evidence that behavioural interference by one  
18 species can impact the spatial distribution of another. Furthermore, we identify several gaps  
19 where more empirical work is needed to robustly test predictions from theory. Finally, we  
20 outline several avenues for future research, providing suggestions for how interspecific  
21 behavioural interference could be incorporated into existing biotic-interactions frameworks of  
22 range expansion, such as species distribution models, to build a stronger understanding of the  
23 potential consequences of behavioural interference on the outcome of future range dynamics.

24

25 *Keywords (5-10)*

26 *interspecific behavioural interference, reproductive interference, interspecific aggression,*  
27 *range dynamics, systematic review, elevational gradients, invasion biology, range shift*

28

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## 44 **I. Introduction**

45           As anthropogenic changes continue to alter the availability and distribution of  
46 habitats, the spatial distribution of species' niches will shift, in turn driving shifts in species'  
47 ranges (Parmesan and Yohe 2003). Given that species vary in their niches and in their  
48 responses to environmental change, communities will not shift in concert, resulting in a  
49 global reshuffling of diversity and the formation of novel species assemblages. Similarly,  
50 invasions due to anthropogenic factors can have disruptive effects on species assemblages.  
51 Interactions between species--whether between previously coexisting species or between  
52 newly co-occurring species in shifting communities--play key roles in determining the ability  
53 of species' ranges to track suitable habitats (Alexander, Diez, and Levine 2015; Blois et al.  
54 2013; Early and Keith 2019; Ockendon et al. 2014). For instance, the arrival of novel  
55 predators can drive prey species to extinction (e.g., brown tree snakes [*Boiga irregularis*]  
56 drove the local extinction of several bird species after they were introduced to Guam,  
57 (Savidge 1987); conversely, the local extinction of one species can destabilize interaction  
58 networks, driving secondary extinctions (e.g., experimental removal of a keystone predator  
59 [*Pisaster ochraceus*] led to a decline in diversity in the marine intertidal zone, (Paine 1966)).  
60 By and large, studies on the impacts of biotic interactions on population and range dynamics  
61 have predominantly focused on interactions across trophic levels or, to a lesser extent,  
62 exploitative competition between species of the same trophic level (Sirén and Morelli 2020;  
63 Early and Keith 2019; Louthan, Doak, and Angert 2015; Svenning et al. 2014; Legault et al.  
64 2020; Ortego and Knowles 2020).

65           Yet, an important type of competition between closely related animal species is often  
66 overlooked: interspecific behavioural interference (Grether et al. 2017). Behavioural  
67 interference encompasses any aggressive, territorial, or mating behaviour by one species that  
68 has a negative impact on the fitness of another species (Grether et al. 2017; Gröning and

69 Hochkirch 2008; Burdfield-Steel and Shuker 2011) and has been documented across a wide  
70 range of taxa (Gröning and Hochkirch 2008; Peiman and Robinson 2010). In general,  
71 aggressive and sexual interactions arise between species that are phenotypically and  
72 ecologically similar owing to recent shared ancestry (e.g., species with similar sexual signals  
73 and/or perceptual systems). Such interactions are costly and lead to decreased fitness as  
74 individuals waste energy, are driven to use suboptimal habitat, or miss out on mating  
75 opportunities with conspecifics. Consequently, behavioural interference can decrease  
76 population growth rates, cause exclusion from adequate habitat, and reduce or prevent  
77 dispersal into novel areas (Grether et al. 2017). Thus, interspecific behavioural interference is  
78 likely to have important impacts on range dynamics.

79         Several theoretical investigations of behavioural interference have modelled the  
80 factors that promote or preclude coexistence (T. J. Case and Gilpin 1974; Kuno 1992; Liou  
81 and Price 1994; Amarasekare 2002; Mikami and Kawata 2004; Kishi and Nakazawa 2013;  
82 Kyogoku and Sota 2017; Iritani and Noriyuki 2021; Irwin and Schluter 2022; Grether and  
83 Okamoto 2022) and a handful have even explicitly analysed how processes affecting  
84 coexistence locally scale up to influence the outcome of movement across landscapes  
85 (Ribeiro and Spielman 1986; Crowder et al. 2011; Nishida, Takakura, and Iwao 2015;  
86 Ruokolainen and Hanski 2016; Legault et al. 2020). One key insight from these models is  
87 that the impact of interspecific behavioural interference is likely to be highest when one of  
88 the interacting species occurs at a much lower frequency than the other, as interspecific  
89 interference will be more common than intraspecific interactions for the rarer species (e.g.,  
90 (Amarasekare 2002; Kuno 1992). Consequently, Allee effects resulting from behavioural  
91 interference may make it very difficult for viable populations to become established in novel  
92 geographic areas (Grether et al. 2017) or may drive precipitous local extinction once  
93 population densities fall below a certain threshold. A common result in models incorporating

94 behavioural interference is the formation and maintenance of abutting (parapatric) range  
95 limits, which may move according to the magnitude of and degree of asymmetry in  
96 interference (Ribeiro and Spielman 1986; Nishida, Takakura, and Iwao 2015). Another  
97 insight from these models relates to the interactive effect of resource competition and  
98 behavioural interference--several models also show dynamics of systems with both resource  
99 competition and behavioural interference are markedly different than systems with resource  
100 competition alone (Ribeiro and Spielman 1986; Amarasekare 2002; Crowder et al. 2011),  
101 which underscores the importance of further research into behavioural interference in  
102 attempts at predicting species responses to shifting assemblages.

103         Insights derived from theory about the impact of behavioural interference on range  
104 dynamics are now backed up by a growing body of empirical research. Interspecific  
105 behavioural interference has been shown to impact a range of spatial dynamics, ranging from  
106 local-scale habitat use (Vallin et al. 2012) to large-scale range limit shifts (Duckworth and  
107 Badyaev 2007). Here we present the results of the first synthesis of this body of work through  
108 a systematic literature review, and, in light of the widespread evidence that behavioural  
109 interference impacts range dynamics, we discuss patterns emerging from existing studies,  
110 highlight key gaps in the literature, and suggest several avenues for future research.

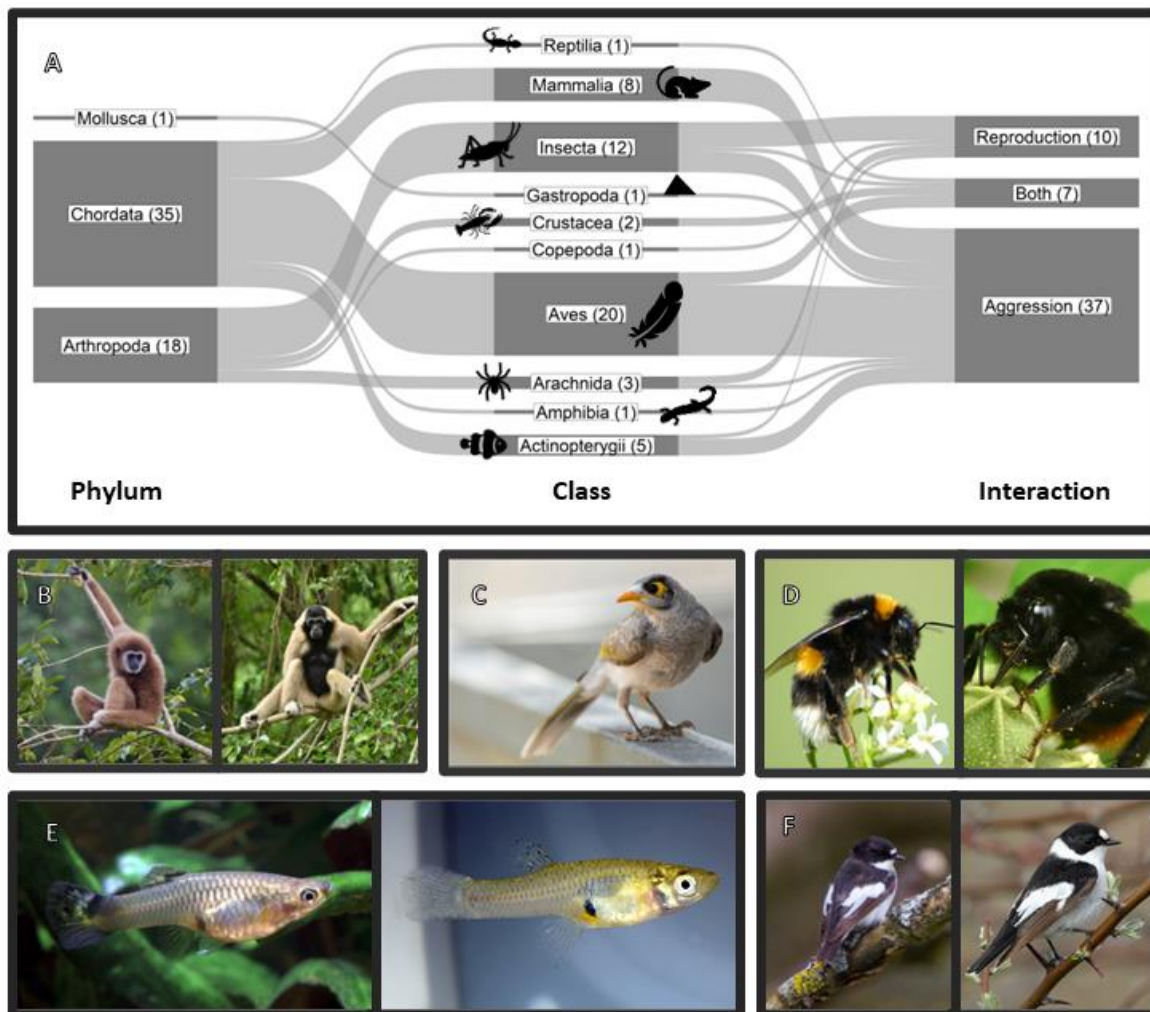
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## 112 **II. Systematic literature review**

113         To identify examples of interspecific behavioural interference influencing the spatial  
114 distribution of a species, we conducted a search of peer-review literature using the “all  
115 databases” option in Web of Science (<https://www.webofscience.com/>). We used the search  
116 term “*TS=(((behaviour\* OR behavior\*) NEAR/6 interference) OR (reproduct\* NEAR/6*  
117 *interference) OR (interspecific NEAR/6 (behaviour\* OR behavior\*) NEAR/6 competition)*  
118 *OR ((interspecific OR heterospecific) NEAR/6 aggress\*) OR ((interspecific OR*

119 *heterospecific) NEAR/6 dominan\*) OR ((interspecific OR heterospecific) NEAR/6 territor\*)*  
120 *OR ((interspecific OR heterospecific) NEAR/6 interference) OR (sister AND (taxa OR*  
121 *species) AND (competition OR aggress\* OR territor\*OR dominan\* OR interference))) AND*  
122 *TS= ((range\* NEAR/6 shift\*) OR (species NEAR/6 distribution\*) OR (range\* NEAR/6*  
123 *expansion\*) OR (range\* NEAR/6 dynamic\*) OR (species NEAR/6 displace\*) OR (species*  
124 *NEAR/6 replace\*) OR (Altitud\* NEAR/6 (zonat\* OR zone)))". As of the search date (2022-*  
125 *10-13), this produced a database of 338 unique peer-reviewed articles, which both authors*  
126 *contributed to reading and extracting data from. To reduce bias in data extraction between*  
127 *readers, the first 37 papers (10%) were independently read by both of us and data extraction*  
128 *compared. For the 10% of papers initially read by both readers, the interpretation of the paper*  
129 *and data extracted was concordant. We only included cases for which there are direct*  
130 *observations of interspecific behavioural interference and an explicit link between that*  
131 *interference to spatial dynamics, which added 72 papers in our final set. For instance, in cases*  
132 *where species have abutting boundaries (e.g., parapatric range limits), we only included cases*  
133 *where behavioural interference has been documented and this boundary does not also*  
134 *coincide with clear shifts in habitat types. Similarly, for instances of microhabitat segregation*  
135 *or mosaic distribution patterns, we required the study to demonstrate that shifts in habitat use*  
136 *directly result from behavioural interference. While reading these papers, we also noted*  
137 *papers that the authors cited as further evidence for behavioural interference and/or range*  
138 *dynamics within their own or other study systems which added 26 additional papers to our*  
139 *final set. Of the 98 studies in our final set, 62 studies provided clear evidence that*  
140 *interspecific behavioural interference impacts the spatial distribution of a species, with 19*  
141 *additional studies providing corroborating evidence in combination with other papers. The*  
142 *remaining papers either found no effect (n=15) or were inconclusive (n=2). The 81 papers*  
143 *that, either provide evidence directly or in collaboration with other studies, found clear*

144 evidence in favour of interspecific behavioural interference impacting the spatial distribution  
 145 of a species and were sorted into 54 unique study systems (Figure 1, Table 1).



146  
 147 Figure 1. There is widespread evidence that behavioural interference influences spatial  
 148 dynamics in animals. **A.** The breakdown of study systems that directly measured the impact  
 149 of interspecific behavioural interference on the spatial distribution of one of more species by  
 150 phylum, class, and whether the study covered aggressive, reproductive behavioural  
 151 interference, or both. All studies investigated the impact of intraclass behavioural  
 152 interference, except for one case of interphylum behavioural interference between a  
 153 Crustacean and Actinopterygii (Bubb et al. 2009). The interphyla study is counted here as  
 154 Crustacea study as the Crustacea was the more aggressive species. Sankey diagram was



155 created using the R package ggsankey **B.** In Thailand, two species of gibbon, the white-  
156 handed gibbon (*Hylobates lar*) and the pileated gibbon (*Hylobates pileatus*), have a  
157 parapatric distribution with only a small (<1km wide) boundary where the species are found  
158 in sympatry. Both *H. lar* and *H. pileatus* hold territories that are controlled exclusively by  
159 monogamous pairs. Detailed mapping of territories and observation of conflict events show  
160 that where the two species are found in sympatry, pairs defend territories from conspecifics  
161 and heterospecifics (Asensio et al. 2017). The relatively low abundance of hybrids at the  
162 boundary suggests that there is strong reproductive isolation between the two species.  
163 However, interspecific aggression persists which prevents the two species from dispersing  
164 into each other's ranges. **C.** Indiscriminate hyperaggression of Noisy miners (*Manorina*  
165 *melanocephala*) has led to shift in the whole structure of avian communities (Mac Nally et al.  
166 2012). **D.** In Japan, the invasive bumblebee *Bombus terrestris* engages in reproductive  
167 interference with two species of native bumblebee species. Copulation between male *B.*  
168 *terrestris* and female *Bombus hypocrita sapporoensis* or *Bombus ignites* results in unviable  
169 eggs being laid the following spring when there are no further intraspecific mating  
170 opportunities. Consequently, *B. ignities* and *B. h. sapporeensis* have declined rapidly in areas  
171 with *B. terrestris* and could lead to the extinction of the native bumblebee species (Tsuchida  
172 et al. 2019). (<https://github.com/davidsjoberg/ggsankey>). **E.** The accidental introduction of  
173 guppies *Poecilia reticulata* led to the eradication of invasive mosquito fish  
174 (*Gambusia affinis*) in Okinawa owing to reproductive interference, and consequently guppies  
175 have been proposed as a potential control agent for mosquito fish elsewhere (Tsurui-Sato et  
176 al. 2019). **F.** Pied flycatchers (*Ficedula hypoleuca*) are driven to use sub-optimal habitat by  
177 the high aggression of collared flycatchers (*Ficedula albicollis*) (Vallin et al. 2012; Rybinski  
178 et al. 2016). All photos under creative commons by Wikimedia-user:Kongkham6211, JJ

- 179 Harrison, flickr-user:coniferconifer, Vera Buhl, Rex Boggs, Andrej Chudý, Ron Knight,  
180 Holger Krisp, and Wikimedia-user:Fredlyfish4.  
181  
182

183 **Table 1:** All 54 study systems identified during the literature review that found clear  
 184 evidence that interspecific behavioural interference (IBI) impacts the spatial distribution of a  
 185 species. An expanded table which includes a description of each study system can be found in  
 186 Supplementary Table 1.

<b>Interacting Species</b>	<b>IBI.Type</b>	<b>Elevational (Y/N)</b>	<b>Invasion (Y/N)</b>	<b>Comparative (Y/N)</b>	<b>References</b>
<b>Aves</b>					
Great reed warblers ( <i>Acrocephalus arundinaceus</i> ) & marsh warblers ( <i>Acrocephalus palustris</i> )	Aggression	N	N	N	(Rolando and Palestini 1989)
Bicknell's thrushes ( <i>Catharus bicknelli</i> ) & Swainson's thrushes ( <i>Catharus ustulatus</i> )	Aggression	Y	N	N	(Freeman and Montgomery 2015)
Black-headed nightingale thrushes ( <i>Catharus mexicanus</i> ) & ruddy-capped nightingale-thrushes ( <i>Catharus frantzii</i> )	Aggression	Y	N	N	(Jones et al. 2020)
Collared ( <i>Ficedula albicollis</i> ) & pied ( <i>Ficedula hypoleuca</i> ) flycatchers	Aggression	N	N	N	(Vallin et al. 2012; Rybinski et al. 2016)
Several species of wood wrens ( <i>Henicorhina leucophrys</i> & <i>Henicorhina leucosticta</i> ) and thrushes ( <i>Catharus mexicanus</i> & <i>Catharus aurantiirostris</i> ) along an elevational gradient in Costa Rica.	Aggression	Y	N	N	(Jankowski, Robinson, and Levey 2010)
Narrow-billed woodcreepers ( <i>Lepidocolaptes angustirostris</i> ) & scaled woodcreepers ( <i>Lepidocolaptes squamatus</i> )	Aggression	N	N	N	(Maldonado-Coelho et al. 2017)
Common nightingales ( <i>Luscinia megarhynchos</i> ) & thrush nightingales ( <i>Luscinia luscinia</i> )	Aggression	N	N	N	(Sorjonen 1986; Reif et al. 2015; 2018)
Noisy miners ( <i>Manorina melanocephala</i> ) & local bird assemblages	Aggression	N	N	N	(Mac Nally et al. 2012; Lill and Muscat 2015)
Flame robins ( <i>Petroica phoenicea</i> ) & Norfolk robins ( <i>Petroica multicolor</i> )	Aggression	N	N	N	(Robinson 1992)
Carolina chickadees ( <i>Poecile carolinensis</i> ) and black-capped chickadees ( <i>Poecile atricapillus</i> )	Aggression and Reproductive Interference	N	N	N	(Bronson et al. 2003; McQuillan and Rice 2015)
Invasive ring-necked parakeets ( <i>Psittacula krameri</i> ) and native communities	Aggression	N	Y	N	(Hernández-Brito et al. 2014)
Townsend's warblers ( <i>Setophaga townsendi</i> ) and hermit warblers ( <i>Setophaga occidentalis</i> )	Aggression and Reproductive Interference	N	N	N	(Pearson 2000; Pearson and Rohwer 2000)
Western bluebirds ( <i>Sialia mexicana</i> ) & mountain bluebirds ( <i>Sialia currucoides</i> )	Aggression	N	N	N	(Duckworth and Badyaev 2007; Duckworth 2013; Duckworth, Belloni, and Anderson 2015)
Spotted owls ( <i>Strix occidentalis</i> ) & barred owls ( <i>Strix varia</i> )	Aggression	N	Y	N	(Gutiérrez et al. 2007; Van Lanen et al. 2011; Wiens, Anthony, and Forsman 2014)
Dominant and subordinate congeneric birds in urban environments	Aggression	N	N	Y	(Martin and Bonier 2018; Martin, Burke, and Bonier 2021)
Dominant and subordinate birds from North America	Aggression	N	N	Y	(Freshwater, Ghalambor, and Martin 2014)
Birds along an elevational gradient in Borneo	Aggression	Y	N	Y	(Boyce and Martin 2019)
North american perching birds (passerines)	Aggression and	N	N	Y	(Cowen, Drury, and Grether 2020)

	Reproductive Interference				
Birds along an elevational gradient in Papua New Guinea	Aggression	Y	N	Y	(Freeman, Class Freeman, and Hochachka 2016)
<b>Amphibia</b>					
Southern Appalachian salamander ( <i>Plethodon teyahalee</i> ) & red-cheeked salamanders ( <i>Plethodon jordani</i> )	Aggression	Y	N	N	(Hairston, Nishikawa, and Stenhouse 1987; Gifford and Kozak 2012)
<b>Actinopterygii</b>					
Damselfish ( <i>Dischistodus</i> spp.) in the Great Barrier Reef	Aggression	N	N	N	(Bay, Jones, and McCormick 2001)
Guppies ( <i>Poecilia reticulata</i> ) & mosquitofish ( <i>Gambusia affinis</i> )	Reproductive Interference	N	Y	N	(Tsurui-Sato et al. 2019)
Obscure damselfish ( <i>Pomacentrus adelus</i> ) & speckled damselfish ( <i>Pomacentrus bankanensis</i> )	Aggression	N	N	N	(Eurich, McCormick, and Jones 2018)
Invasive brown trout ( <i>Salmo trutta</i> ) & white-spotted charr ( <i>Salvelinus leucomaenis</i> ) in Japan	Aggression	N	Y	N	(Takami et al. 2002; Hasegawa et al. 2004; Hasegawa and Maekawa 2009)
Gopher rockfish ( <i>Sebastes carnatus</i> ) & Black-and-yellow rockfish ( <i>Sebastes chrysomelas</i> )	Aggression	N	N	N	(Larson 1980)
<b>Arachnida</b>					
Invasive sheet-web spiders ( <i>Linyphia triangularis</i> ) & bowl-and-doily spiders ( <i>Frontinella communis</i> )	Aggression	N	Y	N	(Houser, Ginsberg, and Jakob 2014)
<b>Copepoda</b>					
<i>Skistodiaptomus</i> copepods	Reproductive Interference	N	N	N	(Thum 2007)
<b>Crustacea</b>					
Invasive rusty crayfish ( <i>Orconectes rusticus</i> ) and native Sanborn crayfish ( <i>Orconectes sanborni</i> )	Aggression and Reproductive Interference	N	Y	N	(Butler and Stein 1985)
Invasive signal crayfish ( <i>Pacifastacus leniusculus</i> ) in Europe & native communities	Aggression and Reproductive Interference	N	Y	N	Svärdson et al. 1991  (Björn Söderbäck 1994; B. Söderbäck 1995; Westman and Savolainen 2001; Westman, Savolainen, and Julkunen 2002; Bubb et al. 2009)
<b>Gastropoda</b>					
Keyhole limpets ( <i>Siphonaria lessonii</i> ) & pulmonate limpets ( <i>Fissurella crassa</i> )	Aggression	N	N	N	(Aguilera and Navarrete 2012)
<b>Insecta</b>					
<i>Aedes</i> mosquitos ( <i>Ae. albopictus</i> & <i>Ae. aegypti</i> )	Reproductive Interference	N	Y	N	(Nasci, Hare, and Willis 1989; Irka E. Bargielowski, Lounibos, and Carrasquilla 2013; Irka Ewa Bargielowski and Lounibos 2016; Lounibos and Juliano 2018; Zhou et al. 2022)
Two tick species ( <i>Amblyomma variegatum</i> & <i>Amblyomma hebraeum</i> )	Reproductive Interference	N	N	N	(Bournez et al. 2015)
Whiteflies ( <i>Bemisia tabaci</i> spp.)	Reproductive Interference	N	Y	N	(Liu et al. 2007; Crowder et al. 2011; Wang, Crowder, and Liu 2012)
Invasive buff-tailed bumblebees ( <i>Bombus terrestris</i> ) & native bumblebees ( <i>Bombus h. sapporoensis</i> 7 <i>Bombus ignitus</i> ) in Japan	Reproductive Interference	N	Y	N	(Tsuchida et al. 2019)
Rubyspot damselflies ( <i>Hetaerina</i> spp.)	Aggression	N	N	Y	(McEachin et al. 2022)

Two ant species ( <i>Iridomyrmex</i> spp.)	Aggression	N	N	N	(Haering and Fox 1987)
Arboreal termite species in Papua New Guinea ( <i>Microcerotermes biroi</i> , <i>Nasutitermes novarumhebridiarum</i> , & <i>Nasutitermes princeps</i> )	Aggression	N	N	Y	(Leponce, Roisin, and Pasteels 1997)
White-crossed seed bugs ( <i>Neacoryphus bicrurus</i> ) and co-occurring insect communities	Aggression and Reproductive Interference	N	N	N	(McLain and Shure 1987)
Invasive southern green stink bugs ( <i>Nezara viridula</i> ) & native green stink bugs ( <i>Nezara antennata</i> )	Reproductive Interference	N	Y	N	(Kiritani 2011)
Alpine dark bush-crickets ( <i>Pholidoptera aptera</i> ) & Transylvanian dark bush-crickets ( <i>Pholidoptera transylvanica</i> )	Reproductive Interference	N	N	N	(Dorková et al. 2020)
Eastern subterranean termites ( <i>Reticulitermes flavipes</i> ) & Western subterranean termites ( <i>Reticulitermes grassei</i> )	Aggression	N	Y	N	(Perdereau et al. 2011)
Invasive Asian blue ticks ( <i>Rhipicephalus [Boophilus] microplus</i> ) & African blue ticks ( <i>Rhipicephalus [Boophilus] decoloratus</i> ) in South Africa	Reproductive Interference	N	Y	N	(Sutherst 1987; Tønnesen et al. 2004)
Cepero's groundhoppers ( <i>Tetrix ceperoi</i> ) & slender groundhoppers ( <i>Tetrix subulata</i> )	Reproductive Interference	N	N	N	(Gröning et al. 2007; Hochkirch, Gröning, and Bücker 2007; Hochkirch and Gröning 2012)
Arboreal ant species in Papua New Guinea	Aggression	N	N	Y	(Mottl et al. 2021)
<b>Mammalia</b>					
Fallow deer ( <i>Dama dama</i> ) & roe deer ( <i>Capreolus capreolus</i> )	Aggression	N	Y	N	(Ferretti and Mori 2020)
White-handed gibbons ( <i>Hylobates lar</i> ) & Pileated gibbons ( <i>Hylobates pileatus</i> )	Aggression	N	N	N	(Suwanvecho and Brockelman 2012; Asensio et al. 2017)
Least chipmunks ( <i>Neotamias minimus</i> ) & yellow-pine chipmunks ( <i>Neotamias amoenus</i> )	Aggression	Y	N	N	(Chappell 1978; Heller 1971)
Townsend's chipmunks ( <i>Neotamias townsendii</i> ) & yellow-pine chipmunks ( <i>Neotamias amoenus</i> )	Aggression	N	N	N	(Trombulak 1985)
Uinta chipmunks ( <i>Neotamias umbrinus</i> ) & Colorado chipmunks ( <i>Neotamias quadrivittatus</i> )	Aggression	Y	N	N	(Bergstrom 1992)
Stoats ( <i>Mustela erminea</i> ) & least weasels ( <i>Mustela nivalis</i> )	Aggression	N	N	N	(Erlinge and Sandell 1988)
Pied tamarins ( <i>Saguinus bicolor</i> ) & Golden-handed tamarins ( <i>Saguinus midas</i> )	Aggression	N	N	N	(Sobroza et al. 2021)
Chiriquí singing mice ( <i>Scotinomys xerampelinus</i> ) & Alston's singing mice ( <i>Scotinomys teguina</i> )	Aggression	Y	N	N	(Pasch, Bolker, and Phelps 2013)
<b>Reptilia</b>					
Invasive house geckos ( <i>Hemidactylus frenatus</i> ) & native communities	Aggression and Reproductive Interference	N	Y	N	(Bolger and Case 1992; Petren, Bolger, and Case 1993; Ted J. Case, Bolger, and Petren 1994; Dame and Petren 2006)

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190 **(1) Reproductive interference versus interspecific aggression**

191 We identified more study systems where aggressive interference (N = 37) influenced range  
192 dynamics than reproductive interference (N = 10). Seven study systems found both  
193 reproductive and aggression influencing range dynamics (Figure 1, Table 1). This suggest  
194 that competitive exclusion via interference competition is likely to be more widespread than  
195 sexual exclusion. Nevertheless, it is also possible that the role of reproductive interference in  
196 such cases has been overlooked. Indeed, interspecific territoriality often occurs between  
197 species that engage in reproductive interference (Drury et al. 2015; Drury, Cowen, and  
198 Grether 2020; Grether et al. 2020; Payne 1980), including in several case studies uncovered  
199 by the systematic literature review (Vallin et al. 2012; Wiens, Anthony, and Forsman 2014;  
200 Reif et al. 2018), so the abundance of examples of aggressive interference influencing spatial  
201 dynamics in vertebrates may also be indicative of undetected reproductive interference.  
202 Further empirical and theoretical work would help clarify the relative importance as well as  
203 the interactive, potentially non-additive, impacts of different types of behavioural interference  
204 on spatial dynamics.

205 The taxonomic distribution of case studies was the most apparent difference among  
206 the factors associated with different types of behavioural interference (Figure 1). Most  
207 examples of reproductive interference influencing range dynamics were conducted on  
208 arthropods (9 out of 10). This contrasts with studies of aggressive interference that were  
209 dominated by vertebrates (30 out of 37), especially birds (n = 17). Empirical examples of  
210 reproductive interference are taxonomically widespread (Gröning and Hochkirch 2008), so it  
211 is surprising to see that evidence of reproductive interference influencing the spatial  
212 dynamics of a species come predominantly from insects and arachnids. One potential  
213 explanation for this apparent bias is that it reflects a biological reality about the costs of  
214 reproductive interference in arthropods; the fitness cost of reproductive interference may be

215 especially high in arthropods because of females' short reproductive lifespans, and, because  
216 in some species, females produce no viable offspring after interspecific mating (Ribeiro and  
217 Spielman 1986), which makes a species particularly vulnerable to local extinction (Irwin and  
218 Schluter 2022). Alternatively, the bias may reflect a methodological convenience of working  
219 with invertebrates—reproductive interference may be hard to measure in the field without  
220 experimental mating trials, making larger scale field research of the sort necessary to build a  
221 link between reproductive interference and range dynamics more feasible on arthropods.

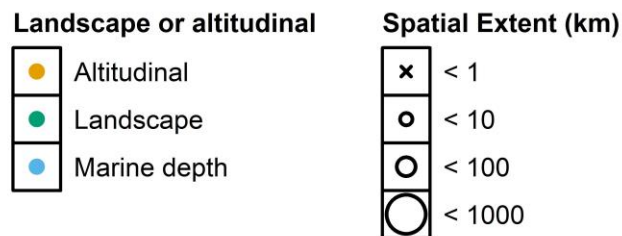
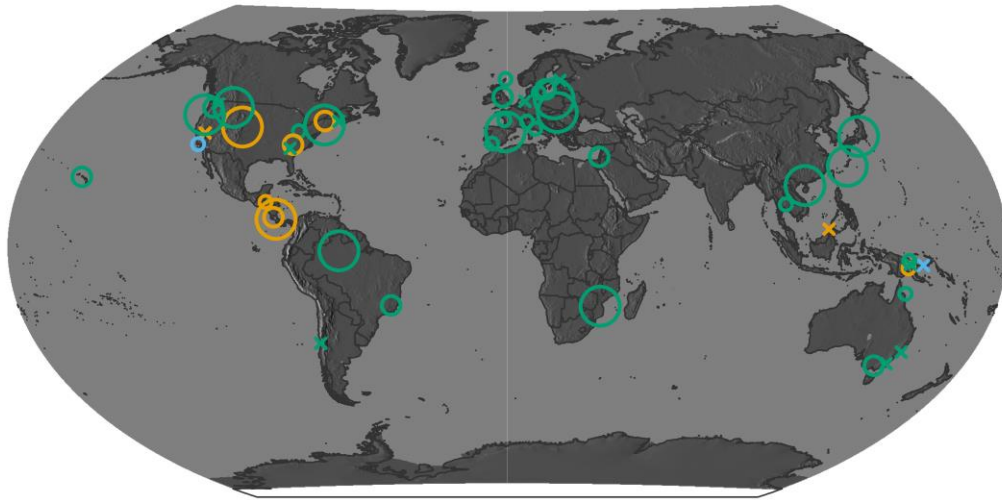
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## 223 **(2) Elevational gradients**

224         Range dynamics along elevational gradients have long been of interest to ecologists  
225 and evolutionary biologists. For instance, a classic hypothesis posits that abiotic factors are  
226 likely to play a more important role than biotic factors at high-elevation range limits  
227 (Louthan, Doak, and Angert 2015). As a result, there may be an increased risk of extinction  
228 in montane ecosystems caused by the 'escalator to extinction' (Sekercioglu et al. 2008;  
229 Freeman et al. 2018) in which warming conditions cause high-elevation species' climate  
230 niches to disappear. Given the interest in biotic interactions along elevational gradients, it is  
231 not surprising that we identified multiple examples of interspecific behavioural interference  
232 of one species influencing the elevational distribution of another species (17% of cases  
233 documenting an impact of behavioural interference on range dynamics). Due to rapid habitat  
234 turnover with altitude, range boundaries across elevational gradient are often sharply defined,  
235 making studies of range limits inherently simpler along an elevational gradient (Žagar et al.  
236 2015; Pasch, Bolker, and Phelps 2013; Jones et al. 2020), so it would be premature to  
237 conclude how likely that behavioural interference is to influence elevational range limits in  
238 comparison to range boundaries across landscape scales.

239           Several key patterns emerge from studies along elevational gradients. First,  
240 interspecific territoriality plays a key role in creating and maintaining elevational range  
241 limits. Comparative analyses, for instance, have shown that bird species have wider  
242 elevational ranges in mountains without competitors (Burner et al. 2020). Moreover, the  
243 response of several species of montane birds to heterospecific songs decreases with distance  
244 from their parapatric boundary, indicating a learned response to the presence of an aggressive  
245 congener (Jankowski, Robinson, and Levey 2010; Freeman and Montgomery 2015; Freeman,  
246 Class Freeman, and Hochachka 2016; Jones et al. 2020; Boyce and Martin 2019).  
247 Additionally, asymmetries in dominance are not consistently biased in favour of low  
248 elevation species, as there are examples of species pairs with subordinate high elevation  
249 species (e.g., *Catharus* thrushes, (Freeman and Montgomery 2015) and of pairs in which the  
250 lower elevation species is subordinate (e.g., *Scotinomys* singing mice (Pasch, Bolker, and  
251 Phelps 2013), *Neotamias* chipmunks (Bergstrom 1992) and, if aquatic depth gradients are  
252 comparable to elevational gradients, *Pomacentrus* damselfish (Eurich, McCormick, and Jones  
253 2018)) (see also Freeman 2020). These examples demonstrate the varied and often  
254 unpredictable role that behavioural interference can play in influencing elevational range  
255 limits, thereby challenging the hypothesis that abiotic factors are likely to play a more  
256 important role than biotic factors at high-elevation range limits (Louthan, Doak, and Angert  
257 2015). We also note a bias in the geographic locations of studies investigating behavioural  
258 interference across elevational gradients, with two exceptions in Borneo and Papa New  
259 Guinea, all study systems were located Northern and Central America (Figure 2). Studies  
260 across landscapes were found across a wider area, but still with noted gaps in Africa and  
261 Asia, likely due to an underlying geographic bias in scientific research (Culumber et al.  
262 2019).





263

264 Figure 2. The global distribution of field studies that found an effect of Interspecific  
 265 behavioural interference on the spatial distribution of a one of more species. Colour denotes  
 266 whether the study investigated the spatial distributions across a landscape (i.e., latitude and  
 267 longitude), across an elevational gradient (altitudinal), or across a sea-depth gradient (marine  
 268 depth). Size indicates the maximum spatial extent for where data was collected for study but  
 269 is not to scale, excluding comparative studies which had a greater than 1000km global  
 270 distribution (N = 7).

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### (3) Invasion biology

Anthropogenic influences have led to a dramatic rise in the number of non-native species that become invasive after being translocated to novel regions (Blackburn et al. 2011). As the ranges of invasive species expand they may engage in interspecific behavioural interference, driving displacement of native species (Rowles and O’Dowd 2007; Lounibos and Juliano 2018; Pereira, Lourenço, and Mota 2020; Kyogoku and Sota 2017). The systematic review identified multiple examples of invasive species engaging in reproductive interference (Tsurui-Sato et al. 2019; Lounibos and Juliano 2018; Tsuchida et al. 2019; Tønnesen et al. 2004; Westman, Savolainen, and Julkunen 2002) and aggressive interference (Bubb et al. 2009; Houser, Ginsberg, and Jakob 2014; Westman, Savolainen, and Julkunen 2002; Rowles and O’Dowd 2007) with native species (15/54 =28% of cases). For instance, invading Argentine ants in Australia outcompete native ant species through direct aggressive interactions (Rowles & O’Dowd 2007). Similarly, in Japan, invasive buff-tailed bumblebees (*Bombus terrestris*) engage in reproductive interference with two species of native bumblebee species. Copulation between male *B. terrestris* and female *Bombus hypocrite sapporoensis* or *Bombus ignites* results in unviable eggs being laid the following spring when there are no further intraspecific mating opportunities. Consequently, *B. ignities* and *B. h. sapporeensis* have declined rapidly in areas with *B. terrestris*, and further declines could lead to the extinction of the native bumblebee species (Tsuchida et al. 2019). Other well-established cases where invading lineages quickly replace previously established lineages include the replacement of asexual gecko lineages throughout the Pacific that have been displaced by interference from invasive common house geckos (Dame & Petren 2016, Bolger & Case 1992, Petren et al. 1993), and the replacement of *Aedes aegypti* by *Ae. albopictus* both throughout the southern U.S. (Nasci, Hare, and Willis 1989) and in China (Zhou et al. 2022).

297            Yet, behavioural interference is not always beneficial to invasive species and  
298 detrimental to native species. Invasive species may be unable to establish in areas which  
299 contain a more aggressive congener, and higher levels of aggressive or reproductive  
300 interference could allow native species to tolerate the presence of the invading species  
301 (Crowder et al. 2011), or even prevent its spread (Cisterne, Schwarzkopf, and Pike 2019;  
302 Bizwell and Mattingly 2010). Whether asymmetries in behavioural interference generally  
303 influence the outcome of translocations of animal species is, therefore, an important open  
304 question.

305            In addition to being a potentially accelerating factor in biological invasions,  
306 behavioural interference has also been suggested as a management tool for invasive species.  
307 On Okinawa, for instance, the accidental introduction of guppies (*Poecilia reticulata*) led to  
308 the eradication of invasive mosquito fish (*Gambusia affinis*) (Tsurui-Sato et al. 2019).  
309 Laboratory experiments indicate that male guppies attempt to mate with female mosquito  
310 fish, thereby reducing their reproductive output. Introduced guppies also have negative  
311 impacts on native taxa, but by introducing only males, or mixed populations into  
312 environments with lethal winter temperatures, guppies could be used to eradicate mosquito  
313 fish from other river systems (Tsurui-Sato et al. 2019). Similarly, a study on aggression  
314 between invasive brown trout and native white-spotted charr demonstrated that habitat  
315 modifications in the form of visual barriers could reduce observed levels of interspecific  
316 aggression (Hasegawa & Maekawa 2009).

317

#### 318 **(4) Empirical validation of theoretical predictions**

319            The formation of parapatric ranges, where two species have adjacent ranges with little  
320 or no overlap, is a key prediction of the theoretical models of how interspecific behavioural  
321 interference impacts range dynamics when the impacts of behavioural interference are

322 symmetrical (Ribeiro and Spielman 1986). In line with this prediction, we found that, where  
323 the impact of behavioural interference is equal, the ranges of interacting species pairs are  
324 stable (Asensio et al. 2017; Bull and Burzacott 1994; Thum 2007). If the impact of  
325 behavioural interference is asymmetrical, however, replacement of one species by the other  
326 commonly results (Tønnesen et al. 2004; Tsuchida et al. 2019; Tsurui-Sato et al. 2019;  
327 Duckworth and Badyaev 2007; Vallin et al. 2012; Sobroza et al. 2021). Some studies found  
328 that the ranges of the two species were stable even in the presence of asymmetrical  
329 behavioural interference because the more dominant species was limited by an abiotic or a  
330 different biotic factor (Pasch, Bolker, and Phelps 2013; Bergstrom 1992).

331         Although Allee effects are common in theoretical models of behavioural interference,  
332 relatively few case studies identified by our literature review explicitly tested for Allee  
333 effects, though several investigators of these studies suggest that Allee effects generate range  
334 turnovers (Soderback 1994, Tønnesen et al. 2004, Thum 2007, Kiritani 2011). The paucity of  
335 direct evidence for Allee effects was surprising, given documented Allee effects in laboratory  
336 studies (e.g., Kyogoku & Nishida 2012) and frequency- and/or density-dependent impacts of  
337 interspecific interference in the field (Svensson et al. 2018, Gomez-Llano et al. 2018). Future  
338 research, therefore, should aim to understand the importance of Allee effects in determining  
339 the outcome of spatial dynamics. For instance, a key test of the impact of behavioural  
340 interference on range dynamics would be to artificially induce an Allee effect in field systems  
341 known to engage in behavioural interference, by heightening or inverting the densities and/or  
342 frequencies of two species that engage in behavioural interference.

343         Similarly, though several models incorporate both behavioural interference and  
344 resource competition (Ribeiro and Spielman 1986; Amarasekare 2002; Crowder et al. 2011),  
345 our literature search found few explicit analyses disentangling the relative impacts of

346 behavioural interference and resource competition, or the predicted interactive dynamics of  
347 both, on range dynamics (but see Duckworth 2014, Cowen 2020).

348

### 349 **III. Future Directions**

350 Our systematic literature review demonstrated that there are now many studies that  
351 show varied impacts of behavioural interference on range expansion, but it also highlighted  
352 several gaps in our understanding. Here, we argue that further research is needed in several  
353 key areas, including the role that behavioural interference has played in shaping historical  
354 patterns of range dynamics, the impacts of behavioural interference on future range dynamics  
355 under climate change, and the extent to which evolution influences outcomes.

356

#### 357 **(1) Identifying the impact of behavioural interference on historical spatial processes**

358 There are several existing approaches for studying historical range dynamics that  
359 would be useful to develop further to understand outcomes of behavioural interference across  
360 a range of timescales. For instance, at a deep evolutionary timescale, models of ancestral  
361 biogeography have proven to be useful tools for making inferences about the pace and  
362 trajectory of range evolution within independently evolving lineages (Ronquist 2011).  
363 Recently, there have been calls for extending these methods to incorporate ecological factors  
364 such as species interactions (Sukumaran and Knowles 2018), and the development of tools  
365 for identifying the signature of competitive exclusion in range data (Quintero and Landis  
366 2020). Incorporating the possibility for the presence and/or magnitude of behavioural  
367 interference to modulate the impacts of competition on range dynamics into these models,  
368 similar to advances already developed for trait-mediated dispersal (Klaus and Matzke 2020),  
369 could provide a novel tool that would make it possible to test a range of hypotheses that  
370 cannot be tested with current methods (Fig 3A).

371           At shallower evolutionary scales, existing population genomic techniques leverage the  
372 signatures of historical processes preserved in genomes to test hypotheses about spatial (Peter  
373 and Slatkin 2013; Petkova, Novembre, and Stephens 2015; Al-Asadi et al. 2019; He, Prado,  
374 and Knowles 2017) and demographic (Gutenkunst et al. 2009; Gronau et al. 2011; Excoffier  
375 et al. 2021) dynamics that have unfolded over scales of thousands to millions of years.  
376 Largely, these developments have been designed to examine dynamics within independently  
377 evolving lineages. Within this constraint, one way forward would be to conduct comparative  
378 analyses to test the hypothesis that lineages (e.g., populations, species) experiencing higher  
379 levels of behavioural interference expand their ranges at different rates than lineages  
380 experiencing little or no behavioural interference (Fig 3B). Recently, Ortego & Knowles  
381 (2020) developed an analytical pipeline that explicitly tests for the impact of facilitation  
382 and/or competition between species on generating contemporary geographic patterns of  
383 genomic diversity. Extending these models to explicitly test for impacts of behavioural  
384 interference is an exciting possibility that would generate new insights.

385           On a more contemporary scale, long-term census data have proven to be a useful tool  
386 for monitoring dynamics of species assemblages over the past century (Rosenberg et al. 2019,  
387 Saunders et al. 2022). Such datasets contain interacting species, and understanding how those  
388 interactions impact temporal dynamics is one way forward (Fig 3C). One recent attempt has  
389 shown that species-pairs that are interspecifically territorial have increased their fine scale  
390 habitat overlap more than non-interspecifically territorial pairs (Nesbit et al. 2022).

391

## 392 **(2) Predicting the impact of behavioural interference in novel assemblages**

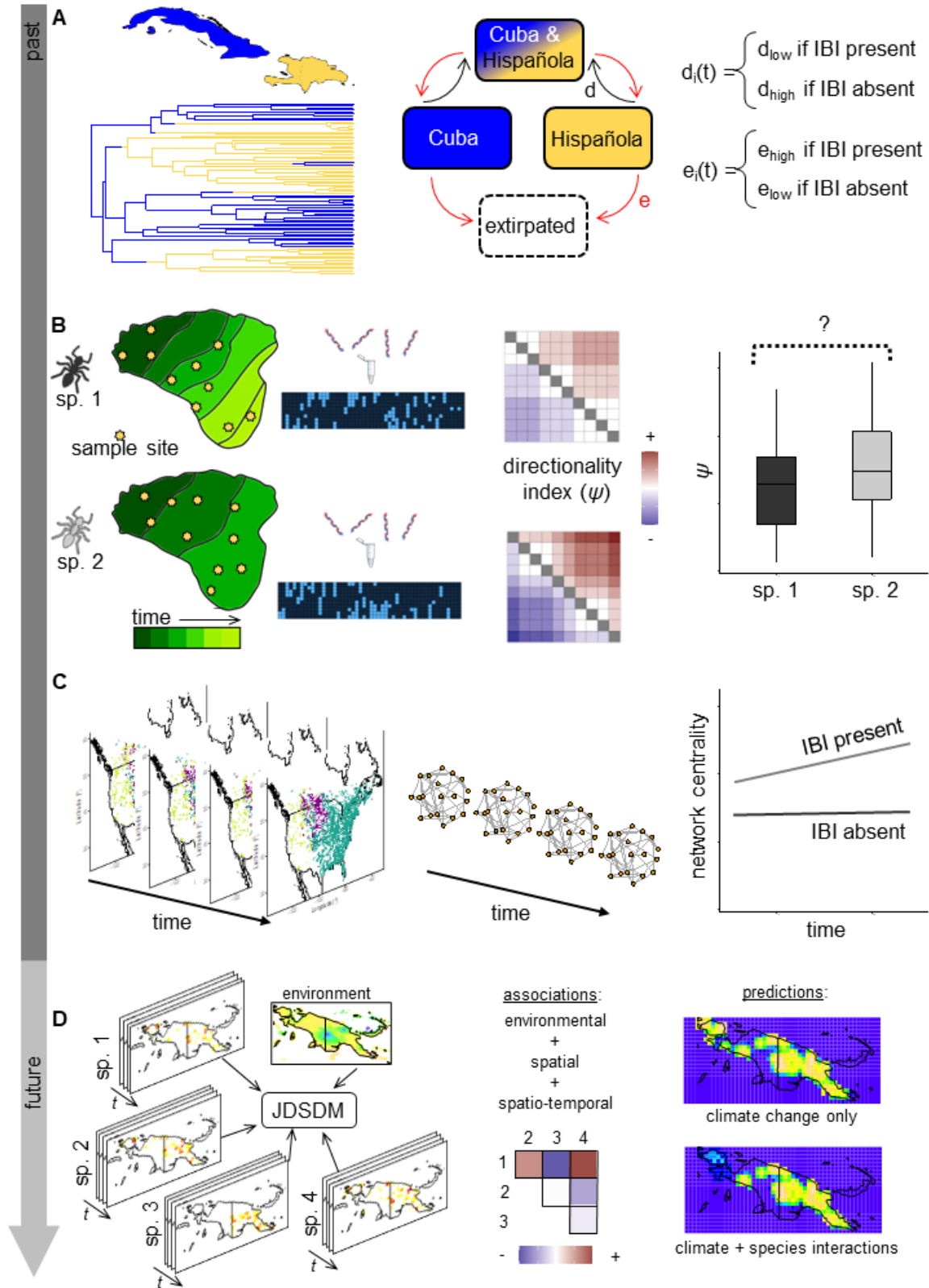
393           Insights generated from investigations of the impacts of behavioural interference on  
394 historical range dynamics will be essential for generating predictions about the future impacts  
395 of behavioural interference on climate-change driven range dynamics. At the heart of

396 attempts to predict how species' ranges will shift in response to global changes are species  
397 distribution models (SDMs). SDMs use measures of abiotic factors and presence-absence  
398 data to project the species' current released range onto future climate models (Elith and  
399 Leathwick 2009; Titley et al. 2021).

400 Attempts to incorporate biotic factors into species distribution models have given rise to joint  
401 species distribution models (JSDMs) (Wilkinson et al. 2019; Tikhonov et al. 2017). Yet,  
402 implementing and validating JSDMs is fraught with difficulties because positive and negative  
403 occurrence patterns often correlate with abiotic factors (Poggiato et al. 2021). Consequently,  
404 many examples of interspecific behavioural interference limiting the spatial distribution of  
405 species would not be detected using JSDMs, although some attempts to implement  
406 behavioural interference into SDMs/JSDMs have been conducted (Bastianelli et al. 2017;  
407 Engler et al. 2013). Despite challenges, joint species distribution modelling remains an active  
408 area of research with many promising recent developments (Pichler and Hartig 2021;  
409 Escamilla Molgora et al. 2022). For instance, joint *dynamic* species distribution models  
410 (JDSDMs) use time-series data on abundance to examine the impact of concurrent changes in  
411 abundance across assemblages more directly (Thorson, Pinsky, and Ward 2016; Elo et al.  
412 2023). Consequently, we imagine that these tools will be useful for generating predictive  
413 models of future range dynamics in the presence of behavioural interference (Fig. 3d), for  
414 instance by comparing the marginal predictions of such models (i.e., the effects of  
415 environmental variables only), to conditional predictions which also incorporate impacts of  
416 changing species interactions (Wilkinson et al. 2021) (Wilkinson et al. 2020). Recently, for  
417 instance, (Novella-Fernandez et al. 2021) devised an index of 'geographic avoidance' by  
418 comparing species suitable ranges (calculated from SDMs) to their observed ranges. Using  
419 this index, they found that two pairs of cryptic species of bats in Europe exhibited spatial  
420 partitioning consistent with interspecific competition driving exclusion. They then examined

421 range overlap under future climate projections, demonstrating that some predicted range  
422 shifts may not be possible due to predicted range overlap with competitors (Novella-  
423 Fernandez et al. 2021), see also Engler et al. 2013 and McQuillan and Rice 2015 for a similar  
424 approach). Future attempts to generate predictions of range dynamics in the presence of  
425 behavioural interference could also be used to disentangle and quantify the differing impacts  
426 of behavioural interference versus resource competition.





430 Fig 3. Possible directions for future research into the historical (A-C) and forecasted (D)  
431 impacts of behavioural interference (BI) on range dynamics. Approaches to test for historical  
432 impacts of BI include (A) extending models of ancestral biogeography to include separate  
433 parameters for species that engage in BI and those that do not, (B) deploying genomic tools  
434 to test whether the historical dynamics of range expansion differ between species that engage  
435 in BI (sp. 2, in this example) and species that do not by calculating pairwise indices of  
436 directional movement such as the  $\psi$  index (Peter and Slatkin 2013), and (C) using long-term  
437 census data to analyse how BI has impacted dynamics of species cooccurrence through time  
438 using tools from network analyses (e.g., indices of network centrality). Developments for  
439 forecasting and mitigating the impacts of BI on global-change induced range shifts might  
440 include (D) fitting joint dynamic species distribution models (JDSDMs) and using model  
441 inferences to compare future ranges under pure climate-tracking scenarios to scenarios that  
442 incorporate species interactions inferred from JDSDMs.  
443

444           The preceding approaches largely rely on metrics of cooccurrence to make inferences  
445 about the impacts of behavioural interference, under the assumption that cooccurring lineages  
446 are likely to interact. Yet, range overlap per se is not robust evidence that interactions occur.  
447 One way forward is to use measurements of fine-scale range overlap (i.e., 'syntopy'), which  
448 may be more indicative of the opportunity for species interactions (Drury, Cowen, and  
449 Grether 2020). Still, there is no substitute to direct observations of behaviour across large  
450 spatiotemporal scales. For instance, a large-scale study of spatiotemporal variation in  
451 agonistic behaviour in damselfish shows that interactions between individuals of different  
452 species increase after coral bleaching events (Keith et al. 2023). Future studies should  
453 directly observe behaviours to demonstrate concrete links between behavioural interference  
454 and range dynamics.

455

### 456 **(3) The role of evolution in mediating responses to behavioural interference**

457           Historically, empirical research into behavioural interference has largely focused on  
458 understanding factors that lead to behavioural interference (e.g., Drury, Cowen, and Grether  
459 2020; Leighton et al. 2023) and its evolutionary consequences, such as its impact on trait  
460 evolution (Grether et al. 2009; Pfennig and Pfennig 2009) or other aspects of the speciation  
461 cycle (Tobias, Ottenburghs, and Pigot 2020). This work has shown that the likelihood of  
462 behavioural interference decreases with increasing divergence time (e.g., Drury, Cowen, and  
463 Grether 2020; Barley et al. 2022) likely owing to the relative similarity in perceptual systems  
464 and agonistic and/or mating signals used in closely related species (Grether et al. 2009;  
465 Orians and Willson 1964). Consequently, behavioural interference is thought to have a strong  
466 impact on the rate of speciation by limiting the rate at which two recently diverged allopatric  
467 lineages can coexist in secondary sympatry (Tobias, Ottenburghs, and Pigot 2020). One  
468 possible evolutionary outcome of behavioural interference is divergent reproductive or

469 agonistic character displacement, in which selection acts on mating or agonistic signals or  
470 perceptual systems to prevent or reduce the occurrence of behavioural interference (Grether  
471 et al. 2009; Pfennig and Pfennig 2009). Yet, the benefits of diverging in signals and/or  
472 perceptual systems do not always outweigh the costs--for instance, because of the continued  
473 pressure of stabilising selection for intraspecific mate recognition (Drury et al. 2019) or  
474 because interspecific competitor recognition may be an adaptive pathway to interspecific  
475 resource partitioning (Grether and Okamoto 2022) -- and consequently, selection may  
476 preclude divergence or even drive convergence between interacting lineages.

477         The evolutionary responses to behavioural interference in shifting ranges should,  
478 therefore, play an important role in determining the outcome of range dynamics. For instance,  
479 in the case of *Aedes* mosquitoes, reproductive character displacement appears to have slowed  
480 down the invasion of *Ae. albopictus* in Florida (Irka E. Bargielowski, Lounibos, and  
481 Carrasquilla 2013; I. Bargielowski, Blosser, and Lounibos 2015). Similarly, native  
482 bumblebees in Japan have evolved polyandrous mating systems in response to reproductive  
483 interference from invasive buff-tailed bumblebees (Tsuchida et al. 2019). The extent to which  
484 and circumstances under which evolutionary changes mediate the impact of behavioural  
485 interference on range dynamics are thus open questions. Future long-term studies of zones  
486 where behavioural interference occurs, in addition to comparisons between sympatric and  
487 allopatric populations, could shed further light on these questions.

488

#### 489 **IV. Concluding remarks**

490 (1) Multiple lines of evidence now demonstrate that interspecific behavioural interference can  
491 limit the spatial distribution of species. Case studies demonstrate that this is true across a  
492 wide range of animal taxa, and that both reproductive interference and interspecific  
493 aggression can influence spatial dynamics.

494

495 (2) In line with predictions derived from theoretical models of behavioural interference, the  
496 case studies we compiled demonstrate that symmetry (or lack thereof) in behavioural  
497 interference determines the spatial outcome of interactions. Further work is necessary to test  
498 other key predictions of theoretical models, such as the presence of Allee effects and  
499 interactive impacts of behavioural interference and exploitative competition for resources.

500

501 (3) We identified several other gaps that remain in our broad-scale understanding of the  
502 impacts of behavioural interference on spatial dynamics. For instance, which factors (e.g.,  
503 phylogenetic distance, life history, climate niche, etc.) explain variation in the presence or  
504 magnitude of the effect of behavioural interference on range dynamics?

505

506 (4) Several recent developments have paved the way for modelling the impacts of species  
507 interactions on both historical and future spatial dynamics, and future work adapting these  
508 methods to further explore the links between behavioural interference and range dynamics is  
509 an important way forward.

510

511 (5) In addition to modelling approaches, further work aimed at quantifying the interactive  
512 effects of evolutionary change and spatial movement is crucial for predicting the outcome of  
513 range dynamics in the presence of behavioural interference.

514

515 (6) The spatial distribution of species has implication for conservation, human health, and  
516 agriculture. Alongside other abiotic and biotic factors, our study highlights the need to  
517 include interspecific behavioural interference in predicting and managing the current and  
518 future distribution of species.

519

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521

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526

527

528 **VI. References**

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## 1062 SUPPLEMENTARY INFORMATION

1063 Supplementary Table 1: All 54 study systems identified during the literature review that found clear evidence that interspecific behavioural interference (IBI)  
 1064 impacts the spatial distribution of a species.

Interacting Species	IBI.Type	Elevational (Y/N)	Invasion (Y/N)	Comparative (Y/N)	Impacts of IBI on Spatial Dynamics	References	Additional Explanations?
<b>Aves</b>							
<b>Great reed warblers (<i>Acrocephalus arundinaceus</i>) &amp; marsh warblers (<i>Acrocephalus palustris</i>)</b>	Aggression	N	N	N	Territorial mapping and behavioural observations demonstrate that great reed warblers and marsh warblers are interspecifically territorial, with great reed warblers dominating interactions. In areas where both species occur, marsh warblers use habitat further from reed habitats than sites where great reed warblers are absent.	(Rolando and Palestini, 1989)	
<b>Bicknell's thrushes (<i>Catharus bicknelli</i>) &amp; Swainson's thrushes (<i>Catharus ustulatus</i>)</b>	Aggression	Y	N	N	Playback experiments between two parapatric thrush species. Lower elevation Swainson's thrushes respond aggressively to the calls of higher elevation Bicknell's thrushes, but not vice versa. The aggressive responses of Swainson's thrush toward heterospecifics increases with altitude (i.e., closer to range boundary).	(Freeman and Montgomery, 2015)	
<b>Black-headed nightingale thrushes (<i>Catharus mexicanus</i>) &amp; ruddy-capped nightingale-thrushes (<i>Catharus frantzii</i>)</b>	Aggression	Y	N	N	Playback experiments showed that lower elevation black-capped nightingale-thrushes respond aggressively to the ruddy-capped nightingale-thrush, but not vice-versa.	(Jones <i>et al.</i> , 2020)	Habitat segregation
<b>Collared (<i>Ficedula albicollis</i>) &amp; pied (<i>Ficedula hypoleuca</i>) flycatchers</b>	Aggression	N	N	N	Collared and pied flycatchers have recently (150 years ago) come into sympatry. Collared flycatchers are more aggressive, which shifts the nest occupancy of pied flycatchers into suboptimal habitat. However, pied flycatchers that nest in suboptimal habitat are less likely to hybridise with Collared flycatchers, this reinforces the habitat use of the two species.	(Vallin <i>et al.</i> , 2012; Rybinski <i>et al.</i> , 2016)	Exploitative competition for nestboxes (but nestbox access mediated by aggression)
<b>Several species of wood wrens (<i>Henicorhina leucophrys</i> &amp; <i>Henicorhina leucosticta</i>) and thrushes (<i>Catharus mexicanus</i> &amp; <i>Catharus aurantiirostris</i>) along an elevational gradient in Costa Rica.</b>	Aggression	Y	N	N	Playback experiments show aggressive responses to heterospecific congeners, with the magnitude of such responses increase toward contact zones.	(Jankowski, Robinson and Levey, 2010)	Habitat turnover
<b>Narrow-billed woodcreepers (<i>Lepidocolaptes angustirostris</i>) &amp; scaled woodcreepers (<i>Lepidocolaptes squamatus</i>)</b>	Aggression	N	N	N	Fragmentation of the Atlantic Forest in Brazil has facilitated range expansion of narrow-billed woodcreepers. Scaled woodcreepers have been forced to recede into the remaining fragments of forest. However, narrow-billed woodcreepers regularly join mixed-species flocks within the forest and aggressively exclude scaled woodcreepers from joining flocks	(Maldonado-Coelho <i>et al.</i> , 2017)	
<b>Common nightingales (<i>Luscinia megarhynchos</i>) &amp; thrush nightingales (<i>Luscinia luscinia</i>)</b>	Aggression	N	N	N	Common and thrush nightingales are interspecifically territorial and exhibit evidence of song convergence in sympatry. This aggression drives shifts in habitat preferences in sympatry compared to allopatric populations.	(Sorjonen, 1986; Reif <i>et al.</i> , 2015, 2018)	

<b>Noisy miners (<i>Manorina melanocephala</i>) &amp; local bird assemblages</b>	Aggression	N	N	N	Noisy miners are extremely aggressive towards nearly all heterospecific birds, even those with little overlap in diet and foraging behaviour, and their presence shapes the structure of entire avian assemblages.	(Mac Nally <i>et al.</i> , 2012; Lill and Muscat, 2015)	
<b>Flame robins (<i>Petroica phoenicea</i>) &amp; Norfolk robins (<i>Petroica multicolor</i>)</b>	Aggression	N	N	N	Both species are interspecifically territorial. Migratory flame robins displace the less aggressive Norfolk robin upon returning to breeding habitat, likely displacing Norfolk robins into suboptimal habitat.	(Robinson, 1992)	
<b>Carolina chickadees (<i>Poecile carolinensis</i>) and black-capped chickadees (<i>Poecile atricapillus</i>)</b>	Aggression and Reproductive Interference	N	N	N	Carolina chickadees are more aggressive (dominant) than black-capped chickadees, and that dominant chickadees are preferred by females of both species in mate choice trials. SDMs show that Carolina chickadees' distribution limit largely matches climatic predictors, whereas black-capped chickadee distribution does not, suggesting that it is limited instead by interactions with Carolina chickadees.	(Bronson <i>et al.</i> , 2003; McQuillan and Rice, 2015)	
<b>Invasive ring-necked parakeets (<i>Psittacula krameri</i>) and native communities</b>	Aggression	N	Y	N	Invasive ring-necked parakeets tend to be dominant in aggressive interactions, and consequently the parakeets exclude other species that use tree cavities, including greater noctules ( <i>Nyctalus lasiopterus</i> ), a threatened bat species. Although many birds currently appear to benefit from parakeet aggression towards predators, greater noctules decline where parakeets occur.	(Hernández-Brito <i>et al.</i> , 2014)	
<b>Townsend's warblers (<i>Setophaga townsendi</i>) and hermit warblers (<i>Setophaga occidentalis</i>)</b>	Aggression and Reproductive Interference	N	N	N	Moving hybrid zone attributed to asymmetries in behavioural interference. Both species defend mutually exclusive territories, though Townsend warblers are likely to be more aggressive toward hermit warblers than vice versa. Similarly, though mating is largely assortative, exceptions are more likely with Townsend males mating with hermit females (not vice versa).	(Pearson, 2000; Pearson and Rohwer, 2000)	
<b>Western bluebirds (<i>Sialia mexicana</i>) &amp; mountain bluebirds (<i>Sialia currucoides</i>)</b>	Aggression	N	N	N	As western bluebirds range shifts into mountain bluebirds range, mountain bluebird populations are going locally extinct due to aggression from western bluebirds limiting nesting opportunities.	(Duckworth and Badyaev, 2007; Duckworth, 2013; Duckworth, Belloni and Anderson, 2015)	Exploitative competition for nestboxes (but nestbox access mediated by aggression)
<b>Spotted owls (<i>Strix occidentalis</i>) &amp; barred owls (<i>Strix varia</i>)</b>	Aggression	N	Y	N	Barred owls are invading spotted owls' range and driving declines in spotted owls. Playback experiments with mounts demonstrate asymmetric aggression from barred owls toward spotted owls, and tracking data suggest they exclude spotted owls from breeding territories.	(Gutiérrez <i>et al.</i> , 2007; Van Lanen <i>et al.</i> , 2011; Wiens, Anthony and Forsman, 2014)	Habitat loss, exploitative competition
<b>Dominant and subordinate congeneric birds in urban environments</b>	Aggression	N	N	Y	Subordinate species are less likely to occur and less abundant in cities where dominant species are widespread breeders (compared to in cities where the sub-dominant species is found in allopatry).	(Martin and Bonier, 2018; Martin, Burke and Bonier, 2021)	Exploitative competition for resources not ruled out
<b>Dominant and subordinate birds from North America</b>	Aggression	N	N	Y	Subordinate species migrate further distances than dominant species	(Freshwater, Ghalambor and Martin, 2014)	
<b>Birds along an elevational gradient in Borneo</b>	Aggression	Y	N	Y	Simulated intrusion paper testing whether interspecific aggression drives parapatric ranges along an elevational gradient for different pairs of birds. They found support for this hypothesis in bulbuls: ochraceous bulbuls ( <i>Alophoixus ochraceus</i> ) respond aggressively to pale-faced bulbuls ( <i>Pycnonotus leucops</i> ). However, they did not find evidence that parapatric white-eyes ( <i>Zosterops</i> sp.) are aggressive to congeners.	(Boyce and Martin, 2019)	

<b>North american perching birds (passerines)</b>	Aggression and Reproductive Interference	N	N	Y	Analyses of sister taxa show that transitions from allopatry to secondary sympatry are best predicted by the interactive effect of interspecific territoriality and hybridization.	(Cowen, Drury and Grether, 2020)	
<b>Birds along an elevational gradient in Papua New Guinea</b>	Aggression	Y	N	Y	Playback experiments on five species pairs demonstrate that the lower elevation species are more aggressive toward heterospecifics than upper elevation conspecific counterparts, and that species only engaged in aggression towards HS at the range boundary, for three of the five species pairs.	(Freeman, Class Freeman and Hochachka, 2016)	
<b>Amphibia</b>							
<b>Southern Appalachian salamander (<i>Plethodon teyahalee</i>) &amp; red-cheeked salamanders (<i>Plethodon jordani</i>)</b>	Aggression	Y	N	N	Extensive observational and experimental data (from removal experiments and behavioural experiments) demonstrate that aggressive interference is the cause of the species parapatric elevational ranges in the Great Smokey Mountains. Later modelling suggesting interspecific interactions prevent the low elevation southern Appalachian salamander from expanding into higher elevations.	(Hairston, Nishikawa and Stenhouse, 1987; Gifford and Kozak, 2012)	
<b>Actinopterygii</b>							
<b>Damselfish (<i>Dischistodus</i> spp.) in the Great Barrier Reef</b>	Aggression	N	N	N	Four species of damselfish have non overlapping habitat use within reef. Aquarium studies show the damselfish have wider habitat use than seen in the field and simulated intruder experiments in the field reveal high levels of interspecific aggression between species that use adjacent habitat.	(Bay, Jones and McCormick, 2001)	Habitat segregation
<b>Guppies (<i>Poecilia reticulata</i>) &amp; mosquitofish (<i>Gambusia affinis</i>)</b>	Reproductive Interference	N	Y	N	Mosquitofish decline upon introduction of guppies, and experimental evidence shows that reproductive interference occurs asymmetrically, with negative fitness impacts on mosquitofish, but not guppies.	(Tsurui-Sato <i>et al.</i> , 2019)	
<b>Obscure damselfish (<i>Pomacentrus adelus</i>) &amp; speckled damselfish (<i>Pomacentrus bankanensis</i>)</b>	Aggression	N	N	N	Species are interspecifically territorial, and upon removal of obscure damsels, speckled damsels expand territories to occupy vacant space, with knock-on effects for other habitat use of other reef fish.	(Eurich, McCormick and Jones, 2018)	
<b>Invasive brown trout (<i>Salmo trutta</i>) &amp; white-spotted charr (<i>Salvelinus leucomaenis</i>) in Japan</b>	Aggression	N	Y	N	Introduced brown trout has expanded throughout drainage, except upstream of weirs where white-spotted charr are more abundant. Experimental data shows that brown trout are dominant in behavioural trials.	(Takami <i>et al.</i> , 2002; Hasegawa <i>et al.</i> , 2004; Hasegawa and Maekawa, 2009)	
<b>Gopher rockfish (<i>Sebastes carnatus</i>) &amp; Black-and-yellow rockfish (<i>Sebastes chrysomelas</i>)</b>	Aggression	N	N	N	Lab experiments show interspecific aggression for territories and removal experiments in the field show that the removal of both species allows the other to expand its depth range.	(Larson, 1980)	
<b>Arachnida</b>							
<b>Invasive sheet-web spiders (<i>Linyphia triangularis</i>) &amp; bowl-and-doily spiders (<i>Frontinella communis</i>)</b>	Aggression	N	Y	N	An invasive species of spider displaces a native species from their constructed web. Furthermore, field experiments demonstrate that bowl-and-doily spiders are less likely to settle in plots where the invasive species is present and that introducing the invasive species leads to declines in bowl-and-doily spiders.	(Houser, Ginsberg and Jakob, 2014)	Exploitative competition for resources ruled out
<b>Copepoda</b>							
<b><i>Skistodiaptomus</i> copepods</b>	Reproductive Interference	N	N	N	<i>S. oregonensis</i> and <i>S. pygmaeus</i> exhibit a parapatric boundary. Laboratory studies demonstrate high levels of reproductive interference	(Thum, 2007)	Ecological gradients ruled out as possible explanation

(though no evidence of introgression), suggesting that Allee effects generated by reproductive interference maintain this parapatric boundary.

### Crustacea

<b>Invasive rusty crayfish (<i>Orconectes rusticus</i>) and native Sanborn crayfish (<i>Orconectes sanborni</i>)</b>	Aggression and Reproductive Interference	N	Y	N	An invasive crayfish ( <i>O. rusticus</i> ) that replaces native crayfish ( <i>O. sanborni</i> ) tends to be dominant, and because females of the invasive species are larger, males of the native species prefer to mate with invasive females, reducing native female fitness.	(Butler and Stein, 1985)	Juvenile susceptibility to predation of native species
<b>Invasive signal crayfish (<i>Pacifastacus leniusculus</i>) in Europe &amp; native communities</b>	Aggression and Reproductive Interference	N	Y	N	Signal crayfish have been introduced in many locations throughout Europe, and in several instances, have coincided with decline of native species. In Finland & Sweden, longitudinal data show replacement of native <i>Astacus astacus</i> , with experimental evidence that both reproductive interference and aggression implicated in the decline. Agonistic interactions with bullhead ( <i>Cottus gobio</i> ) drive bullhead out of shelters, which may explain pattern where density of signal crayfish is negatively correlated with that of bullhead.	Svärdson et al. 1991 (Söderbäck, 1994, 1995; Westman and Savolainen, 2001; Westman, Savolainen and Julkunen, 2002; Bubb et al., 2009)	Signal crayfish are resistant to crayfish plague that contributes to decline of native crayfish species; Life history traits (e.g., developmental time)

### Gastropoda

<b>Keyhole limpets (<i>Siphonaria lessonii</i>) &amp; pulmonate limpets (<i>Fissurella crassa</i>)</b>	Aggression	N	N	N	Mesocosm experiments demonstrate that large keyhole limpets aggressively displace smaller pulmonate limpets from crevices, and that displacement has fitness consequences not related to exploitative competition.	(Aguilera and Navarrete, 2012)	
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### Insecta

<b><i>Aedes</i> mosquitos (<i>Ae. albopictus</i> &amp; <i>Ae. aegypti</i>)</b>	Reproductive Interference	N	Y	N	In places where <i>Ae. aegypti</i> is established, males in invading populations of <i>Ae. albopictus</i> mate with <i>Ae. aegypti</i> females, greatly reducing their fitness and leading to replacement of <i>Ae. aegypti</i> by <i>Ae. albopictus</i> .	(Nasci, Hare and Willis, 1989; Bargielowski, Lounibos and Carrasquilla, 2013; Bargielowski and Lounibos, 2016; Lounibos and Juliano, 2018; Zhou et al., 2022)	Larval resource competition
<b>Two tick species (<i>Amblyomma variegatum</i> &amp; <i>Amblyomma hebraeum</i>)</b>	Reproductive Interference	N	N	N	Two species of tick are largely parapatric. In sympatry, interspecific copulations are commonly observed, with little geographic overlap, suggesting symmetric reproductive interference may maintain parapatric boundary.	(Bournez et al., 2015)	
<b>Whiteflies (<i>Bemisia tabaci</i> spp.)</b>	Reproductive Interference	N	Y	N	Invading whitefly species have replaced native strains in several locations owing to asymmetric reproductive interference, in which matings from invading males reduce fitness of native females.	(Liu et al., 2007; Crowder et al., 2011; Wang, Crowder and Liu, 2012)	Life history traits (e.g., developmental time, relative fecundity; though not sufficient without asymmetric reproductive interference to explain rapid replacement)
<b>Invasive buff-tailed bumblebees (<i>Bombus terrestris</i>) &amp; native bumblebees (<i>Bombus h. sapporoensis</i> 7 <i>Bombus ignitus</i>) in Japan</b>	Reproductive Interference	N	Y	N	The invasive bumblebee species <i>bombus terrestris</i> engages in reproductive interference with two species of native bumblebee. Copulation between <i>B. terrestris</i> and <i>B. h. sapporoensis</i> or <i>B. ignitus</i> results in unviable eggs being laid the following spring, driving declines native bumblebee species.	(Tsuchida et al., 2019)	Exploitative competition for nectar and nest sites

<b>Rubyspot damselflies (<i>Hetaerina</i> spp.)</b>	Aggression	N	N	Y	Rubyspot damselflies, which engage in high levels of reproductive interference and interspecific territoriality, have diverged in microhabitat use in a way that reduces the effects of behavioural interference.	(McEachin <i>et al.</i> , 2022)	
<b>Two ant species (<i>Iridomyrmex</i> spp.)</b>	Aggression	N	N	N	Removal experiments that two species hold mutually exclusive territories and compete for space to build colonies. Over a short period of time (11 months), one species ("C") replaced by another ("A"), in part due to asymmetric competition.	(Haering and Fox, 1987)	Habitational succession
<b>Arboreal termite species in Papua New Guinea (<i>Microcerotermes biroi</i>, <i>Nasutitermes novarumhebridarum</i>, &amp; <i>Nasutitermes princeps</i>)</b>	Aggression	N	N	Y	Long term mapping of arboreal termite nests and their territories in combination with behavioural observations shows that species defend mutually exclusive territories. Removal experiments of <i>N. princeps</i> drives concomitant increase in <i>M. biroi</i> home range.	(Leponce, Roisin and Pasteels, 1997)	
<b>White-crossed seed bugs (<i>Neacoryphus bicrurus</i>) and co-occurring insect communities</b>	Aggression and Reproductive Interference	N	N	N	White-crossed seed bugs engage in asymmetrical reproductive interference (misdirected courtship) and aggression towards many species, and removal experiments demonstrate that several other species increase in density when white-crossed seed bugs are removed.	(McLain and Shure, 1987)	
<b>Invasive southern green stink bugs (<i>Nezara viridula</i>) &amp; native green stink bugs (<i>Nezara antennata</i>)</b>	Reproductive Interference	N	Y	N	Invasive southern green stink bugs are expanding in Japan into the range of and replacing native green stink bugs. In regions of coexistence, heterospecific copulations are commonly observed, and reproductive interference is suspected to drive declines of native species.	(Kiritani, 2011)	Shifting climatic suitability
<b>Alpine dark bush-crickets (<i>Pholidoptera aptera</i>) &amp; Transylvanian dark bush-crickets (<i>Pholidoptera transsylvanica</i>)</b>	Reproductive Interference	N	N	N	Bush-crickets exhibit a 'mosaic' pattern of distribution, where the two species are rarely found in syntopy. Experiments demonstrate that heterospecific matings resulting in transfer of spermatophores are common.	(Dorková <i>et al.</i> , 2020)	Habitat segregation ruled out
<b>Eastern subterranean termites (<i>Reticulitermes flavipes</i>) &amp; Western subterranean termites (<i>Reticulitermes grassei</i>)</b>	Aggression	N	Y	N	Invasive eastern subterranean termites are dominant in aggressive interactions over native western subterranean termites; success of invasion is attributed to this asymmetry.	(Perdereau <i>et al.</i> , 2011)	Lack of intraspecific aggression in invasive species; demographic factors (large colony size)
<b>Invasive Asian blue ticks (<i>Rhipicephalus [Boophilus] microplus</i>) &amp; African blue ticks (<i>Rhipicephalus [Boophilus] decoloratus</i>) in South Africa</b>	Reproductive Interference	N	Y	N	Invasive Asian blue ticks have replaced African blue ticks in South Africa. Interspecific matings lead to sterile hybrids, so rapid demographic increases in invader populations lead to Allee effects driving local extinction of native species.	(Sutherst, 1987; Tønnesen <i>et al.</i> , 2004, 2004)	Life history traits (e.g., developmental time); host resistance
<b>Cepero's groundhoppers (<i>Tetrix ceperoi</i>) &amp; slender groundhoppers (<i>Tetrix subulata</i>)</b>	Reproductive Interference	N	N	N	Groundhoppers exhibit a 'mosaic' pattern of distribution, where the two species are rarely found in syntopy. Laboratory and field experiments demonstrate that extensive reproductive interference is likely responsible for this spatial distribution.	(Gröning <i>et al.</i> , 2007; Hochkirch, Gröning and Bücken, 2007; Hochkirch and Gröning, 2012)	Habitat segregation ruled out
<b>Arboreal ant species in Papua New Guinea</b>	Aggression	N	N	Y	Colony mapping and behavioural experiments demonstrate that interspecific aggression is the key factor shaping the spatial distribution of ant species in a 9 hectare plot	(Mottl <i>et al.</i> , 2021)	Habitat segregation ruled out
<b>Mammalia</b>							

<b>Fallow deer (<i>Dama dama</i>) &amp; roe deer (<i>Capreolus capreolus</i>)</b>	Aggression	N	Y	N	Fallow deer displace roe deer but not vice versa, and that habitat use by roe deer is affected by presence of fallow deer. Together, these suggest behavioural interference has led to decline in roe deer populations as fallow deer populations have increased.	(Ferretti and Mori, 2020)	Exploitative competition for resources not ruled out
<b>White-handed gibbons (<i>Hylobates lar</i>) &amp; Pileated gibbons (<i>Hylobates pileatus</i>)</b>	Aggression	N	N	N	Two species of gibbon are largely parapatric, with a small contact zone that is maintained by interspecific territorial aggression.	(Suwanvecho and Brockelman, 2012; Asensio <i>et al.</i> , 2017)	Niche partitioning (via habitat segregation or diet divergence) ruled out.
<b>Least chipmunks (<i>Neotamias minimus</i>) &amp; yellow-pine chipmunks (<i>Neotamias amoenus</i>)</b>	Aggression	Y	N	N	Removal experiments of two species of chipmunk that engage in aggressive interference. When yellow-pine chipmunks were removed, least chipmunks captures increased; the converse did not occur.	(Chappell, 1978; Heller, no date)	
<b>Townsend's chipmunks (<i>Neotamias townsendii</i>) &amp; yellow-pine chipmunks (<i>Neotamias amoenus</i>)</b>	Aggression	N	N	N	Removal experiments of two species of chipmunk that engage in aggressive interactions with one another show that when heterospecifics are removed, the range size of the retained species and juvenile recruitment increases.	(Trombulak, 1985)	Habitat segregation ruled out
<b>Uinta chipmunks (<i>Neotamias umbrinus</i>) &amp; Colorado chipmunks (<i>Neotamias quadrivittatus</i>)</b>	Aggression	Y	N	N	Colorado chipmunks cannot move into higher elevational because of aggressive interactions with Uinta chipmunks. Uinta chipmunks hypothesised to be restricted to higher elevations because of the high parasitic load of a bot fly found at lower elevations.	(Bergstrom, 1992)	
<b>Stoats (<i>Mustela erminea</i>) &amp; least weasels (<i>Mustela nivalis</i>)</b>	Aggression	N	N	N	Experimental data demonstrates that stoats are dominant over weasels, and observational data shows that weasels are very rarely found in preferred habitat when a stoats held a territory in the area. Distributional data collected over several years shows that when stoats declined, weasels increased locally.	(Erlinge and Sandell, 1988)	
<b>Pied tamarins (<i>Saguinus bicolor</i>) &amp; Golden-handed tamarins (<i>Saguinus midas</i>)</b>	Aggression	N	N	N	Playback experiment of two species on Tamarin, in allopatry and sympatry. Pied tamarins are critically endangered and experiencing range fragmentation, while red-handed tamarins have expanded their range into the range of pied tamarins. Playback experiments show that red-handed tamarin respond more aggressively than the pied tamarins.	(Sobroza <i>et al.</i> , 2021)	
<b>Chiriquí singing mice (<i>Scotinomys xerampelinus</i>) &amp; Alston's singing mice (<i>Scotinomys teguina</i>)</b>	Aggression	Y	N	N	Playback experiments, laboratory experiments, and removal experiments all demonstrate that the higher elevation species ( <i>Scotinomys xerampelinus</i> ) is dominant and preempts range intrusions from lower elevation species. In removal experiments, <i>Scotinomys xerampelinus</i> didn't descend to occupy areas where <i>Scotinomys teguina</i> was removed, but <i>Scotinomys teguina</i> did invade higher elevation areas when <i>Scotinomys xerampelinus</i> was removed.	(Pasch, Bolker and Phelps, 2013)	
<b>Reptilia</b>							
<b>Invasive house geckos (<i>Hemidactylus frenatus</i>) &amp; native communities</b>	Aggression and Reproductive Interference	N	Y	N	Comprehensive longitudinal data, in combination with laboratory and field experiments, show that introduced house geckos are aggressive to and avoided by native species, leading to the decline of native species across many different locations. Reproductive interference has also been demonstrated in some locations.	(Bolger and Case, 1992; Petren, Bolger and Case, 1993; Case, Bolger and Petren, 1994; Dame and Petren, 2006)	Competitive exclusion due to differential resource acquisition (though this results from interference competition)

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