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

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Novel biotic interactions in shifting communities play a key role in determining the ability of species' ranges to track suitable habitat. To date, the impact of biotic interactions on range dynamics have predominantly been studied in the context of interactions between different trophic levels or, to a lesser extent, exploitative competition between species of the same trophic level. Yet, both theory and a growing number of empirical studies show that interspecific behavioural interference, such as interspecific territorial and mating interactions, can slow down range expansions, preclude coexistence, or drive local extinction, even in the absence of resource competition. We conducted a systematic review of the current empirical research into the consequences of interspecific behavioural interference on range dynamics. Our findings demonstrate there is abundant evidence that behavioural interference by one species can impact the spatial distribution of another. Furthermore, we identify several gaps where more empirical work is needed to robustly test predictions from theory. Finally, we outline several avenues for future research, providing suggestions for how interspecific behavioural interference could be incorporated into existing scientific frameworks for understanding how biotic interactions influence range expansions, such as species distribution models, to build a stronger understanding of the potential consequences of behavioural interference on the outcome of future range dynamics. *Keywords* (5-10) interspecific behavioural interference, reproductive interference, interspecific aggression,

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range dynamics, systematic review, elevational gradients, invasion biology, range shift

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#### I. Introduction

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As anthropogenic changes continue to alter the availability and distribution of habitats, the spatial distribution of species' niches will shift, in turn driving shifts in species' ranges (Parmesan and Yohe 2003). Given that species vary in their niches and in their responses to environmental change, communities will not shift in concert, resulting in a global reshuffling of diversity and the formation of novel species assemblages. Similarly, invasions due to anthropogenic factors can have disruptive effects on species assemblages. Interactions between species—whether between previously coexisting species or between newly co-occurring species in shifting communities—play key roles in determining the ability of species' ranges to track suitable habitats (Alexander, Diez, and Levine 2015; Blois et al. 2013; Early and Keith 2019; Ockendon et al. 2014). For instance, the arrival of novel predators can drive prey species to extinction (e.g., brown tree snakes [Boiga irregularis] drove the local extinction of several bird species after they were introduced to Guam, (Savidge 1987); conversely, the local extinction of one species can destabilize interaction networks, driving secondary extinctions (e.g., experimental removal of a keystone predator [Pisaster ochraceus] led to a decline in diversity in the marine intertidal zone, (Paine 1966)). By and large, studies on the impacts of biotic interactions on population and range dynamics have predominantly focused on interactions across trophic levels or, to a lesser extent, exploitative competition between species of the same trophic level (Sirén and Morelli 2020; Early and Keith 2019; Louthan, Doak, and Angert 2015; Svenning et al. 2014; Legault et al. 2020; Ortego and Knowles 2020). Yet, an important type of competition between closely related animal species is often overlooked: interspecific behavioural interference (Grether et al. 2017). Behavioural interference encompasses any aggressive or mating behaviour by one species that is directed toward and has a negative impact on the fitness of another species (Grether et al. 2017;

Gröning and Hochkirch 2008; Burdfield-Steel and Shuker 2011). For instance, both territorial aggression between individuals of different species and courtship displays directed by males of one species toward females of another species fall under the umbrella of 'behavioural interference'. Behavioural interference has been documented across a wide range of taxa (Gröning and Hochkirch 2008; Peiman and Robinson 2010), and in general, such aggressive and sexual interactions arise between species that are phenotypically and ecologically similar owing to recent shared ancestry (e.g., species with similar sexual signals and/or perceptual systems), though in some cases, behavioural interference may occur across large phylogenetic distances (e.g., indiscriminate aggression from noisy miners toward a broad range of bird species throughout much of Australia, MacNally et al. 2012, Fig. 1C). Such interactions are costly and lead to decreased fitness as individuals waste energy, are driven to use suboptimal habitat, or miss out on mating opportunities with conspecifics. Consequently, behavioural interference can decrease population growth rates, cause exclusion from adequate habitat, and reduce or prevent dispersal into novel areas (Grether et al. 2017). Thus, interspecific behavioural interference is likely to have important impacts on range dynamics. Several theoretical investigations of behavioural interference have modelled the factors that promote or preclude coexistence (T. J. Case and Gilpin 1974; Kuno 1992; Liou and Price 1994; Amarasekare 2002; Mikami and Kawata 2004; Kishi and Nakazawa 2013; Kyogoku and Sota 2017; Iritani and Noriyuki 2021; Irwin and Schluter 2022; Grether and Okamoto 2022) and a handful have even explicitly analysed how processes affecting coexistence locally scale up to influence the outcome of movement across landscapes (Ribeiro and Spielman 1986; Crowder et al. 2011; Nishida, Takakura, and Iwao 2015; Ruokolainen and Hanski 2016; Legault et al. 2020). One key insight from these models is that the impact of interspecific behavioural interference will be highest on the rarer species, and the magnitude of this impact increases as the asymmetry in frequency increases (e.g.,

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Amarasekare 2002; Kuno 1992). In other words, as interactions between the rarer species and heterospecifics become increasingly more common than interactions with conspecifics. Consequently, Allee effects resulting from behavioural interference may make it very difficult for viable populations to become established in novel geographic areas (Grether et al. 2017) or may drive precipitous local extinction once population densities fall below a certain threshold. A common result in models incorporating behavioural interference is the formation and maintenance of abutting (parapatric) range limits, which may move according to the magnitude of and degree of asymmetry in interference (Ribeiro and Spielman 1986; Nishida, Takakura, and Iwao 2015). Another insight from these models relates to the interactive effect of resource competition and behavioural interference—several models also show dynamics of systems with both resource competition and behavioural interference are markedly different than systems with resource competition alone (Ribeiro and Spielman 1986; Amarasekare 2002; Crowder et al. 2011), which underscores the importance of further research into behavioural interference in attempts at predicting species responses to shifting assemblages.

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

## II. Systematic literature review

119	To identify examples of interspecific behavioural interference influencing the spatial
120	distribution of a species, we conducted a literature search using the "all databases" option in
121	Web of Science ( <a href="https://www.webofscience.com/">https://www.webofscience.com/</a> ). We used the search term
122	"TS=(((behaviour* OR behavior*) NEAR/6 interference) OR (reproduct* NEAR/6
123	interference) OR (interspecific NEAR/6 (behaviour* OR behavior*) NEAR/6 competition)
124	OR ((interspecific OR heterospecific) NEAR/6 aggress*) OR ((interspecific OR
125	heterospecific) NEAR/6 dominan*) OR ((interspecific OR heterospecific) NEAR/6 territor*)
126	OR ((interspecific OR heterospecific) NEAR/6 interference) OR (sister AND (taxa OR
127	species) AND (competition OR aggress* OR territor*OR dominan* OR interference))) AND
128	TS= ((range* NEAR/6 shift*) OR (species NEAR/6 distribution*) OR (range* NEAR/6
129	expansion*) OR (range* NEAR/6 dynamic*) OR (species NEAR/6 displace*) OR (species
130	NEAR/6 replace*) OR (Altitud* NEAR/6 (zonat* OR zone)))" (NEAR/6 returns search results
131	that contain the first phrase within six words of the later phrase). While we designed this set
132	of search terms to focus on behavioural interference, we note that hybridization falls under
133	the general umbrella term of 'reproductive interference'. There is a large, related literature
134	covering the spatial dynamics of hybrid zones (Barton 1979; Barton and Hewitt 1989; Buggs
135	2007), which focuses on the way that clines form in the presence of selection acting on
136	hybrid genotypes. Here, however, we focus on the outcome of reproductive behavioural
137	interactions per se, regardless of whether those interactions result in the formation of hybrids.
138	We note that, although some treatments of reproductive interference include aggression in the
139	context of access to mates (e.g., Groning & Hochkirk 2008), we follow recent literature on
140	behavioural interference in classifying all agonistic interactions directed toward
141	heterospecifics as agonistic interference (Grether et al. 2017).
142	As of the search date (2022-10-13), we obtained a database of 338 unique peer-
143	reviewed articles, which both authors contributed to reading and extracting data from. To

reduce bias in data extraction between readers, the first 37 papers (10%) were independently read by both of us and data extraction compared. Across all 37 papers, the interpretation of the paper and data extracted was concordant. We only included cases for which there are direct observations of interspecific behavioural interference and an explicit link between that interference to spatial dynamics, which totalled 72 papers in our final set. For instance, in cases where species have abutting boundaries (e.g., parapatric range limits), we only included cases where behavioural interference has been documented and this boundary does not also coincide with clear shifts in habitat types. Similarly, for instances of microhabitat segregation or mosaic distribution patterns, we required the study to demonstrate that shifts in habitat use directly result from behavioural interference. While reading these papers, we also noted papers that the authors cited as further evidence for behavioural interference and/or range dynamics within their own or other study systems which added 26 additional papers to our final set. Of the 98 studies in our final set, 62 studies provided clear evidence that interspecific behavioural interference impacts the spatial distribution of a species, with 19 additional studies providing corroborating evidence in combination with other papers. The remaining papers either found no effect (n = 15) or were inconclusive (n = 2). The 81 papers that, either provide evidence directly or in collaboration with other studies, found clear evidence in favour of interspecific behavioural interference impacting the spatial distribution of a species and were sorted into 54 unique study systems (Figure 1, Table 1). Each of the 54 study systems is descripted in greater detail in Supplementary Table 1.

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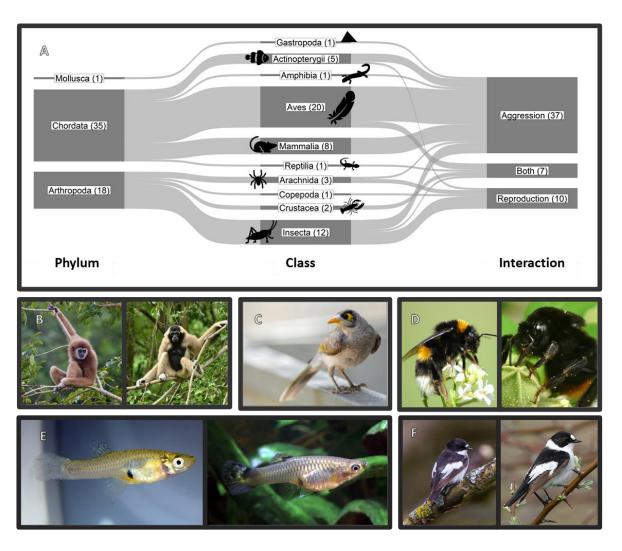


Figure 1. There is widespread evidence that behavioural interference (costly aggressive or reproductive interactions between species) influences spatial dynamics in animals. **A**. The breakdown of study systems that directly measured the impact of interspecific behavioural interference on the spatial distribution of one of more species by phylum, class, and whether the study covered aggressive, reproductive behavioural interference, or both. All study systems investigated the impact of intraclass behavioural interference, except for one case of interphylum behavioural interference between a Crustacean and Actinopterygii (Bubb et al. 2009). The interphyla system is counted here as Crustacea study as the crustacean was the more aggressive species. The Sankey diagram was created using the R package ggsankey (https://github.com/davidsjoberg/ggsankey). **B.** In Thailand, white-handed gibbons (*Hylobates lar*) (left) and pileated gibbons (*Hylobates pileatus*) (right) are interspecifically

territorial at their parapatric range boundary, reinforcing that boundary and, likely, decreasing
the frequency of hybridization (Asensio et al. 2017). C. Indiscriminate hyperaggression of
Noisy miners (Manorina melanocephala) has led to shift in the whole structure of avian
communities (Mac Nally et al. 2012). <b>D.</b> In Japan, the invasive bumblebee <i>Bombus terrestris</i>
(left) engages in reproductive interference with two species of native bumblebee species,
driving rapid declines in B. ignities (right) and B. h. sapporeenis (Tsuchida et al. 2019). E.
The accidental introduction of guppies (Poecilia reticulata) (left) led to the eradication of
invasive mosquito fish (Gambusia affinis) (right) in Okinawa owing to reproductive
interference, and consequently guppies have been proposed as a potential control agent for
mosquito fish elsewhere (Tsurui-Sato et al. 2019). F. Pied flycatchers (Ficedula hypoleuca)
(left) are driven to use sub-optimal habitat by the high aggression of collared flycatchers
(Ficedula albicollis) (right) (Vallin et al. 2012; Rybinski et al. 2016). All photos under
creative commons by Wikimedia-user:Kongkham6211, JJ Harrison, flickr-
user:coniferconifer, Vera Buhl, Rex Boggs, Andrej Chudý, Ron Knight, Holger Krisp, and
Wikimedia-user:Fredlyfish4.

**Table 1:** All 54 study systems identified during the literature review that found clear evidence that interspecific behavioural interference (IBI) impacts the spatial distribution of a species. An expanded table which includes a description of each study system can be found in Supplementary Table 1. The elevational column indicates whether the study investigated range dynamics across an elevational gradient. The invasion column indicates whether the study contained a species outside of its native range. The comparative column indicates whether the study examined variation in behavioural interference across many species and/or environments.

Interacting Species	IBI Type	Elevational (Y/N)	Invasion (Y/N)	Comparative (Y/N)	References
Aves					
Great reed warblers ( <i>Acrocephalus arundinaceus</i> ) & marsh warblers ( <i>Acrocephalus palustris</i> )	Aggression	N	N	N	(Rolando and Palestrini 1989)
Bicknell's thrushes (Catharus bicknelli) & Swainson's thrushes (Catharus ustulatus)	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 (Ficedula albicollis) & pied (Ficedula hypoleuca) flycatchers	Aggression	N	N	N	(Vallin et al. 2012; Rybinski et al. 2016)
Several species of wood wrens (Henicorhina leucophrys & Henicorhina leucosticta) and thrushes (Catharus mexicanus & Catharus aurantiirostris) 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 (Petroica phoenicea) & Norfolk robins (Petroica multicolor)	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 (Psittacula krameri) and native communities	Aggression	N	Y	N	(Hernández-Brito et al. 2014)
Townsend's warblers (Setophaga townsendi) and hermit warblers (Setophaga occidentalis)	Aggression and Reproductive Interference	N	N	N	(Pearson 2000; Pearson and Rohwer 2000)
Western bluebirds (Sialia mexicana) & mountain bluebirds (Sialia currucoides)	Aggression	N	N	N	(Duckworth and Badyaev 2007; Duckworth 2013; Duckworth, Belloni, and Anderson 2015)
Spotted owls (Strix occidentalis) & barred owls (Strix varia)	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 Reproductive Interference	N	N	Y	(Cowen, Drury, and Grether 2020)
Birds along an elevational gradient in Papua New Guinea	Aggression	Y	N	Y	(Freeman, Class Freeman, and Hochachka 2016)
Amphibia					
Southern Appalachian salamander (Plethodon teyahalee) & red-cheeked salamanders (Plethodon jordani)	Aggression	Y	N	N	(Hairston, Nishikawa, and Stenhouse 1987; Gifford and Kozak 2012)
Actinopterygii					
Damselfish ( <i>Dischistodus</i> spp.) in the Great Barrier Reef	Aggression	N	N	N	(Bay, Jones, and McCormick 2001)
Guppies (Poecilia reticulata) & mosquitofish (Gambusia affinis)	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 (Salmo trutta) & white- spotted charr (Salvelinus leucomaenis) in Japan	Aggression	N	Y	N	(Takami et al. 2002; Hasegawa et al. 2004; Hasegawa and Maekawa 2009)
Gopher rockfish (Sebastes carnatus) & Black- and-yellow rockfish (Sebastes chrysomelas)	Aggression	N	N	N	(Larson 1980)
Arachnida					
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)
Copepoda					
Skistodiaptomus copepods	Reproductive Interference	N	N	N	(Thum 2007)
Crustacea					
Invasive rusty crayfish (Orconectes rusticus) and native Sanborn crayfish (Orconectes sanborni)	Aggression and Reproductive Interference	N	Y	N	(Butler and Stein 1985)
Invasive signal crayfish ( <i>Pacifastacus leniusculus</i> ) in Europe & native communities. This includes an example interphylum behavioural interference: aggression by signal crayfish toward native bullhead fish ( <i>Cottus gobio</i> ).	Aggression and Reproductive Interference	N	Y	N	(Björn Söderbäck 1994; B. Söderbäck 1995; Westman and Savolainen 2001; Westman, Savolainen, and Julkunen 2002; Bubb et al. 2009; Svärdson, Fürst, and Fjälling 1991)
Gastropoda					
Keyhole limpets (Siphonaria lessonii) & pulmonate limpets (Fissurella crassa)	Aggression	N	N	N	(Aguilera and Navarrete 2012)
Insecta					
Aedes mosquitos (Ae. albopictus & Ae. aegypti)	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 (Amblyomma variegatum & Amblyomma hebraeum)	Reproductive Interference	N	N	N	(Bournez et al. 2015)
Whiteflies (Bemisia tabaci spp.)	Reproductive Interference	N	Y	N	(Liu et al. 2007; Crowder et al. 2011; Wang, Crowder, and Liu 2012)
Invasive buff-tailed bumblebees (Bombus terrestris) & native bumblebees (Bombus h. sapporoensis & Bombus ignitus) in Japan	Reproductive Interference	N	Y	N	(Tsuchida et al. 2019)
Rubyspot damselflies (Hetaerina spp.)	Aggression	N	N	Y	(McEachin et al. 2022)
Two ant species (Iridomyrmex spp.)	Aggression	N	N	N	(Haering and Fox 1987)
Arboreal termite species in Papua New Guinea (Microcerotermes biroi, Nasutitermes novarumhebridiarum, & Nasutitermes princeps)	Aggression	N	N	Y	(Leponce, Roisin, and Pasteels 1997)
White-crossed seed bugs (Neacoryphus bicrurus) and co-occurring insect communities	Aggression and Reproductive Interference	N	N	N	(McLain and Shure 1987)
Invasive southern green stink bugs (Nezara viridula) & native green stink bugs (Nezara antennata)	Reproductive Interference	N	Y	N	(Kiritani 2011)
Alpine dark bush-crickets ( <i>Pholidoptera aptera</i> ) & Transylvanian dark bush-crickets ( <i>Pholidoptera transsylvanica</i> )	Reproductive Interference	N	N	N	(Dorková et al. 2020)
Eastern subterranean termites (Reticulitermes flavipes) & Western subterranean termites (Reticulitermes grassei)	Aggression	N	Y	N	(Perdereau et al. 2011)
Invasive Asian blue ticks (Rhipicephalus [Boophilus] microplus) & African blue ticks (Rhipicephalus [Boophilus] decoloratus) 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)
Mammalia					
Fallow deer (Dama dama) & roe deer (Capreolus capreolus)	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 (Neotamias minimus) & yellow- pine chipmunks (Neotamias amoenus)	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 (Mustela erminea) & least weasels (Mustela nivalis)	Aggression	N	N	N	(Erlinge and Sandell 1988)
Pied tamarins (Saguinus bicolor) & Golden- handed tamarins (Saguinus midas)	Aggression	N	N	N	(Sobroza et al. 2021)
Chiriquí singing mice (Scotinomys xerampelinus) & Alston's singing mice (Scotinomys teguina)	Aggression	Y	N	N	(Pasch, Bolker, and Phelps 2013)
Reptilia					
Invasive house geckos (Hemidactylus frenatus) & 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)

## (1) Reproductive interference versus interspecific aggression

Our search terms returned more study systems where aggressive interference (n = 44) influenced range dynamics than reproductive interference (n = 17) (Figure 1A, Table 1, Supplementary Table 1). At face value, these figures suggest that competitive exclusion via aggressive interference is more widespread than sexual exclusion. Yet, this conclusion may be premature. For one thing, we avoided searching for cases of hybrid tension zones (see "Systematic literature review", above), and hybridization is among the more highly studied forms of reproductive interference. Moreover, other forms of reproductive interference include behaviours such as misdirected courtship, signal jamming, and heterospecific mating (Groning & Hochkirch 2008), all of which are difficult to detect, especially in species where these processes occur rapidly.

Seven study systems found that both reproductive and aggression influence range dynamics. For instance, where collared (*Ficedula albicollis*) & pied (*Ficedula hypoleuca*) flycatchers have recently (150 years ago) come into sympatry (Fig. 1F), 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, which reenforces the habitat segregation of the two species (Vallin et al. 2012). Given that interspecific aggression often arises as an adaptive response to reproductive interference (Drury et al. 2015; Drury, Cowen, and Grether 2020; Grether et al. 2020; Payne 1980), the abundance of examples of aggressive interference influencing spatial dynamics in vertebrates may be indicative of undetected reproductive interference. Further empirical and theoretical work would help clarify the relative importance as well as the interactive, potentially non-additive, impacts of different types of behavioural interference on spatial dynamics.

The taxonomic distribution of case studies was the most apparent difference among the factors associated with different types of behavioural interference (Figure 1). Most examples of reproductive interference influencing range dynamics were conducted on arthropods (9 out of 10). This contrasts with studies of aggressive interference that were dominated by vertebrates (30 out of 37), especially birds (n = 17). Empirical examples of reproductive interference are taxonomically widespread (Gröning and Hochkirch 2008), so it is surprising to see that evidence of reproductive interference influencing the spatial dynamics of a species come predominantly from insects and arachnids. One potential explanation for this apparent bias is that it reflects a biological reality about the costs of reproductive interference in arthropods; the fitness cost of reproductive interference may be especially high in arthropods because of females' short reproductive lifespans, and, because in some species, females produce no viable offspring after interspecific mating (Ribeiro and Spielman 1986), which makes a species particularly vulnerable to local extinction (Irwin and Schluter 2022). Alternatively, the bias may reflect a methodological convenience of working with invertebrates—reproductive interference may be hard to measure in the field without experimental mating trials, making larger scale field research of the sort necessary to build a link between reproductive interference and range dynamics more feasible on arthropods.

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## (2) Elevational gradients

Range dynamics along elevational gradients have long been of interest to ecologists and evolutionary biologists. For instance, a classic hypothesis posits that abiotic factors are likely to play a more important role than biotic factors at high-elevation range limits (Louthan, Doak, and Angert 2015). As a result, there may be an increased risk of extinction in montane ecosystems caused by the 'escalator to extinction' (Sekercioglu et al. 2008; Freeman et al. 2018) in which warming conditions cause high-elevation species' climate

niches to disappear. Given the interest in biotic interactions along elevational gradients, it is not surprising that we identified multiple examples of interspecific behavioural interference of one species influencing the elevational distribution of another species (17% of cases documenting an impact of behavioural interference on range dynamics). Due to rapid habitat turnover with altitude, range boundaries across elevational gradient are often sharply defined, making studies of range limits inherently simpler along an elevational gradient (Žagar et al. 2015; Pasch, Bolker, and Phelps 2013; Jones et al. 2020), so it would be premature to conclude how likely that behavioural interference is to influence elevational range limits in comparison to range boundaries across landscape scales.

Several key patterns emerge from studies along elevational gradients. First, interspecific territoriality plays a key role in creating and maintaining elevational range limits. Comparative analyses, for instance, have shown that bird species have wider elevational ranges in mountains without competitors (Burner et al. 2020). Additionally, the response of several species of montane birds to heterospecific songs decreases with distance from their parapatric boundary, indicating a learned response to the presence of an aggressive congener (Jankowski, Robinson, and Levey 2010; Freeman and Montgomery 2015; Freeman, Class Freeman, and Hochachka 2016; Jones et al. 2020; Boyce and Martin 2019). Secondly, asymmetries in dominance are not consistently biased in favour of low elevation species, as there are examples of species pairs with subordinate high elevation species (e.g., Catharus thrushes, (Freeman and Montgomery 2015) and of pairs in which the lower elevation species is subordinate (e.g., Scotinomys singing mice (Pasch, Bolker, and Phelps 2013), Neotamias chipmunks (Bergstrom 1992) and, if aquatic depth gradients are comparable to elevational gradients, *Pomacentrus* damselfish (Eurich, McCormick, and Jones 2018)) (see also Freeman 2020). These examples demonstrate the varied and often unpredictable role that behavioural interference can play in influencing elevational range limits, thereby challenging the

hypothesis that abiotic factors are likely to play a more important role than biotic factors at high-elevation range limits (Louthan, Doak, and Angert 2015). Finally, we also note a bias in the geographic locations of studies investigating behavioural interference across elevational gradients, with two exceptions in Borneo and Papa New Guinea, all study systems were located Northern and Central America (Figure 2). Studies across landscapes were found across a wider area, but still with noted gaps in Africa and Asia, likely due to an underlying geographic bias in scientific research (Culumber et al. 2019).

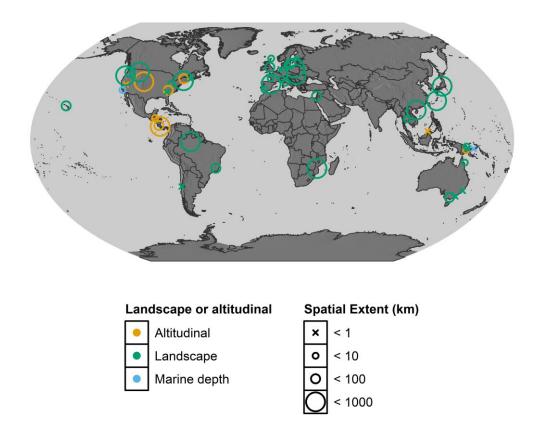


Figure 2. The global distribution of field studies that found an effect of interspecific behavioural interference on the spatial distribution of one or more species. Colour denotes whether the study investigated the spatial distributions across a landscape (i.e., latitude and longitude), across an elevational gradient (altitudinal), or across a sea-depth gradient (marine depth). Size indicates the maximum spatial extent for where data was collected for study but is not to scale, excluding comparative studies that had a greater than 1000km global distribution (n = 7). Across landscapes, we found examples of behavioural interference influencing the spatial distributions of species in studies ranging in spatial scope from local (<1km) scales (e.g. Hochkirch and Gröning 2012, found that, within a single nature reserve, reproductive interference causes two groundhopper species to exhibit a mosaic of small scale habitat use) to continental (<1000km) scales (e.g. Reif et al. 2018; 2015, found that across

Eastern Europe, aggression drives shifts in habitat preferences in sympatry compared to
allopatric populations of common *Luscinia megarhynchos*, and thrush nightingales, *Luscinia*luscinia).

## (3) Invasion biology

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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 (Fig. 1D). 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. sapporeenis 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).

Yet, behavioural interference is not always beneficial to invasive species and detrimental to native species. Invasive species may be unable to establish in areas which contain a more aggressive congener, and higher levels of aggressive or reproductive interference could allow native species to tolerate the presence of the invading species (Crowder et al. 2011), or even prevent its spread. For instance Australian house geckos, *Gehyra dubia*, are more aggressive than the globally invasive Asian house gecko, *Hemidactylus frenatus* which could prevent the invasive species replacing the native (Cisterne, Schwarzkopf, and Pike 2019). Additionally, conservation efforts towards the critically endangered Nashville crayfish, *Orconectes shoupi*, may be aided by its higher aggression toward the invasive bigclaw crayfish, *Orconectes placid* (Bizwell and Mattingly 2010). Whether asymmetries in behavioural interference generally influence the outcome of translocations of animal species is, therefore, an important open question.

In addition to being a potentially accelerating factor in biological invasions, behavioural interference has also been suggested as a management tool for invasive species. On Okinawa, for instance, the accidental introduction of guppies (*Poecilia reticulata*) led to the eradication of invasive mosquito fish (*Gambusia affinis*) (Fig. 1E, Tsurui-Sato et al. 2019). Laboratory experiments indicate that male guppies attempt to mate with female mosquito fish, thereby reducing their reproductive output. Introduced guppies also have negative impacts on native taxa, but by introducing only males, or mixed populations into environments with lethal winter temperatures, guppies could be used to eradicate mosquito fish from other river systems (Tsurui-Sato et al. 2019). Similarly, a study on aggression between invasive brown trout and native white-spotted charr demonstrated that habitat modifications in the form of visual barriers could reduce observed levels of interspecific aggression (Hasegawa & Maekawa 2009).

## (4) Empirical validation of theoretical predictions

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The formation of parapatric ranges, where two species have adjacent ranges with little or no overlap, is a key prediction of the theorical models of how interspecific behavioural interference impacts range dynamics when the impacts of behavioural interference are symmetrical (Ribeiro and Spielman 1986). In line with this prediction, we found that, where the impact of behavioural interference is equal, the ranges of interacting species pairs are stable (Asensio et al. 2017; Bull and Burzacott 1994; Thum 2007). For instance, in Thailand, two species of gibbon, white-handed gibbons (Hylobates lar) and pileated gibbons (Hylobates pileatus), have a parapatric distribution with only a small (<1km wide) boundary where the species are found in sympatry. Both H. lar and H. pileatus hold territories that are controlled exclusively by monogamous pairs. Detailed mapping of territories and observation of conflict events show that, where the two species are found in sympatry, pairs of both species defend territories against both conspecifics and heterospecifics (Fig. 1B, Asensio et al. 2017). If the impact of behavioural interference is asymmetrical, however, replacement of one species by the other commonly results (Tønnesen et al. 2004; Tsuchida et al. 2019; Tsurui-Sato et al. 2019; Duckworth and Badyaev 2007; Vallin et al. 2012; Sobroza et al. 2021). Some studies found that the ranges of the two species were stable even in the presence of asymmetrical behavioural interference because the more dominant species was limited by an abiotic or a different biotic factor (Pasch, Bolker, and Phelps 2013; Bergstrom 1992). Although Allee effects are common in theoretical models of behavioural interference, relatively few case studies identified by our literature review explicitly tested for Allee effects, though several investigators of these studies suggest that Allee effects generate range turnovers (Soderback 1994, Tønnesen et al. 2004, Thum 2007, Kiritani 2011). The paucity of

direct evidence for Allee effects was surprising, given documented Allee effects in laboratory

studies (e.g., Kyogoku & Nishida 2012) and frequency- and/or density-dependent impacts of

interspecific interference in the field (Gómez-Llano et al. 2023; Svensson et al. 2018). Future research, therefore, should aim to understand the importance of Allee effects in determining the outcome of spatial dynamics. For instance, a key test of the impact of behavioural interference on range dynamics would be to artificially induce an Allee effect in field systems known to engage in behavioural interference, by heightening or inversing the densities and/or frequencies of two species that engage in behavioural interference.

Similarly, though several models incorporate both behavioural interference and resource competition (Ribeiro and Spielman 1986; Amarasekare 2002; Crowder et al. 2011), our literature search found few explicit analyses disentangling the relative impacts of behavioural interference and resource competition, or the predicted interactive dynamics of both, on range dynamics (but see (Duckworth 2013; Cowen, Drury, and Grether 2020).

## **III. Future Directions**

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

# $(1) \ Identifying \ the \ impact \ of \ behaviour al \ interference \ on \ historical \ spatial \ processes$

There are several existing approaches for studying historical range dynamics that would be useful to develop further to understand outcomes of behavioural interference across a range of timescales. For instance, at a deep evolutionary timescale, models of ancestral biogeography have proven to be useful tools for making inferences about the pace and

trajectory of range evolution within independently evolving lineages (Ronquist 2011).

Recently, there have been calls for extending these methods to incorporate ecological factors such as species interactions (Sukumaran and Knowles 2018), and the development of tools for identifying the signature of competitive exclusion in range data (Quintero and Landis 2020). Incorporating the possibility for the presence and/or magnitude of behavioural interference to modulate the impacts of competition on range dynamics into these models, similar to advances already developed for trait-mediated dispersal (Klaus and Matzke 2020), could provide a novel tool that would make it possible to test a range of hypotheses that cannot be tested with current methods (Fig 3A).

At shallower evolutionary scales, existing population genomic techniques leverage the signatures of historical processes preserved in genomes to test hypotheses about spatial (Peter and Slatkin 2013; Petkova, Novembre, and Stephens 2015; Al-Asadi et al. 2019; He, Prado, and Knowles 2017) and demographic (Gutenkunst et al. 2009; Gronau et al. 2011; Excoffier et al. 2021) dynamics that have unfolded over scales of thousands to millions of years.

Largely, these developments have been designed to examine dynamics within independently evolving lineages. Within this constraint, one way forward would be to conduct comparative analyses to test the hypothesis that lineages (e.g., populations, species) experiencing higher levels of behavioural interference expand their ranges at different rates than lineages experiencing little or no behavioural interference (Fig 3B). Recently, Ortego & Knowles (2020) developed an analytical pipeline that explicitly tests for the impact of facilitation and/or competition between species on generating contemporary geographic patterns of genomic diversity. Extending these models to explicitly test for impacts of behavioural interference is an exciting possibility that would generate new insights.

On a more contemporary scale, long-term census data have proven to be a useful tool for monitoring dynamics of species assemblages over the past century (Rosenberg et al. 2019,

Saunders et al. 2022). Such datasets contain interacting species, and understanding how those interactions impact temporal dynamics is one way forward. One recent attempt has shown that stably coexisting species-pairs that are interspecifically territorial have increased their fine scale habitat overlap more than non-interspecifically territorial pairs, suggesting that interspecific territoriality may actually stabilise coexistence in species that would otherwise engage in high levels of exploitative competition (Nesbit et al. 2023). Future applications could use tools developed for network analyses (Blonder et al. 2012) to examine how behavioural interference influences dynamics within assemblages (Fig 3C).

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

Insights generated from investigations of the impacts of behavioural interference on historical range dynamics will be essential for generating predictions about the future impacts of behavioural interference on climate-change driven range dynamics. At the heart of attempts to predict how species' ranges will shift in response to global changes are species distribution models (SDMs). SDMs use measures of abiotic factors and presence-absence data to predict species' future ranges under different climate scenarios (Elith and Leathwick 2009; Titley et al. 2021).

Attempts to incorporate biotic factors into species distribution models have given rise to joint species distribution models (JSDMs) (Wilkinson et al. 2019; Tikhonov et al. 2017). Yet, implementing and validating JSDMs is fraught with difficulties because positive and negative occurrence patterns often correlate with abiotic factors (Poggiato et al. 2021). Consequently, although some attempts to implement behavioural interference into SDMs/JSDMs have been conducted (Bastianelli et al. 2017; Engler et al. 2013), many examples of interspecific behavioural interference limiting the spatial distribution of species would not be detected using JSDMs. Despite challenges, joint species distribution modelling

remains an active area of research with many promising recent developments (Pichler and Hartig 2021; Escamilla Molgora et al. 2022). For instance, joint *dynamic* species distribution models (JDSDMs) use time-series data on abundance to examine the impact of concurrent changes in abundance across assemblages more directly (Thorson, Pinsky, and Ward 2016; Elo et al. 2023). Consequently, we imagine that these tools will be useful for generating predictive models of future range dynamics in the presence of behavioural interference (Fig. 3D), for instance by comparing the marginal predictions of such models (i.e., the effects of environmental variables only), to conditional predictions which also incorporate impacts of changing species interactions (Wilkinson et al. 2019; 2021). Recently, for instance, (Novella-Fernandez et al. 2021) devised an index of 'geographic avoidance' by comparing species suitable ranges (calculated from SDMs) to their observed ranges. Using this index, they found that two pairs of cryptic species of bats in Europe exhibited spatial partitioning consistent with interspecific competition driving exclusion. They then examined range overlap under future climate projections, demonstrating that some predicted range shifts may not be possible due to predicted range overlap with competitors (Novella-Fernandez et al. 2021, see also Engler et al. 2013 and McQuillan and Rice 2015 for a similar approach). Future attempts to generate predictions of range dynamics in the presence of behavioural interference could also be used to disentangle and quantify the differing impacts of behavioural interference versus resource competition.

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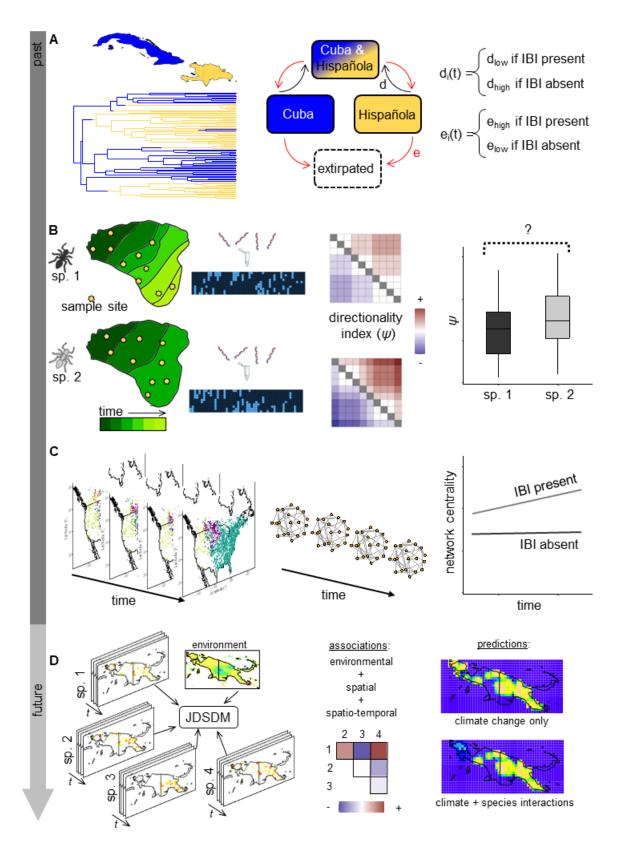


Fig 3. Possible directions for future research into the historical (A-C) and forecasted (D) impacts of behavioural interference (BI) on range dynamics. Approaches to test for historical impacts of BI include (A) extending models of ancestral biogeography to include separate parameters for species that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

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

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

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

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

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

# IV. Concluding remarks

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

539 (2) In line with predictions derived from theoretical models of behavioural interference, the 540 case studies we compiled demonstrate that symmetry (or lack thereof) in behavioural 541 interference determines the spatial outcome of interactions. Further work is necessary to test 542 other key predictions of theoretical models, such as the presence of Allee effects and 543 interactive impacts of behavioural interference and exploitative competition for resources. 544 (3) We identified several other gaps that remain in our broad-scale understanding of the 545 546 impacts of behavioural interference on spatial dynamics. For instance, which factors (e.g., 547 phylogenetic distance, life history, climate niche, etc.) explain variation in the presence or 548 magnitude of the effect of behavioural interference on range dynamics? 549 550 (4) Several recent developments have paved the way for modelling the impacts of species 551 interactions on both historical and future spatial dynamics, and future work adapting these 552 methods to further explore the links between behavioural interference and range dynamics is 553 an important way forward. 554 555 (5) In addition to modelling approaches, further work aimed at quantifying the interactive 556 effects of evolutionary change and spatial movement is crucial for predicting the outcome of 557 range dynamics in the presence of behavioural interference. 558 559 (6) The spatial distribution of species has implication for conservation, human health, and 560 agriculture. Alongside other abiotic and biotic factors, our study highlights the need to 561 include interspecific behavioural interference in predicting and managing the current and

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future distribution of species.

V. Acknowledgements We thank Erandi Bonillas-Monge, Greg Grether, Sal Keith, and Dan Nesbit for helpful comments on the manuscript, and Durham University librarians for assistance. We'd like to thank Darren Irwin and an anonymous reviewer for their additional helpful comments on the manuscript. CP was funded by a Durham Doctoral Studentship, and JPD was funded by NSFDEB-NERC-2040883. 

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<b>Interacting Species</b>	IBI.Type	Elevational (Y/N)	Invasion (Y/N)	Comparative (Y/N)	Impacts of IBI on Spatial Dynamics	References	Additional Explanations?
Aves	1						
Great reed warblers (Acrocephalus arundinaceus) & marsh warblers (Acrocephalus palustris)	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 Palestrini, 1989)	
Bicknell's thrushes (Catharus bicknelli) & Swainson's thrushes (Catharus ustulatus)	Aggression	Y	N	N	Playback experiments between two parapatric thrush species. Lower elevation Swaison's thruses respond aggresively to the calls of higher elevation Bikcnells thrushes, but not vice versa. The aggressive responses of Swaison's thrush toward heterospecifics increases with altitude (i.e., closer to range boundary).	(Freeman and Montgomery, 2015)	
Black-headed nightingale thrushes (Catharus mexicanus) & ruddy-capped nightingale- thrushes (Catharus frantzii)	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 et al., 2020)	Habitat segregation
Collared (Ficedula albicollis) & pied (Ficedula hypoleuca) flycatchers	Aggression	N	N	N	For instance, collared ( <i>Ficedula albicollis</i> ) & pied ( <i>Ficedula hypoleuca</i> ) 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, which reenforces the habitat segregation 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)
Several species of wood wrens (Henicorhina leucophrys & Henicorhina leucosticta) and thrushes (Catharus mexicanus & Catharus aurantiirostris) along an elevational gradient in Costa Rica.	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
Narrow-billed woodcreepers (Lepidocolaptes angustirostris) & scaled woodcreepers (Lepidocolaptes squamatus)	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)	

Common nightingales (Luscinia megarhynchos) & thrush nightingales (Luscinia luscinia)	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)
Noisy miners (Manorina melanocephala) & local bird assemblages	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 et al., 2012; Lill and Muscat, 2015)
Flame robins (Petroica phoenicea) & Norfolk robins (Petroica multicolor)	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)
Carolina chickadees ( <i>Poecile carolinensis</i> ) and black-capped chickadees ( <i>Poecile atricapillus</i> )	Aggression and Reproductive Interference	N	N	N	Carolina chickadees are more aggressive (dominant) than black-capped chickadees, and that dominant chickadees are prefered by females of both species in mate choice trails. SDMs show that Carolina chickadees' distribution limit largely matches climatic predictors, whereas black-capped chickadee distribution does nor, suggesting that it is limited instead by interactions with Carolina chickadees.	
Invasive ring-necked <i>parakeets</i> ( <i>Psittacula krameri</i> ) and native communities	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)
Townsend's warblers (Setophaga townsendi) and hermit warblers (Setophaga occidentalis)	Aggression and Reproductive Interference	N	N	N	Moving hybrid zone attributed to asymmetries in behavioural interference. Both species defend mutually exclusive territories, though Townsend warbler's 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)
Western bluebirds (Sialia mexicana) & mountain bluebirds (Sialia currucoides)	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)
Spotted owls (Strix occidentalis) & barred owls (Strix varia)	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 et al., 2007; Van Habitat loss, exploitative Lanen et al., 2011; Wiens, competition Anthony and Forsman, 2014)
Dominant and subordinate congeneric birds in urban environmetns	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; Exploitative competition for Martin, Burke and Bonier, resources not ruled out 2021)

Dominant and subordinate birds from North America	Aggression	N	N	Y	Subordinate species migrate further distances than dominant species	(Freshwater, Ghalambor and Martin, 2014)	
Birds along an elevational gradient in Borneo	Aggression	Y	N	Y	Simulated instrusion 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: ochraceus bulbuls (Alophoixus ochraceus) respond aggressivly to pale-faced bulbuls (Pycnonotus leucops). However, they did not find evidence that parapatric white-eyes (Zosterops sp.) are aggressive to congeners.	(Boyce and Martin, 2019)	
North american perching birds (passerines)	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)	
Birds along an elevational gradient in Papua New Guinea	Aggression	Y	N	Y	Playback experiments on five species pairs demonstrate that the lower elevation species are more aggressive toward heterospecifics than upper elevation confamilial 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)	
Amphibia							
Southern Appalachian salamander (Plethodon teyahalee) & red-cheeked salamanders (Plethodon jordani)	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)	
Actinopterygii							
Damselfish (Dischistodus spp.) in the Great Barrier Reef	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
Guppies (Poecilia reticulata) & mosquitofish (Gambusia affinis)	Reproductive Interference	N	Y	N	Mosquitofish decline upon introduction of guppies, and experimental evidence shows that reproductive interference occurrs asymetrically, with negative fitness impacts on mosquitofish, but not guppies.	(Tsurui-Sato et al., 2019)	
Obscure damselfish (Pomacentrus adelus) & speckled damselfish (Pomacentrus bankanensis)	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)	
Invasive brown trout (Salmo trutta) & white-spotted charr (Salvelinus leucomaenis) in Japan	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)	

Gopher rockfish (Sebastes carnatus) & Black-and-yellow rockfish (Sebastes chrysomelas)	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 is depth range.	(Larson, 1980)	
Arachnida	1						
Invasive sheet-web spiders (Linyphia triangularis) & bowl-and-doily spiders (Frontinella communis)	Aggression	N	Y	N		(Houser, Ginsberg and Jakob, 2014)	Exploitative competition for resources ruled out
Copepoda	ı						
Skistodiaptomus copepods	Reproductive Interference	N	N	N	S. oregonensis and S. pygmaeus exhibit a parapatric boundary. Laboratory studies demonstrate high levels of reproductive interference (though no evidence of introgression), suggesting that Allee effects generated by reproductive interference maintain this parapatric boundary.	(Thum, 2007)	Ecological gradients ruled out as possible explanation
Crustacea	ı						
Invasive rusty crayfish (Orconectes rusticus) and native Sanborn crayfish (Orconectes sanborni)	Aggression and Reproductive Interference	N	Y	N	An invasive crayfish ( <i>O. rusticus</i> ) that replaces native crafish ( <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
Invasive signal crayfish (Pacifastacus leniusculus) in Europe & native communities	Aggression and Reproductive Interference	N	Y	N	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	Svärdson et al. 1991 (Söderbäck, 1994, 1995; Westman and Savolainen, 2001; Westman, Savolainen and Julkunen, 2002; Bubb <i>et al.</i> , 2009)	Signal crayfish are resistent to crayfish plague that contributes to decline of native crayfish species; Life history traits (e.g., developmental time)
Gastropoda	ı						
Keyhole limpets (Siphonaria lessonii) & pulmonate limpets (Fissurella crassa)	Aggression	N	N	N		(Aguilera and Navarrete, 2012)	
Insecta	1						
Aedes mosquitos (Ae. albopictus & Ae. aegypti)	Reproductive Interference	N	Y	N	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 <i>et al.</i> , 2022)	Larval resource competition

Two tick species (Amblyomma variegatum & Amblyomma hebraeum)	Reproductive Interference	N	N	N	Two species of tick are larglely parapatric . In sympatry, interspecific copulations are commonly observed, with little geographic overlap, suggesting symmetric reproductive interference may maintain parapatric boundary.	(Bournez et al., 2015)	
Whiteflies (Bemisia tabaci spp.)	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)
Invasive buff-tailed bumblebees (Bombus terrestris) & native bumblebees (Bombus h. sapporoensis 7 Bombus ignitus) in Japan	Reproductive Interference	N	Y	N	The invasive bumblebee species bombus terrestris engages in reproductive interference with two species of native bumblebee. Copulation between B. terrestris and B. h. sapporoensis or B. ignitus 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
Rubyspot damselflies ( <i>Hetaerina</i> spp.)	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 et al., 2022)	
Two ant species (Iridomyrmex spp.)	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
Arboreal termite species in Papua New Guinea (Microcerotermes biroi, Nasutitermes novarumhebridiarum, & Nasutitermes princeps)	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.	Pasteels, 1997)	
	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)	
Invasive southern green stink bugs (Nezara viridula) & native green stink bugs (Nezara antennata)	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
Alpine dark bush-crickets (Pholidoptera aptera) & Transylvanian dark bush-crickets (Pholidoptera transsylvanica)	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 et al., 2020)	Habitat segregation ruled out
Eastern subterranean termites (Reticulitermes flavipes) &	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 et al., 2011)	Lack of intraspecific aggression in invasive species;

Western subterranean termits (Reticulitermes grassei)							demographic factors (large colony size)
Invasive Asian blue ticks (Rhipicephalus [Boophilus] microplus) & African blue ticks (Rhipicephalus [Boophilus] decoloratus) in South Africa	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.		Life history traits (e.g., developmental time); host resistance
Cepero's groundhoppers (Tetrix ceperoi) & slender groundhoppers (Tetrix subulata)	Reproductive Interference	N	N	N	the two species are rarely found in syntopy. Laboratory and field experiments demonstrate that extensive reproductive interference		Habitat segregation ruled out
Arboreal ant species in Papua New Guinea	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 et al., 2021)	Habitat segregation ruled out
Mammalia	ı						
Fallow deer (Dama dama) & roe deer (Capreolus capreolus)	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 dear. 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
White-handed gibbons ( <i>Hylobates lar</i> ) & Pileated gibbons ( <i>Hylobates pileatus</i> )	Aggression	N	N	N	Two species of gibbon are largely parapatric, with a small contact zone that is maintained by interspecific territorial aggression.		Niche partitioning (via habitat segregation or diet divergence) ruled out.
Least chipmunks (Neotamias minimus) & yellow-pine chipmunks (Neotamias amoenus)	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)	
Townsend's chipmunks (Neotamias townsendii) & yellow- pine chipmunks (Neotamias amoenus)	Aggression	N	N	N	Removal experiments of two species of chipmunk that engage in aggressive intractions 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
Uinta chipmunks (Neotamias umbrinus) & Colorado chipmunks (Neotamias quadrivittatus)	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 file found at lower elevations.	(Bergstrom, 1992)	
Stoats (Mustela erminea) & least weasels (Mustela nivalis)	Aggression	N	N	N	Experimental data demonstrates that stoats are dominant over weasels, and observational data shows that weasels are very rarely found in prefered 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)	
Pied tamarins (Saguinus bicolor) & Golden-handed tamarins (Saguinus midas)	Aggression	N	N	N	Playback experiment of two species on Tarmarin, in allopatry and sympatry. Pied tamarins are critically edangered and experiencing range fragmentation, while red-handed tamarins have expanded their range into the range of pied tamarins.	(Sobroza et al., 2021)	

					Playback experiments show that red-handed tarmarin respond more agressively than the pied tamarins.		
Chiriquí singing mice (Scotinomys xerampelinus) & Alston's singing mice (Scotinomys teguina)	Aggression	Y	N	N	Playback experiments, laboratory experiments, and removal experiments all demonstrate that the higher elevation species (Scotinomys xerampelinus) is dominant and preempts range intrusions from lower elevation species. In removal experiments, Scotinomys xerampelinus didn't descend to occupy areas where Scotinomys teguina was removed, but Scotinomys teguina did invade higher elevation areas when Scotinomys xerampelinus was removed.	(Pasch, Bolker and Phelps, 2013)	
Reptilia	ı						
Invasive house geckos (Hemidactylus frenatus) & native communities	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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