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Interspecific behavioural interference and range dynamics: current insights and future directions

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ABSTRACT

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 test predictions from theory robustly. 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.

Key words: interspecific behavioural interference, reproductive interference, interspecific aggression, range dynamics, systematic review, elevational gradients, invasion biology, range shift.

CONTENTS

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I. INTRODUCTION

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 & 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 & Levine, 2015; Blois *et al.*, 2013; Early & 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 destabilise 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, on exploitative competition between species of the same trophic level (Sirén & Morelli, 2020; Early & Keith, 2019; Louthan, Doak & Angert, 2015; Svenning *et al.*, 2014; Legault *et al.*, 2020; Ortego & 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 towards and has a negative impact on the fitness of another species (Grether *et al.*, 2017; Gröning & Hochkirch, 2008; Burdfield-Steel & Shuker, 2011). For instance, both territorial aggression between individuals of different species and courtship displays directed by males of one species towards females of another species fall under the umbrella of behavioural interference. Behavioural interference has been documented across a wide range of taxa (Gröning & Hochkirch, 2008; Peiman & 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), although in some cases, behavioural interference may occur across large phylogenetic distances (e.g. indiscriminate aggression from noisy miners *Manorina melanocephala* towards a broad range of bird species throughout much of Australia; Mac Nally *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 (Case & Gilpin, 1974; Kuno, 1992; Liou & Price, 1994; Amarasekare, 2002; Mikami & Kawata, 2004; Kishi & Nakazawa, 2013; Kyogoku & Sota, 2017; Iritani & Noriyuki, 2021; Irwin & Schluter, 2022; Grether & 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 & Spielman, 1986; Crowder *et al.*, 2011; Nishida, Takakura & Iwao, 2015; Ruokolainen & Hanski, 2016; Legault *et al.*, 2020). One key insight from these models is that the impact of interspecific behavioural interference will be highest on rarer species, and the magnitude of this impact increases as the asymmetry in frequency increases (e.g. Amarasekare, 2002; Kuno, 1992), i.e. 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 & Spielman, 1986; Nishida *et al.*, 2015). Another insight from these models relates to the interactive effect of resource competition and behavioural interference – several models show that the dynamics of systems with both resource competition and behavioural interference are markedly different than systems with resource competition alone (Ribeiro & Spielman, 1986; Amarasekare, 2002; Crowder *et al.*, 2011), which underscores the importance of further research into behavioural interference in attempts to predict 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 & 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.
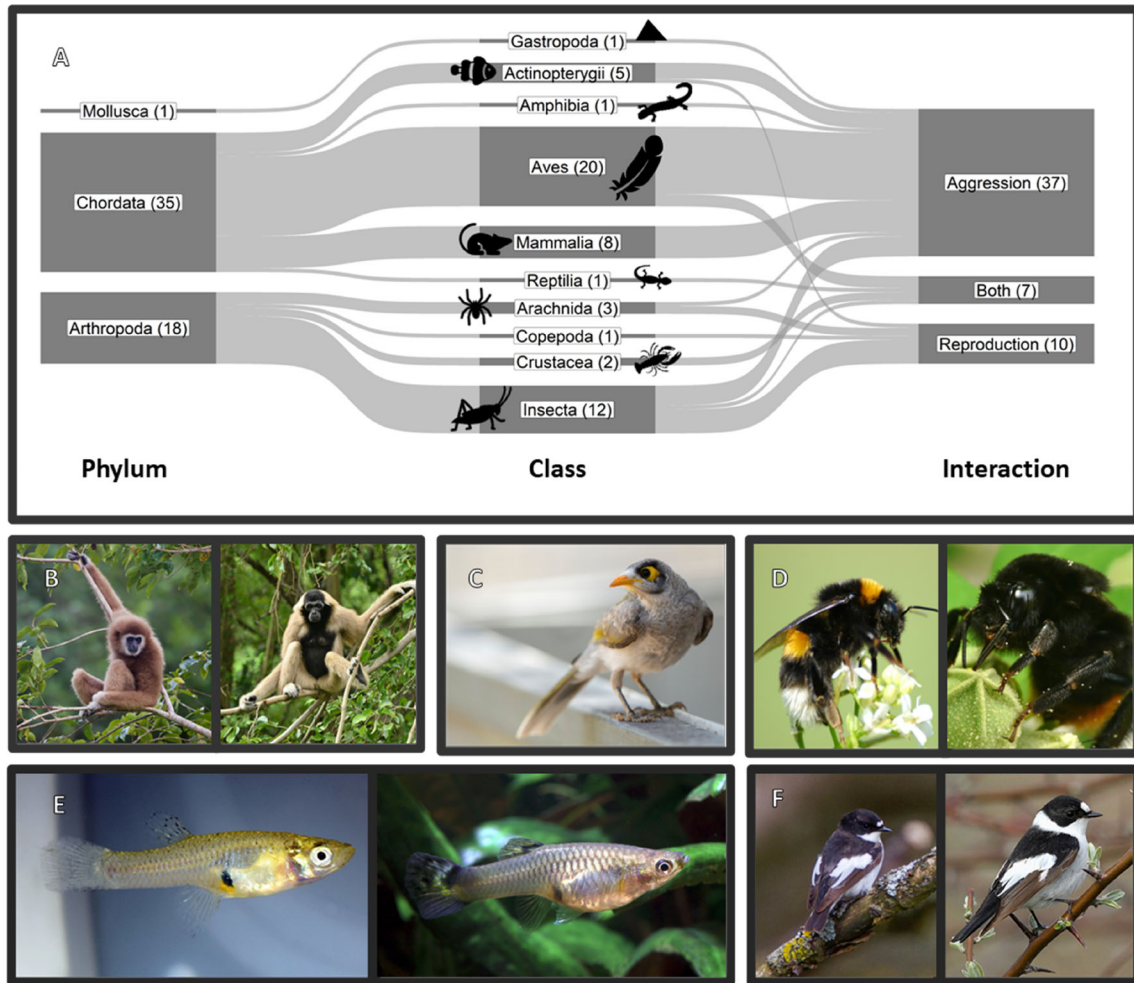
Fig. 1. There is widespread evidence that behavioural interference (costly aggressive or reproductive interactions between species) influences spatial dynamics in animals. (A) Study systems that directly measured the impact of interspecific behavioural interference on the spatial distribution of one of more species by phylum, class, and whether the study covered aggressive or 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 actinopterygians (Bubb *et al.*, 2009). The interphylum system is counted here in Crustacea as the crustacean was the more aggressive species. Sankey diagram 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 hybridisation (Asensio *et al.*, 2017). (C) Indiscriminate hyperaggression of noisy miners (*Manorina melanocephala*) has led to shift in the structure of avian communities (Mac Nally *et al.*, 2012). (D) In Japan, the invasive bumblebee *Bombus terrestris* (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 mosquitofish (*Gambusia affinis*) (right) in Okinawa owing to reproductive interference, and consequently guppies have been proposed as a potential control agent for mosquitofish 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 photographs reproduced 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.

II. SYSTEMATIC LITERATURE REVIEW

(1) Methods

To identify examples of interspecific behavioural interference influencing the spatial distribution of a species, we conducted a literature search using the 'all databases' option in *Web of Science* (https://www.webofscience.com/). We used the search term '*TS=(((behaviour* OR behavior*) NEAR/6 interference) OR (reproduct* NEAR/6 interference) OR (interspecific NEAR/6 (behaviour* OR behavior*) NEAR/6 competition) OR*

((interspecific OR heterospecific) NEAR/6 aggress*) OR ((interspecific OR heterospecific) NEAR/6 dominan*) OR ((interspecific OR heterospecific) NEAR/6 territor*) OR ((interspecific OR heterospecific) NEAR/6 interference) OR (sister AND (taxa OR species) AND (competition OR aggress* OR territor* OR dominan* OR interference))) AND TS= ((range* NEAR/6 shift*) OR (species NEAR/6 distribution*) OR (range* NEAR/6 expansion*) OR (range* NEAR/6 dynamic*) OR (species NEAR/6 displace*) OR (species NEAR/6 replace*) OR (Altitud* NEAR/6 (zonat* OR zone)))' (*NEAR/6* returns search results that contain the first phrase within six words of the later phrase). While we designed this set of search terms to focus on behavioural interference, we note that hybridisation falls under the general umbrella term of 'reproductive interference'. There is a large, related literature covering the spatial dynamics of hybrid zones (Barton, 1979; Barton & Hewitt, 1989; Buggs, 2007), which focuses on the way that clines form in the presence of selection acting on hybrid genotypes. Here, however, we focus on the outcome of reproductive behavioural interactions *per se*, regardless of whether those interactions result in the formation of hybrids. We note that, although some treatments of reproductive interference include aggression in the context of access to mates (e.g. Groning & Hochkirch, 2008), we follow recent literature on behavioural interference in classifying all agonistic interactions directed towards heterospecifics as agonistic interference (Grether *et al.*, 2017).

As of the search date (13 October 2022), we obtained a database of 338 unique peer-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 and 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 result directly 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 (Fig. 1A, Table 1; see online Supporting Information, Table S1, for additional information for each of the 54 study systems).

(2) Reproductive interference *versus* interspecific aggression

Our search terms returned more study systems where aggressive interference ($N = 44$) influenced range dynamics than reproductive interference ($N = 17$) (Fig. 1A, Table 1, Table S1). 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 Section II.1), and hybridisation is among the more highly studied forms of reproductive interference. Moreover, reproductive interference also includes 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 interference and aggression influence range dynamics. For instance, where collared (*Ficedula albicollis*) and 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 reinforces 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 & 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 (Fig. 1A). Most examples of reproductive interference influencing range dynamics were conducted on arthropods (9 out of 10). This contrasts with studies of aggressive interference which were dominated by vertebrates (30 out of 37), especially birds ($N = 17$). Empirical examples of reproductive interference are taxonomically widespread (Gröning & Hochkirch, 2008), so it is surprising to find that evidence of reproductive interference influencing the spatial dynamics of a species comes 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 & Spielman, 1986), which

Table 1. The 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 is provided in Table S1. 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. Y/N, yes/no.

Interacting species	IBI type	Elevational (Y/N)	Invasion (Y/N)	Comparative (Y/N)	References
Aves					
Great reed warblers (*Acrocephalus arundinaceus*) & marsh warblers (*Acrocephalus palustris*)	Aggression	N	N	N	Rolando & Palestrini (1989)
Bicknell's thrushes (*Catharus bicknelli*) & Swainson's thrushes (*Catharus ustulatus*)	Aggression	Y	N	N	Freeman & Montgomery (2015)
Black-headed nightingale thrushes (*Catharus mexicanus*) & ruddy-capped nightingale-thrushes (*Catharus frantzii*)	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 *et al.* (2010)
Narrow-billed woodcreepers (*Lepidocolaptes angustirostris*) & scaled woodcreepers (*Lepidocolaptes squamatus*)	Aggression	N	N	N	Maldonado-Coelho *et al.* (2017)
Common nightingales (*Luscinia megarhynchos*) & thrush nightingales (*Luscinia luscinia*)	Aggression	N	N	N	Sorjonen (1986); Reif *et al.* (2015, 2018)
Noisy miners (*Manorina melanocephala*) & local bird assemblages	Aggression	N	N	N	Mac Nally *et al.* (2012); Lill & Muscat (2015)
Flame robins (*Petroica phoenicea*) & Norfolk robins (*Petroica multicolor*)	Aggression	N	N	N	Robinson (1992)
Carolina chickadees (*Poecile carolinensis*) and black-capped chickadees (*Poecile atricapillus*)	Aggression and reproductive interference	N	N	N	Bronson *et al.* (2003); McQuillan & 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 & Rohwer (2000)
Western bluebirds (*Sialia mexicana*) & mountain bluebirds (*Sialia currucoides*)	Aggression	N	N	N	Duckworth & Badyaev (2007); Duckworth (2013); Duckworth *et al.* (2015)
Spotted owls (*Strix occidentalis*) & barred owls (*Strix varia*)	Aggression	N	Y	N	(Gutiérrez *et al.* (2007); Van Lanen *et al.* (2011); Wiens, *et al.* (2014)
Dominant and subordinate congeneric birds in urban environments	Aggression	N	N	Y	Martin & Bonier (2018); Martin *et al.* (2021)
Dominant and subordinate birds from North America	Aggression	N	N	Y	Freshwater *et al.* (2014)
Birds along an elevational gradient in Borneo	Aggression	Y	N	Y	Boyce & Martin (2019)
North American perching birds (passerines)	Aggression and reproductive interference	N	N	Y	Cowen *et al.* (2020)
Birds along an elevational gradient in Papua New Guinea	Aggression	Y	N	Y	Freeman *et al.* (2016)
Amphibia					
Southern Appalachian salamander (*Plethodon teyahalee*) & red-cheeked salamanders (*Plethodon jordani*)	Aggression	Y	N	N	Hairston *et al.* (1987); Gifford & Kozak (2012)

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Table 1. *(Cont.)*

Interacting species	IBI type	Elevational (Y/N)	Invasion (Y/N)	Comparative (Y/N)	References
Actinopterygii					
Damselfish (*Dischistodus* spp.) in the Great Barrier Reef	Aggression	N	N	N	Bay *et al.* (2001)
Guppies (*Poecilia reticulata*) & mosquitofish (*Gambusia affinis*)	Reproductive interference	N	Y	N	Tsurui-Sato *et al.* (2019)
Obscure damselfish (*Pomacentrus adelus*) & speckled damselfish (*Pomacentrus bankanensis*)	Aggression	N	N	N	Eurich *et al.* (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 & Maekawa (2009)
Gopher rockfish (*Sebastes carnatus*) & black-and-yellow rockfish (*Sebastes chrysomelas*)	Aggression	N	N	N	Larson (1980)
Arachnida					
Invasive sheet-web spiders (*Linyphia triangularis*) & bowl-and-doily spiders (*Frontinella communis*)	Aggression	N	Y	N	Houser *et al.* (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 & Stein (1985)
Invasive signal crayfish (*Pacifastacus leniusculus*) in Europe & native communities. This includes an example of interphylum behavioural interference: aggression by signal crayfish toward native bullhead fish (*Cottus gobio*).	Aggression and reproductive interference	N	Y	N	Söderbäck (1994, 1995); Westman & Savolainen (2001); Westman *et al.* (2002); Bubb *et al.* (2009); Svärdson *et al.* (1991)
Gastropoda					
Keyhole limpets (*Siphonaria lessonii*) & pulmonate limpets (*Fissurella crassa*)	Aggression	N	N	N	Aguilera & Navarrete (2012)
Insecta					
Aedes mosquitos (*Ae. albopictus* & *Ae. aegypti*)	Reproductive interference	N	Y	N	Nasci *et al.* (1989); Bargielowski *et al.* (2013); Bargielowski & Lounibos (2016); Lounibos & 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 *et al.* (2012)
Invasive buff-tailed bumblebees (*Bombus terrestris*) & native bumblebees (*Bombus hypocrita 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 & Fox (1987)
Arboreal termite species in Papua New Guinea (*Microcerotermes biroi*, *Nasutitermes novarumhebridiarum* & *Nasutitermes princeps*)	Aggression	N	N	Y	Leponce *et al.* (1997)
White-crossed seed bugs (*Neacoryphus bicrurus*) and co-occurring insect communities	Aggression and reproductive interference	N	N	N	McLain & Shure (1987)
Invasive southern green stink bugs (*Nezara viridula*) & native green stink bugs (*Nezara antennata*)	Reproductive interference	N	Y	N	Kiritani (2011)

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Table 1. *(Cont.)*

Interacting species	IBI type	Elevational (Y/N)	Invasion (Y/N)	Comparative (Y/N)	References
Alpine dark bush-crickets (*Pholidoptera aptera*) & Transylvanian dark bush-crickets (*Pholidoptera transsylvanica*)	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 (*Tetrix ceperoi*) & slender groundhoppers (*Tetrix subulata*)	Reproductive interference	N	N	N	Gröning *et al.* (2007); Hochkirch, *et al.* (2007); Hochkirch & 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 & Mori (2020)
White-handed gibbons (*Hylobates lar*) & pileated gibbons (*Hylobates pileatus*)	Aggression	N	N	N	Suwanvecho & Brockelman (2012); Asensio *et al.* (2017)
Least chipmunks (*Neotamias minimus*) & yellow-pine chipmunks (*Neotamias amoenus*)	Aggression	Y	N	N	Heller (1971); Chappell (1978)
Townsend's chipmunks (*Neotamias townsendii*) & yellow-pine chipmunks (*Neotamias amoenus*)	Aggression	N	N	N	Trombulak (1985)
Uinta chipmunks (*Neotamias umbrinus*) & Colorado chipmunks (*Neotamias quadrivittatus*)	Aggression	Y	N	N	Bergstrom (1992)
Stoats (*Mustela erminea*) & least weasels (*Mustela nivalis*)	Aggression	N	N	N	Erlinge & 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 *et al.* (2013)
Reptilia					
Invasive house geckos (*Hemidactylus frenatus*) & native communities	Aggression and reproductive interference	N	Y	N	Bolger & Case (1992); Petren *et al.* (1993); Case *et al.* (1994); Dame & Petren (2006)

makes a species particularly vulnerable to local extinction (Irwin & Schluter, 2022). Alternatively, the bias may reflect the 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.

(3) 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 & 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 the climate niches of high-elevation species 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 an elevational gradient are often sharply defined, making studies of range limits inherently simpler along an elevational gradient (Žagar *et al.*, 2015; Pasch, Bolker & Phelps, 2013; Jones *et al.*, 2020), so it would be premature to draw conclusions on the relative importance of behavioural interference on 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 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 & Levey, 2010; Freeman & Montgomery, 2015; Freeman, Class Freeman & Hochachka, 2016; Jones *et al.*, 2020; Boyce & 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 & Montgomery, 2015) and of pairs in which the lower elevation species is subordinate [e.g. *Scotinomys* singing mice (Pasch *et al.*, 2013), *Neotamias* chipmunks (Bergstrom, 1992) and, if aquatic depth gradients are comparable to elevational gradients, *Pomacentrus* damselfish (Eurich, McCormick & 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 *et al.*, 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 Papua New Guinea, all study systems were located in northern and Central America (Fig. 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).

(4) 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 & O'Dowd, 2007; Lounibos & Juliano, 2018; Pereira, Lourenço & Mota, 2020; Kyogoku & Sota, 2017). The systematic review identified multiple examples of invasive species engaging in reproductive interference (Tsurui-Sato *et al.*, 2019; Lounibos & Juliano, 2018; Tsuchida *et al.*, 2019; Tønnesen *et al.*, 2004; Westman, Savolainen & Julkunen, 2002) and aggressive interference (Bubb *et al.*, 2009; Houser, Ginsberg & Jakob, 2014; Westman *et al.*, 2002; Rowles & 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 hypocrita sapporoensis* or *Bombus ignitus* results in unviable eggs being laid the following spring when there are no further intraspecific mating opportunities. Consequently, *B. ignitus* and *B. h. sapporoensis* 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 due to interference from invasive Asian house geckos, *Hemidactylus frenatus* (Dame & Petren, 2006; Bolger & Case, 1992; Petren, Bolger & Case, 1993), and the replacement of *Aedes aegypti* by *Ae. albopictus* both throughout the southern USA (Nasci, Hare & 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 that 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 which could prevent the invasive species replacing the native (Cisterne, Schwarzkopf & 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 & 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 mosquitofish, 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 (*Salmo trutta*) and native white-spotted charr (*Salvelinus leucomaenis*) demonstrated that habitat modifications in the form of visual barriers could reduce observed levels of interspecific aggression (Hasegawa & Maekawa, 2009).

(5) Empirical validation of theoretical predictions

The formation of parapatric ranges, where two species have adjacent ranges with little or no overlap, is a key prediction of the theoretical models of how interspecific behavioural
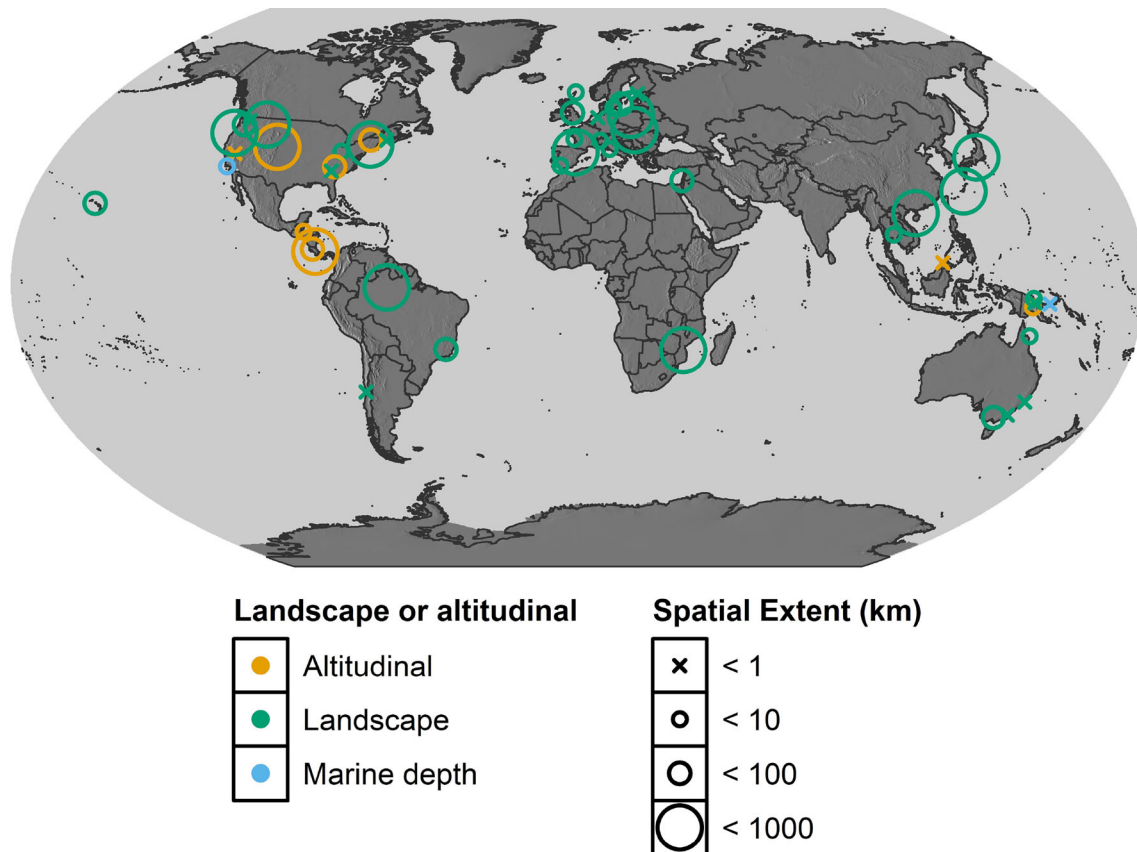
Fig. 2. The global distribution of field studies that found an effect of interspecific behavioural interference on the spatial distribution of one or more species. Colour denotes whether the study investigated the spatial distributions across a landscape (i.e. latitude and longitude), across an elevational 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 1000 km 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 (<1 km) scales [e.g. Hochkirch & 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 (<1000 km) 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*].

interference impacts range dynamics when the impacts of behavioural interference are symmetrical (Ribeiro & 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 & 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 (<1 km 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 observations 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 & 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 *et al.*, 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, although several investigators of these studies suggest that Allee effects generate range turnovers (Söderbäck 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 induce an Allee effect artificially 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, although several models incorporate both behavioural interference and resource competition (Ribeiro & 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) and Cowen, Drury & 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 behavioural 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 proved 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 to extend these methods to incorporate ecological factors such as species interactions (Sukumaran & Knowles, 2018), and for the development of tools to identify the signature of competitive exclusion in range data (Quintero & Landis, 2020). Incorporating the possibility that the presence and/or magnitude of behavioural interference could modulate the impacts of competition on range dynamics into these models, similar to advances already developed for trait-mediated dispersal (Klaus & 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 & Slatkin, 2013; Petkova, Novembre & Stephens, 2015; Al-Asadi *et al.*, 2019; He, Prado & 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 test explicitly for impacts of behavioural interference is an exciting possibility that would generate new insights.

On a more contemporary scale, long-term census data have proved to be a useful tool for monitoring dynamics of species assemblages over the past century (Rosenberg *et al.*, 2019; Saunders *et al.*, 2022). Such data sets 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 & 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
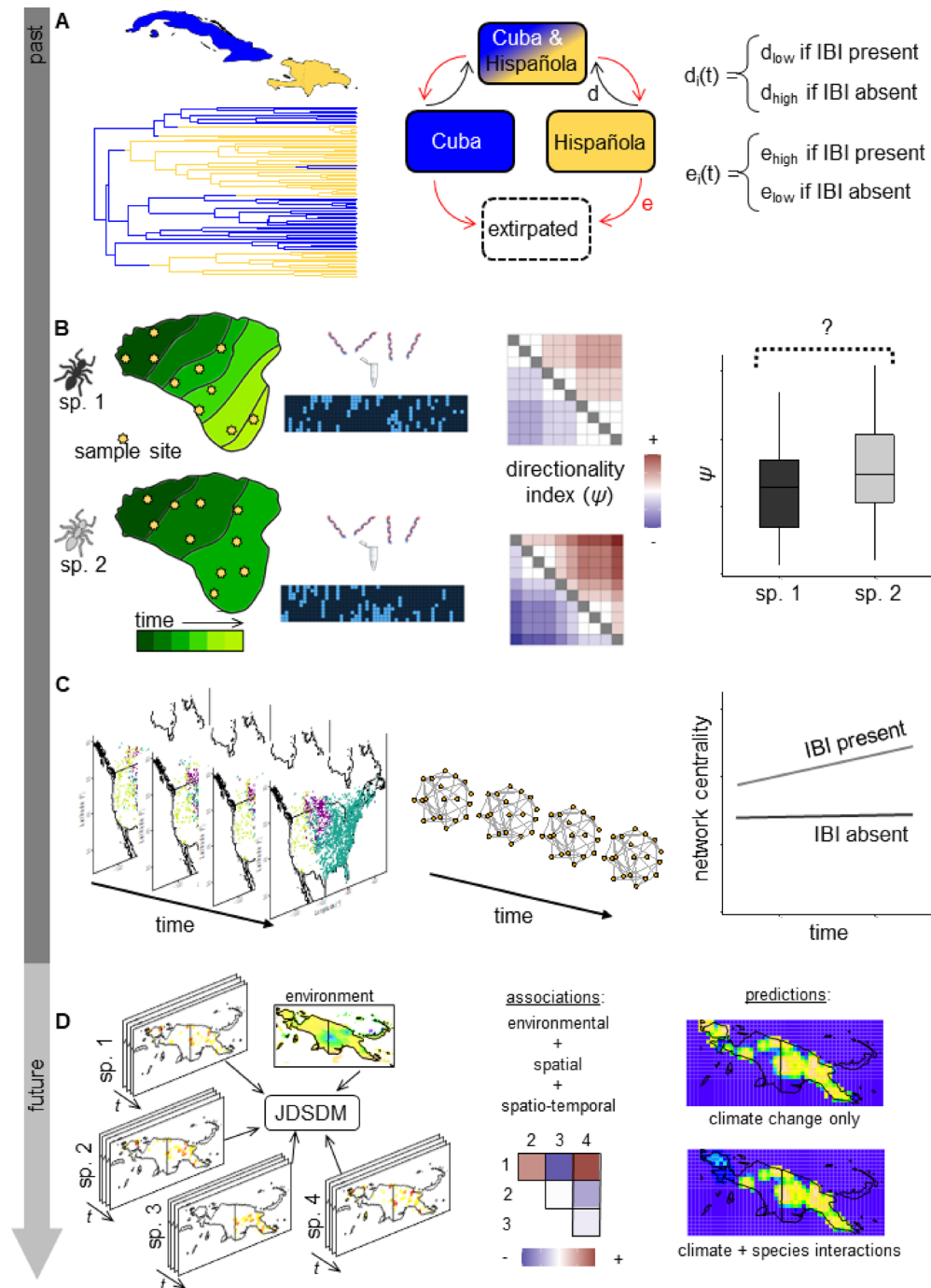
Fig. 3. Possible directions for future research into the historical (A–C) and potential future (D) impacts of interspecific behavioural interference (IBI) on range dynamics. Approaches to test for historical impacts of IBI include (A) extending models of ancestral biogeography to include separate parameters for species that engage in IBI and those that do not; (B) deploying genomic tools to test whether the historical dynamics of range expansion differ between species that engage in IBI (sp. 2, in this example) and species that do not by calculating pairwise indices of directional movement such as the ψ index (Peter & Slatkin, 2013); and (C) using long-term census data to analyse how IBI has impacted the dynamics of species co-occurrence through time using tools from network analysis (e.g. indices of network centrality). Developments for forecasting and mitigating the impacts of IBI 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.

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 & 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 that 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 & 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.

The preceding approaches largely rely on metrics of co-occurrence to make inferences about the impacts of behavioural interference, under the assumption that co-occurring 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 *et al.*, 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 (genus *Chaetodon*) 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 *et al.*, 2020; Leighton *et al.*, 2023) and its evolutionary consequences, such as its impact on trait evolution (Grether *et al.*, 2009; Pfennig & Pfennig, 2009) or other aspects of the speciation cycle (Tobias, Ottenburghs & Pigot, 2020). This work has shown that the likelihood of behavioural interference decreases with increasing divergence time (e.g. Drury *et al.*, 2020; Barley *et al.*, 2022) likely owing to relative similarity in the perceptual systems and agonistic and/or mating signals used in closely related species (Grether *et al.*, 2009; Orians & 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 *et al.*, 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 & 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 & 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 (Bargielowski, Lounibos & Carrasquilla, 2013; Bargielowski, Blosser & 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. CONCLUSIONS

(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.
(2) In line with predictions derived from theoretical models of behavioural interference, the case studies we compiled demonstrate that symmetry (or lack thereof) in behavioural interference determines the spatial outcome of interactions. Further work is necessary to test other key predictions of

theoretical models, such as the presence of Allee effects and interactive impacts of behavioural interference and exploitative competition for resources.

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

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

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

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

V. ACKNOWLEDGEMENTS

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VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. The 54 study systems identified during the literature review that found clear evidence that interspecific behavioural interference (IBI) impacts the spatial distribution of a species.