

Review

Causes and Consequences
of Behavioral Interference
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Behavioral interference between species, such as territorial aggression, courtship, and mating, is widespread in animals. While aggressive and reproductive forms of interspecific interference have generally been studied separately, their many parallels and connections warrant a unified conceptual approach. Substantial evidence exists that aggressive and reproductive interference have pervasive effects on species coexistence, range limits, and evolutionary processes, including divergent and convergent forms of character displacement. Alien species invasions and climate change-induced range shifts result in novel interspecific interactions, heightening the importance of predicting the consequences of species interactions, and behavioral interference is a fundamental but neglected part of the equation. Here, we outline priorities for further theoretical and empirical research on the ecological and evolutionary consequences of behavioral interference.

Interspecific Aggression and Reproductive Interference

Few subjects in animal behavior have attracted more attention than aggression and sex, yet research tends to stop at species boundaries even when the behaviors themselves do not. Aggressive and sexual interactions between species are surprisingly common and share many parallels in their causes and ecological and evolutionary effects [1–6]. Both types of behavioral interference (Box 1) have been hypothesized to: (i) arise as a byproduct of intraspecific interactions (Box 2); (ii) cause local extinction as well as temporal and spatial habitat partitioning; (iii) prevent species from coexisting that otherwise would be expected to coexist; (iv) enable coexistence between species that otherwise would not be expected to coexist; (v) promote or prevent species range shifts and the spread of invasive species; (vi) cause sympatric species to diverge or converge through character displacement processes; (vii) cause populations within a species to diverge from each other due to character displacement in areas of sympatry; and (viii) contribute to reproductive isolation and speciation (Figure 1).

Despite their connections, **aggressive interference** and **reproductive interference** (see Glossary) have largely been studied by different researchers in relation to different theoretical frameworks [2,4,7] and in different study systems [3], even though many closely related species interfere with each other in both ways (see Table S1 in [8]). We do not believe that these two categories of interspecific interactions should be synonymized, because this would obscure important differences between them. Instead, we propose that their similarities and interrelationships merit a common conceptual framework, which we introduce here (Figure 1).

Trends

Aggressive and reproductive forms of behavioral interference between species are widespread in animals and share many parallels in their underlying causes and their ecological and evolutionary effects.

Behavioral interference can determine whether species coexist and, thus, affects species ranges, the persistence of native species, and the spread of invasive species.

As species ranges shift under environmental change and new interspecific interactions arise, it will be important to incorporate knowledge of behavioral interference into ecological forecasts and conservation planning.

Behavioral interference can drive both divergent and convergent character displacement processes and thereby contribute to phenotypic diversity and speciation.

Evidence is accumulating that behavioral interference has shaped large-scale ecological and evolutionary patterns.

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Box 1. Behavioral Interference

We use the term 'behavioral interference' to encompass aggressive and sexual interactions between species and their fitness consequences. By aggressive interactions, we mean not only physical aggression, but also associated behaviors (e.g., displays or territorial signaling). Likewise, sexual interactions include not only mating and mating attempts, but also associated behaviors (e.g., courtship signaling or mate guarding). In both cases, the key factor is that the behaviors negatively affect individuals of another species (see [Box 2](#) in the main text). We do not presume that interference behaviors have evolved for a particular purpose, that they necessarily reduce access to a shared limiting resource, or that they negatively affect both species. Rather, these are among the empirical questions of interest.

Prior Usage

The term 'behavioral interference' has appeared sporadically in the literature, usually in reference to behavioral interactions between species at the same trophic level that negatively affect one or both species. The term is most commonly used in cases where behavioral interactions between consumers (herbivores, predators, or parasitoids) are hypothesized to reduce per capita resource exploitation efficiency. While aggression is the most commonly invoked mechanism in empirical studies, the term is not behavior or context specific.

Related Terms

Gröning and Hochkirch's [4] definition of reproductive interference includes aggressive interactions over access to mates, but excludes aggressive interactions in other contexts. Pfennig and Pfennig's [26] definition of competition encompasses not only aggressive and sexual interactions between species, but also depletion of common resources (i. e., exploitative competition). Interference competition includes aggressive and chemical interference, but does not include sexual interactions between species.

Focusing on behavioral interference now is timely given the rapid pace of anthropogenic and climate change-induced range shifts, exotic species invasions, and shrinking populations of native species ([Box 3](#)) [9–12]. Some of the best-studied cases involve species that are currently expanding their range and displacing a congener [13–16]. A growing body of evidence suggests that behavioral interference also places constraints on geographical ranges and population sizes, for example in altitudinal and latitudinal replacement zones [17–19].

Box 2. Evolutionary Origins and Fitness Considerations

Interspecific behavioral interference is generally assumed to have intraspecific origins. Under the null model commonly referred to as the mistaken identity hypothesis, behavioral interference arises when species first come into contact as a byproduct of (misdirected) intraspecific behavior and persists in unmodified form because selection is weak or gene flow from allopatry swamps selection in sympatry [1,2,4,7]. Alternatively, selection in sympatry might subsequently augment, diminish, or otherwise modify the initial responses toward heterospecifics, depending on the average fitness consequences for individuals [1,2,4,7]. These two hypotheses are most frequently contrasted in the interspecific aggression literature but also apply to reproductive interference (with the added complication of introgression in hybridizing taxa).

Interspecific interactions are often classified in terms of their effects on population mean fitness (i.e., the instantaneous rate of population growth). The term 'interference' implies that both species are negatively affected (–/–) or that one species is negatively affected and the other species is not affected (–/0). This classification might be the basis of the common misconception that interspecific interference should necessarily be selected against and decrease in occurrence and intensity over evolutionary time. Intraspecific interference is also a –/– interaction, yet interference behaviors, such as territoriality and mate guarding, have obvious adaptive value. The classification of an interaction as –/– only means that the fitness of both entities (individuals and/or populations) would be higher in the absence of the other. Interference behaviors that increase the fitness of the individual actor relative to other individuals in the same population are still favored by natural selection. For example, if males cannot reliably distinguish between conspecific and heterospecific females, indiscriminate mating might be the best strategy for males, even though this is a mutually wasteful interaction at the population level. However, thinking in terms of population mean fitness is useful for predicting the outcome of species interactions, and there are situations in which behavioral interference could raise the population mean fitness of one of the two species, relative to the alternative of coexisting without behavioral interference. For example, when species overlap in resource use, interspecific territorial aggression might increase the population mean fitness of a dominant species by reducing exploitative competition with a subordinate species [59,60]. Understanding fitness effects at both the population and individual levels is key to predicting the ecological and evolutionary consequences of behavioral interference.

Glossary**Aggressive interference:**

intimidating or violent interactions between individuals of different species, including threats, displays, and territoriality, but not including predator–prey interactions; a subset of interference competition.

Agonistic character**displacement, divergent (ACDd):**

the process of phenotypic evolution caused by aggressive interference resulting in trait divergence between species and a reduction in the frequency or costs of the interaction; the expected mode of ACD when species do not interfere with each other reproductively or overlap sufficiently in resource use for interspecific resource defense to be adaptive for either species (divergence need not be mutual) [1,7,8].

Agonistic character**displacement, convergent**

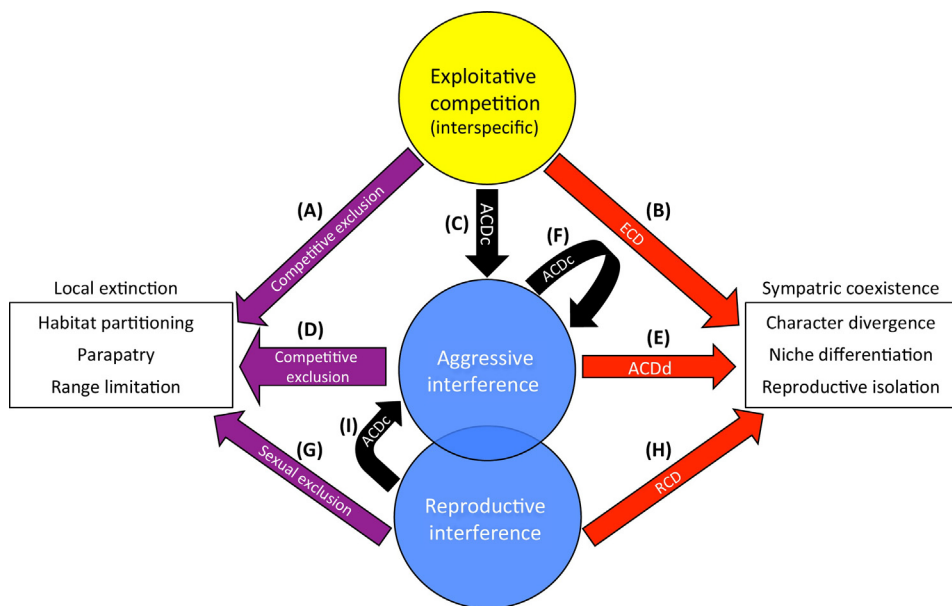
(ACDc): the process of phenotypic evolution caused by interspecific competition for mates or other resources and which can result in trait convergence between species and enhanced competitor recognition and/or interspecific fighting ability; the expected mode of ACD when species interfere with each other reproductively or overlap sufficiently in resource use for interspecific resource defense to be adaptive (convergence need not be mutual) [1,7,8,30].

Behavioral interference: the union of all behaviorally mediated forms of interference between species, including aggressive interference and most forms of reproductive interference (see [Box 1](#)).

Competitive exclusion: local extinction of one species resulting from exploitative or interference competition with another species; can occur at multiple spatial scales, from habitat patches to the entire range of a species.

Competitive mimicry: an evolved phenotypic resemblance that affects the behavior of another class of individuals in such a way that it facilitates access to a defended resource or the defense of a resource.

Competitor recognition: the process of discriminating among different classes of individuals in relation to levels of competition for resources or mates.



Trends in Ecology & Evolution

Figure 1. Conceptual Framework for Behavioral Interference between Species. This diagram summarizes parallels and connections between reproductive and aggressive forms of behavioral interference (blue circles) and their relationship with interspecific exploitative competition for resources other than mates (yellow circle; interspecific exploitative competition for mates is subsumed by reproductive interference). The two forms of behavioral interference are depicted as overlapping to accommodate definitions of reproductive interference that include aggressive interactions between species related to mate acquisition (see [Box 1](#) in the main text). Arrows represent ecological and evolutionary processes that can occur under specific circumstances (purple arrows depict ecological processes; red arrows depict evolutionary processes that result in trait divergence and reductions in the frequency or intensity of the interaction; black arrows depict evolutionary processes that result in trait convergence or enhancements in interspecific interference competitive ability). Exploitative resource competition between species can (A) cause the local elimination of a species by competitive exclusion, (B) cause species to evolutionarily diverge in ways that reduce niche overlap (ecological character displacement, ECD [26]), or (C) when resources are defendable, lead to the evolution (or persistence) of aggressive interference between species (convergent agonistic character displacement, ACDc [1,2]). Aggressive interference between species can (D) result in competitive exclusion [7], (E) cause species that are not competing exploitatively to diverge in ways that reduce the occurrence of interspecific aggression (divergent agonistic character displacement, ACDd [1]), or (F) drive the evolution of enhanced interspecific competitive ability (ACDc [1,2]). Reproductive interference between species can (G) result in sexual exclusion [4,20], (H) cause species to diverge in ways that reduce the occurrence of interspecific sexual interactions (reproductive character displacement, RCD [4,26]), or (I) lead to the evolution (or persistence) of aggressive interference between species (ACDc [8]). Outcomes in the box on the right correspond to species coexisting in sympatry with enhanced mate recognition, competitor recognition, or niche differentiation, relative to the ancestral, presecondary contact condition. Outcomes in the box on the left correspond to effects of competitive or sexual exclusion at different spatial scales. These processes and outcomes are not all mutually exclusive and can interact in complex ways.

Consequently, a deeper understanding of behavioral interference is urgently required to improve our predictions of how environmental change will affect species and ecological communities ([Box 3](#)).

Although behavioral interference has been studied sporadically for decades, this is not a mature field in which most ideas have been modeled and most models have been extensively tested. Instead, theory has moved ahead of empirical research on some fronts, but only a small subset of empirically relevant scenarios has been explored with formal models. To clarify the distinction between theory and empirical results, and to help identify where further research is needed, we start with theory and then review empirical studies selected to illustrate the diversity of phenomena and problems that this subject encompasses.

Ecological character

displacement (ECD): the process of phenotypic evolution caused by interspecific exploitative competition and which usually results in niche divergence and hence reduced resource overlap (divergence need not be mutual).

Ecological sorting: the process of community assembly by which exploitative or interference competition with another species reduces the likelihood of colonization or invasion (see 'niche incumbency'). Unlike character displacement, this process is ecological rather than evolutionary, but theoretically produces a similar pattern of increased trait differences in sympatric species.

Exploitative competition: occurs indirectly through depletion of a shared, limiting resource (e.g., food, refuges, nesting sites, or mates).

Interference competition: any costly interaction between individuals over access to a resource, aside from resource depletion, regardless of whether the resource is shared or limiting; includes fighting, dominance, territoriality, and allelopathy (chemical inhibition).

Learned recognition: the process of changing discrimination toward an individual or classes of individual on the basis of prior interference interactions (i.e., a plastic discrimination response) distinct from innate recognition (a fixed discrimination regardless of prior experience); includes behavioral modulation, signal copying, and cultural co-responses.

Mate recognition: the process of discriminating among different classes of individual in relation to levels of mate suitability.

Niche incumbency: the condition of a niche being already filled by an ecological competitor, typically placing constraints on colonization or invasion through resource depletion or aggressive interaction.

Reproductive character

displacement (RCD): the process of phenotypic evolution caused by reproductive interference and that reduces the frequency or costs of the interaction (divergence need not be mutual).

Reproductive interference: sexual interactions between individuals of different species, including courtship, hybridization, and other pre- and

Box 3. Behavioral Interference and Ecological Forecasting under Environmental Change

Shifting geographical ranges are natural features of biodiversity over longer timescales. However, the rate at which species colonize new environments has increased dramatically because of climate change, land-use change, and the introduction of alien species. Clearly, this process will give rise to numerous novel interactions among species, yet the behavioral component of these interactions is often ignored when predicting the impacts of environmental change.

A prominent approach to ecological forecasting uses environmental niche models to predict future geographical ranges under the assumption that populations will track changes in the geographical distribution of environmental conditions (e.g., [84]). There have been many calls to incorporate 'biotic interactions' into such models (e.g., [85]). However, progress toward this goal has been slow, and most current methods do not account for interference (but see [12]). Interspecific competition might give rise to niche incumbency, and the ecological sorting of competing lineages into nonoverlapping geographical ranges [46], but predicting which species will co-occur in the future, and which will undergo population declines or ecological sorting, requires an improved understanding of behavioral interference and its consequences. An important step is to quantify how the strength or outcome of behavioral interference is correlated with other measurable variables, such as phylogenetic, ecological, or trait similarity. The simplest method is to quantify current patterns of divergence in these variables in relation to geographical range overlap across species [46]. The next step is to use these patterns to refine models forecasting the structure and distribution of biodiversity under scenarios of environmental change, perhaps incorporating alternative predictors of aggressive or reproductive interference where data are available.

A different set of challenges is faced by studies assessing how biodiversity is affected by habitat fragmentation or restoration. In these cases, behavioral interference can determine which species are lost or gained after land-use change. For example, two species might co-occur in larger patches of habitat, but when these patches shrink one of the species might be driven to extinction by elevated competition associated with spatial constraints and a dwindling pool of resources [86]. More information about how behavioral interference is mediated by frequency dependence, dominance asymmetries, and other mechanisms that reduce the fitness of one or both species will help us to predict the rate and order of local extinctions in response to land-use change.

postmating sexual behaviors, such as mate guarding.

Sexual exclusion: local extinction of one species resulting from reproductive interference with another species; can occur at multiple spatial scales, from habitat patches to the entire range of a species.

Species recognition: the concept that organisms have the ability to distinguish between what scientists classify as different species [100]; mate recognition and competitor recognition are more precise and operational terms because they do not imply that class boundaries recognized by the animals necessarily correspond with species boundaries [1,100].

Behavioral Interference Theory**Species Coexistence versus Exclusion**

Behavioral interference can be positively frequency dependent in that the more rare of the two species suffers disproportionately from the interaction [20]. Thus, the expected ecological outcome (exclusion of one species, or coexistence) can depend strongly on the initial population sizes [21,22]. Behavioral interference can be an important cause of Allee effects [23] and impede the spread of non-native species, which often have small initial population sizes in their introduced range. However, the ecological outcome should also depend on asymmetries in the costs of interference. When exotic species do greater harm to native species than vice versa, interference can accelerate invasions [13,20,22].

Ecological outcomes can also be shaped by the interplay between behavioral interference and **exploitative competition**. Based on existing models, reproductive interference more readily leads to exclusion than does resource competition [20,21], and even low levels of reproductive interference can cause local extinction [21]. When exploitative competition and reproductive interference asymmetries are aligned, exclusion can occur more rapidly than under resource competition alone [20]. Conversely, if the species that is inferior in resource competition is superior in reproductive interference (i.e., has a stronger negative effect on the other species), this can prevent competitive exclusion of the inferior resource competitor or even reverse the outcome and cause **sexual exclusion** of the superior resource competitor [20]. However, under special circumstances, reproductive interference could promote coexistence between ecological competitors. For example, ecologically identical species that exploit ephemeral food patches might be able to coexist if reproductive interference triggers dispersal that reduces interspecific spatial overlap [24].

Aggressive interference is also expected, in most cases, to hasten competitive exclusion [22]. As with reproductive interference, asymmetries in aggressive interference ability can counteract

asymmetries in resource exploitation ability and result in the extinction of the superior exploitative competitor [22]. However, asymmetries in aggressive interference are also expected to increase temporal or spatial habitat segregation between species, and the resulting reduction in interspecific exploitative competition could lead to stable coexistence between species that otherwise would be unable to coexist [7,25].

Divergent Character Displacement Processes

Species that engage in behavioral interference are likely to evolve in response to each other. Evolved responses to reproductive interference that reduce the frequency or costs of the interaction are classified as **reproductive character displacement** (RCD; Figure 1) [4]. When RCD increases the level of prezygotic isolation between hybridizing species, it is synonymous with reinforcement [26]. Evolved responses to aggressive interference are classified as agonistic character displacement (ACD; Figure 1) [1]. ACD can cause species to diverge or converge phenotypically, depending on whether they compete exploitatively for resources (or mates) at a sufficient level for interspecific resource (or mate) defense to be adaptive [1,8]. In theory, both RCD and **divergent ACD** (ACDd) can drive species apart in signals and signal perception ('**species recognition**' traits), habitat preferences, and temporal activity patterns, including the timing of migration and breeding [1,4,27]. While only RCD is driven by selection against interspecific mating, all forms of character displacement can potentially increase the level of reproductive isolation between sympatric species as well as cause populations in sympatry to diverge from those in allopatry, and thereby contribute to allopatric speciation [26].

The effects of RCD and ACDd can be indistinguishable when the same traits are used for competitor recognition in one sex and **mate recognition** in the other. In this situation, the rate of trait divergence is governed by the cost of reproductive interference, not by the cost of aggressive interference [28]. The dominance of RCD over ACDd stems from the need for males to be recognized by conspecific females [28].

As traditionally defined, character displacement does not include phenotypically plastic responses that have similar effects on trait divergence (Box 4) but does include genetic changes that alter the ability or propensity to exhibit such plastic responses, if they evolve in response to the species interaction [1,29].

Box 4. Learning

Many aspects of interspecific interactions have the potential to be influenced by learning, just as with intraspecific interactions [87], yet the ecological and evolutionary consequences of learning remain an understudied topic. Here, we sketch the diverse ways that learning influences interference interactions and permits feedbacks between individual behavior, population ecology, and evolutionary responses. First, learning affects the opportunity for interference interactions. It can enhance competitor recognition [88] and modify the frequency of interactions through effects on niche overlap [89]. Second, **learned recognition** allows for rapid behavioral responses to novel species interactions [88–91]. For example, song learning has enabled some bird species to converge in territorial signals more rapidly than intergenerational responses due to selection, gene flow, or drift [89,92]. Third, learned recognition can reduce the frequency and costs of interference during reproduction [93–95] and over territories [87]. However, learning can be costly, such as when it results in the copying of maladaptive behavior that leads to the rejection of conspecific or acceptance of heterospecific mates, or misidentification of competitors [82,94]. Fourth, learning influences the strength and direction of selection by shaping phenotypic variation and its relationship to genetic variation [81]. For example, learned recognition can permit selection causing character displacement of recognition traits [82]. Fifth, learning likely has complex effects on recognition mechanisms of species, classes (e.g., mates or competitors) or individuals. While costly interspecific interactions favor innate recognition mechanisms [96] and greater variation in the frequency or intensity of interactions favor learning [97], most recognition systems likely comprise varying degrees of both components [88]. Finally, learning that increases assortative mating between partially diverged populations can contribute to speciation [90,93,96,98], whereas learning that contributes to stochasticity in mate choice would erode assortative mating and promote gene flow that could limit adaptive divergence and speciation, such as might occur when mate choice is flexible [99].

Convergent Character Displacement and Competitive Mimicry

Exploitative competition between species for defensible resources, including mates, can make interspecific defense adaptive and thereby prevent species from diverging or cause them to converge in agonistic signals and competitor recognition functions [1,8]. Regardless of whether the outcome is stasis maintained by selection or convergence, the process is classified as **convergent ACD** (ACDc; Figure 1) [1,7]. Convergence in agonistic signals and competitor recognition increases the probability that heterospecifics are recognized as competitors and, thus, can not only increase the frequency of aggressive interactions between species, but also reduce interaction costs when the traits involved are dominance or territory deterrence signals that reduce the likelihood or intensity of direct confrontations [1,30]. Interaction costs can also be reduced by learning (Box 4).

Just as **interference competition** for mates and other resources is thought to have led to the evolution of alternative strategies within species (e.g., territory holders, mate guarders, female mimics, or sneakers), interference competition between species can lead to the evolution of distinct species roles, with strategies similar to their intraspecific analogs, including various forms of competitive mimicry (Figure 1) [31–37]. For example, in theory, asymmetries in social dominance between competing species can lead to mimicry of dominant species by subordinate species [33,37].

Convergent ACD and competitive mimicry are overlapping but not identical concepts. Signal convergence between ecological competitors can be classified in both ways, for example, but competitive mimicry also encompasses forms of mimicry driven by intraspecific competition, such as males mimicking females to avoid aggression from conspecific males [31], whereas ACD includes evolutionary changes that do not increase the phenotypic resemblance between species, such as enhancements in competitor recognition and interspecific fighting ability [1].

Persistence of Reproductive Interference

By conventional thinking, reproductive interference is self-destructive in that it should either result in sexual exclusion or cause species to diverge in ways that eliminate wasteful interspecific sexual interactions. If so, why is it so common? [4,6,38]. Traditional RCD theory focuses on the costs of interspecific mating for females, but divergence in male traits and female mate recognition does not automatically reduce the rate at which males attempt to mate with heterospecific females. Indiscriminate mating might remain the best strategy for males if more-discriminating males risk rejecting conspecific females [39]. Perceptual and ecological constraints can also impede refinements in mate recognition [8] (Box 4). Reproductive interference should persist indefinitely wherever interspecific mating yields a net fitness payoff [40].

Empirical Advances in Behavioral Interference

Behavioral Interference in Competition Experiments

A recent review of competition experiments on bean beetles (*Callosobruchus*), flour beetles (*Tribolium*), and fruit flies (*Drosophila*) concluded that outcomes originally attributed to resource competition were likely caused by a combination of resource competition and reproductive interference [41]. In fact, in *Drosophila* and *Callosobruchus*, asymmetries in reproductive interference evidently outweighed asymmetries in resource competition [41]. In general, the presence of frequency dependence and priority effects in competition experiments implicates behavioral interference, because such effects are not expected under exploitative resource competition alone [20,22,41].

Species Range Limits, Invasions, and Replacements

Aggressive interactions between species are usually asymmetric [42] and this can have a major role in determining species range limits [7,43–46]. On the mountains of Costa Rica and

Panama, the singing mouse *Scotinomys teguina* is abruptly replaced by the larger *Scotinomys xerampelinus* above a certain elevation (Figure 2 [18]). Behavioral trials, song playbacks, and removal experiments strongly suggest that the upper altitudinal limit of *S. teguina* is enforced by aggression from *S. xerampelinus*, while the lower altitudinal limit of *S. xerampelinus* is determined by its own thermal habitat preference (Figure 2 [18]). Aggressive asymmetries are also common in avian altitudinal replacement zones [45]. Mismatches of fundamental versus realized altitudinal distributions provide indirect evidence of behavioral interference, and greater mismatch in one species suggests that aggressive interactions are asymmetrical [47]. These scenarios raise the prospect under climate change of subordinate high-elevation species being squeezed into extinction if dominant low-elevation species shift upslope, or of dominant high-elevation species preventing the upward movement of subordinate species, which are then left occupying a physiologically suboptimal habitat [17,19].

As well as limiting ranges, behavioral interference has been implicated in some ongoing species replacements [4,7,15,48,49]. Aggressive interference in conjunction with habitat changes appears to account for the cyclical replacement of mountain bluebirds (*Sialia currucoides*) by western bluebirds (*Sialia mexicana*) in the northwestern USA [15]. Likewise, aggressive and reproductive interference combined with climate change appear to be driving the replacement of pied flycatchers (*Ficedula hypoleuca*) by collared flycatchers (*Ficedula albicollis*) on the Swedish Island of Öland [16,48].

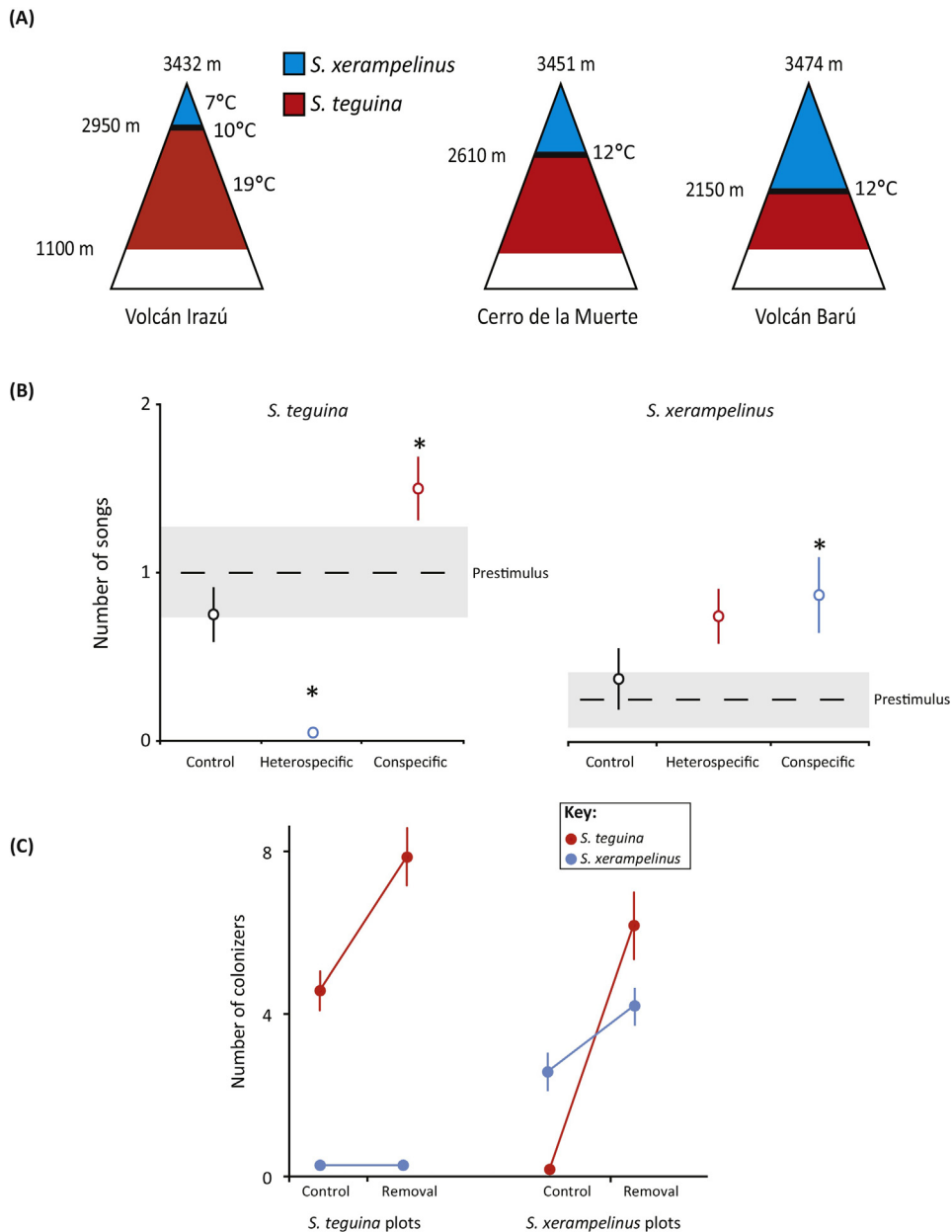
Species replacements can also be affected by how standing behavioral variation within the invading population is spatially structured [15,50–52]. For example, male western bluebirds at the invasion front are more aggressive than those in the resident population [15]. The propensity to disperse is a maternally inherited trait that responds to local bluebird density, such that increases in density accelerate the invasion [15]. In other cases, less aggressive individuals might drive invasion fronts because they are displaced from preferred habitats by aggressive conspecifics [53].

Some of the most thoroughly studied cases of behavioral interference involve disease vectors and agricultural pests [13,14,54]. The invasive mosquitos *Aedes aegypti* (from Africa) and *Aedes albopictus* (from Asia) are the primary vectors of the Zika, dengue, and chikungunya viruses. *Ae. aegypti* became established in North America over 300 years ago, but *Ae. albopictus* has recently invaded and replaced *Ae. aegypti* in some areas due, in part, to asymmetrical reproductive interference [14,54]. Interspecific mating occurs in both directions, but *Ae. albopictus* seminal products cause female *Ae. aegypti* to become refractory to future mating, which effectively sterilizes them [14]. Evolved resistance to interspecific mating (i.e., RCD) might be enabling *Ae. aegypti* to rebound in some areas [14,54].

All the above examples involve close relatives (congeners), but some well-documented cases of behavioral interference involve more distantly related species. For example, in Australia, the native hyperaggressive noisy miner (*Manorina melanocephala*) attacks most other birds. The resultant population declines of other species led to *M. melanocephala* being identified as a reverse keystone species by virtue of its subcontinental-scale effect on entire avifauna assemblages [55–57].

Habitat Partitioning and Coexistence

The altitudinal replacements examples (above) illustrate how aggressive interference could foster coexistence between species on a regional scale where, in the absence of interference, one species might expand its niche and drive the other extinct [17–19]. Similar outcomes are possible on a finer geographic scale when habitats occur in a mosaic of low- and high-quality patches. The coexistence of pied and collared flycatchers in a mosaic of coniferous and



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Figure 2. Evidence that Aggressive Interference Mediates Altitudinal Zonation in Neotropical Singing Mice. (A) Altitudinal distribution of two species of singing mice on three mountains in Central America (replacement zone, black; allopatric zones, red and blue). Average temperatures are shown on the right side of the triangles. (B) Results of a field song playback experiment showing a reduction in singing by *Scotinomys teguina* in response to playbacks of *Scotinomys xerampelinus*, compared with the pre-playback period and conspecific playbacks, and no such reduction in the singing of *S. xerampelinus* in response to *S. teguina* playbacks, corroborating that *S. xerampelinus* is socially dominant to *S. teguina*. (C) Results of a removal experiment carried out in the replacement zone, showing that the smaller, subordinate *S. teguina* colonized plots where *S. xerampelinus* was removed (but not control plots), whereas *S. xerampelinus* did not colonize plots where *S. teguina* was removed. Modified, with permission, from [18].

deciduous forest in Central Europe is a possible example [58,59]. In other cases, aggressive interference can enable coexistence by causing temporal shifts in habitat use. For example, interference appears to stabilize coexistence between two species of gerbils by causing a temporal shift in the activity pattern of the smaller species [60,61]. In the absence of interference, the smaller species, which can forage more efficiently at lower resource levels, would be expected to drive the larger species extinct [60,61]. In general, avoidance of aggressive interactions is common in mammal communities and might help stabilize them [5,62,63].

Interspecific Communication and Competitive Mimicry

Behavioral interference can shape signal evolution and signaling behavior in many ways. At a community level, signal design and the timing of signal production can be partitioned to reduce interference, such as when the acoustic mating signals and responses of anurans are differentiated to avoid interactions between heterospecifics [64,65]. Alternatively, if aggressive signaling is adaptive, for example when it mediates interspecific territoriality, signal design can converge and signaling schedules can become behaviorally synchronized among species [66].

Numerous examples of interspecific competitive mimicry have been proposed [31,32,35,36,67]. For example, males of a subordinate species might gain access to prime habitat by mimicking females of a dominant species [34] and juveniles of one species might gain foraging access to the territories of a dominant species by mimicking the adults of a third, noncompetitor species [68]. Some cases involve parallel morphological variation across geographic ranges of closely related species, while others involve convergence between members of different clades [36,67]. The quality of the empirical evidence ranges from anecdotal to well substantiated [31,32,34–36]. Prum [32] compiled a list of 50 cases of plumage convergence in birds and proposed that the overall patterns, and most individual cases, can be explained by a form of competitive mimicry in which individuals of a subordinate species gain access to resources defended by a dominant species by mimicking the dominant species itself. Alternatively, subordinate mimics convergent on a dominant model might benefit through increased dominance in behavioral interactions with a wider suite of competitors (e.g., multiple frugivorous species gathering at fruiting trees) [69]. Direct behavioral evidence for these mechanisms remains scarce, but Prum's list [32] should inspire further study.

Predicting Behavioral Interference

A few recent comparative studies have tested hypotheses about the evolution and persistence of behavioral interference. In North American wood warblers (Parulidae), a young radiation of ecologically similar species, hybridization and interspecific territoriality primarily occur between closely related species [70,71]. After accounting for shared ancestry, the only significant predictors of interspecific territoriality were similarity in territorial signals and degree of syntopy [71]. Interspecific territoriality was positively related to syntopy, and was not related to habitat complexity, casting doubt on the longstanding hypothesis that interspecific territoriality only persists when species rarely encounter each other or when niche divergence is restricted [71]. However, these results are consistent with the hypothesis that territorial signals converge (or are under selection not to diverge) between strong ecological competitors following secondary contact [1]. In rubyspot damselflies (*Hetaerina* spp.), species differences in female coloration directly affect reproductive interference because males use coloration to distinguish between conspecific and heterospecific females [8]. Variation in reproductive interference among species pairs strongly predicts levels of aggressive (male–male) interference in this genus, in accordance with the hypothesis that interspecific mate competition maintains interspecific territoriality [8].

Macroevolution, Macroecology, and Community Ecology

Most research on behavioral interference has focused on how local conditions affect pairs or small groups of related species, yet interference can potentially shape biodiversity over large spatial and temporal scales. For example, the songs of sympatric pairs of antbirds (Thamnophilidae) are more divergent than related species pairs occurring in allopatry, consistent with the hypothesis that behavioral interference shapes macroevolutionary patterns by promoting species differences in interacting lineages [72]. However, variation in species age can also generate such patterns because new species tend to form in geographic isolation and often take millions of years before they are sufficiently differentiated to coexist in sympatry. Controlling for such biases can alter the picture markedly. For instance, using phylogenetic data to account for species age in 350 lineages of ovenbirds (Furnariidae) revealed that sympatry was not associated with greater divergence in ecological traits, but instead with greater similarity of territorial songs [73]. This implies that ECD is a weaker predictor of broad-scale patterns of phenotypic radiations than was previously believed, whereas the effects of behavioral interference mediated by ACDc might be more widespread than was previously thought.

Behavioral interference can also contribute to our understanding of the processes underpinning community ecology, functional ecology, and biogeography (Box 3). Although overdispersion of traits or phylogenetic history in ecological communities is often interpreted as evidence of interspecific competition [74], the nature of this competition is generally left ambiguous or assumed to be exploitative. Thus, the role of behavioral interference is potentially overlooked, particularly in tropical systems, where stable environmental conditions might maximize the diversity, dietary specialization, and niche packing of sedentary species, and, hence, promote intense biotic interactions [75,76]. For example, aggressive interference in tropical bird species can lead to checkerboard distributions or mosaic parapatry at local scales [25,77], as well as maintaining true parapatry at larger scales [17,46], through territorial interactions, **niche incumbency**, and other **ecological sorting** mechanisms. Moreover, aggressive interference can even shape foraging niches, which has implications for understanding how communities will function under global change [78] (Box 3).

Concluding Remarks and Future Directions

We have characterized the current state of theory, reviewed recent empirical advances, and presented our case for unifying the study of aggressive and sexual interactions between species under the common organizing framework of behavioral interference (Figure 1 and Box 1).

The principal limitation of existing theory is that only a small subset of plausible scenarios has been modeled. For example, the generalization that interspecific interference usually impedes coexistence might not hold when interference causes spatial or temporal resource partitioning (e.g., territoriality or habitat shifts). Current theory also fails to fully address the consequences of asymmetries in behavioral interference [79,80], while empirical research suggests that asymmetries are common and closely linked to the ecological and evolutionary consequences of the interactions [25,27,42,45,47]. Learned mate and competitor recognition also pose interesting and largely unexplored challenges (Box 4; see Outstanding Questions) [81,82]. Further integration of theoretical and empirical research is needed.

Integration of empirical research on aggressive and reproductive interference is also likely to be fruitful, as indicated by the few cases in which both types of interaction have been studied. In particular, when reproductive interference results in mate competition between species, it might be the ultimate reason for aggressive interference [8]. Another promising avenue for empirical research is to incorporate measurements of behavioral interference into phylogenetic

Outstanding Questions

How often do interference behaviors evolve *de novo* as opposed to being co-opted from intraspecific interactions?

Under what conditions will species competing exploitatively start interacting directly so that interference behaviors begin to be involved?

Under what circumstances does behavioral interference stabilize coexistence between species that compete exploitatively for common resources?

How do interference interactions within and between species drive the evolution of learning and how does the evolution of learning feed back through recognition to affect interference interactions?

What factors govern the role of learning in recognition of mates and competitors, and is learning in the two contexts genetically correlated?

How does learning affect the frequency of interactions, direct fitness costs, and reciprocal population responses of signals?

How does behavioral interference vary taxonomically and spatially (e.g., latitudinally), and can this variation be detected using comparative analyses or functional traits across broad temporal and spatial scales?

How can the contribution of behavioral interference be distinguished from exploitative competition in studies of species interactions?

How can phenotypic or phylogenetic data be used to predict which species combinations are likely to result in behavioral interference, or the forms that interference will take?

Can such phenotypic or phylogenetic metrics be incorporated into forecasting models designed to predict the effects of environmental change on species distributions and ecological communities?

How should behavioral interference be considered when developing plans for the recovery of endangered species, or for the control of invasive species?

comparative analyses to directly test for effects of behavioral interference on character evolution [71,83].

We have identified numerous ways in which aggressive and reproductive interference can have a prominent role in affecting fitness and selection within populations. We also argue that extensions of these processes can shape general patterns in biodiversity, including the macroevolution of entire radiations, and community assembly from local to macroecological scales. For these reasons, any predictions about the consequences of species range shifts, translocations, and reintroductions might be critically flawed unless they take behavioral interference into account [5]. Behavioral interference should be considered a key component of complex biological systems and fundamental to conservation and management programs in the face of rapid environmental change.

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