Received: 17 March 2022 | Revised: 21 July 2022 | Accepted: 24 July 2022

DOI: 10.1111/ele.14091

LETTER

ECOLOGY LETTERS WILEY

Eco-evolutionary dynamics of interference competition

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Funding information
National Science Foundation, Grant/Award Number: DEB-1020586, DEB-1457844 and DEB-NERC-2040883

Editor: Puni Jeyasingh

Abstract

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

KEYWORDS

coexistence, competition, competitive exclusion, interference competition, interspecific territoriality, Red Queen hypothesis

INTRODUCTION

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

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

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

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

Asymmetries in interference competition should be able to mediate trade-offs that promote coexistence between resource competitors. For example, if species 1 can profitably exclude species 2 from high-suitability habitat patches, but species 2 is a superior exploitative competitor that can persist in habitat patches too low in suitability to support species 1, it follows that there must be a region of parameter space within which the species can coexist indefinitely. This is essentially the situation hypothesised to enable pied flycatchers and collared flycatchers to coexist in a mosaic of deciduous and coniferous forests (Qvarnström et al., 2009; Veen et al., 2010). However, our goal was not to evaluate whether interspecifically territorial species could coexist in some static region of parameter space, but instead to determine whether species could evolve into that parameter space, under realistic conditions, and remain there indefinitely. More specifically, we sought to determine whether a superior interference competitor could be rescued from extinction by agonistic character displacement, without driving a superior exploitative competitor extinct. Agonistic character displacement (ACD) can be defined as phenotypic evolution caused by interspecific interference competition (Grether et al., 2009). ACD can cause species to diverge or converge in competitor recognition and the traits used to recognise competitors, depending on whether recognising individuals of other species as competitors is adaptive (i.e. increases an individual's fitness) (Grether et al., 2009). If our hypothetical species came into secondary contact and were similar enough phenotypically to recognise each other as competitors but were not actually in competition for limiting resources, they would be expected to diverge in competitor recognition until interference competition was eliminated. If instead the species overlapped substantially in resource use, interspecific territoriality might be adaptive for species 1 (the superior interference competitor) but not for species 2 (the superior exploitative competitor), in which case species 1 would be under selection to converge whilst species 2 was under selection to diverge, potentially resulting in species 1 chasing species 2 through evolutionary time. Could species 1 converge rapidly enough to avoid extinction, and if so, would species 2 go extinct, or would the species' population sizes stabilise in a type of coevolutionary stalemate or a zero-sum game?

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

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

MATERIALS AND METHODS

The model

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

Territoriality is governed by four polygenic male traits: a phenotypic cue (z) that is visible or audible from a distance (e.g. a prominent colour patch), the central location (μ) and width (σ) of a Gaussian recognition function (Okamoto & Grether, 2013), and a fighting ability state variable. As the sender's value of z approaches the receiver's value of μ, the probability that the receiver recognises the sender as a competitor increases. The width of the function (σ) determines how close the sender's value of z must be to the receiver's value of μ for a given probability of recognition.

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

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

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

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

Model implementation

We built the model on the sPEGG (simulating Phenotypic Evolution on General Purpose Graphics Processing Units) modelling framework (Okamoto & Amarasekare, 2018). sPEGG is a library of open-source code for explicitly tracking the survival, reproduction and genotypes of individuals, with customizable modules for mutation, recombination, migration, gene flow, etc. Individual-level processes (birth, death, behaviour, inheritance, development) were characterised as realisations of stochastic processes. We customised sPEGG for the life cycle and reproductive biology of passerine

birds and added modules simulating habitat selection and territoriality.

Allopatric period and secondary contact

For the first 1000 generations (years) of each simulation, populations of the two species breed in different communities with identical habitats. Initially, both species are genetically homogeneous. As genetic variation builds gradually through mutation and recombination, the species evolve to their respective optima for σ and degrees of separation between z and μ, and population sizes stabilise. The first generation is highly territorial because z equals μ within species, but if territoriality proved maladaptive, traits z and μ would diverge from each other until the probability of males recognising conspecific males as competitors was negligible. Thus, intraspecific territoriality is not assumed by the model and would be lost if selection opposed it. It is even possible to have interspecific territoriality without intraspecific territoriality if one species' mean value of μ diverged from its mean value of z and in doing so converged on the other species' mean value of z, although it is difficult to imagine a scenario in which selection would favour that outcome.

With the model parameterised with estimates of clutch size, nestling survival, and adult survival from the published literature on pied and collared flycatchers (Table S1), intraspecific territoriality is adaptive for both species, albeit more strongly so for species 1 than species 2, because species 1's baseline nestling survival is lower, and thus the fitness consequences of not being territorial are more severe for species 1. Starting in the 1001st year, individuals move from one community to the other between breeding seasons, with a probability of 0.5, which brings the species into contact. Simulations ran for 10,001 years in total.

Parameter sets, model output, and outcome classifications

We varied dietary overlap (27 levels), the fraction of refuge territories (14 levels), the species difference in fighting ability (6 levels), and the initial phenotypic difference between the species in traits z and μ (2 levels), in a fully factorial design, for a total of 4536 parameter sets. Each parameter set was run multiple times (mean ± SD = 13.5 ± 1.6) with different random seeds (61,386 simulations in total). Parameter settings remained constant for the duration of a simulation. The model recorded the species, sex, age, phenotypes, and nestling survival of all individuals in selected years.

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

Forking, defined as one species' mean values of z and μ being on opposite sides of the other species' mean values of z and μ, occurred in 1584 (2.6%) of the simulations. The usual cause was that z_2 and μ_2 separated somewhat during the allopatric period and were on opposite sides of z_1 and μ_1 when contact occurred (Figure S8). We do not consider forking to be a plausible outcome in nature and, therefore, re-ran simulations in which forking occurred, using different random seeds.

RESULTS

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

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

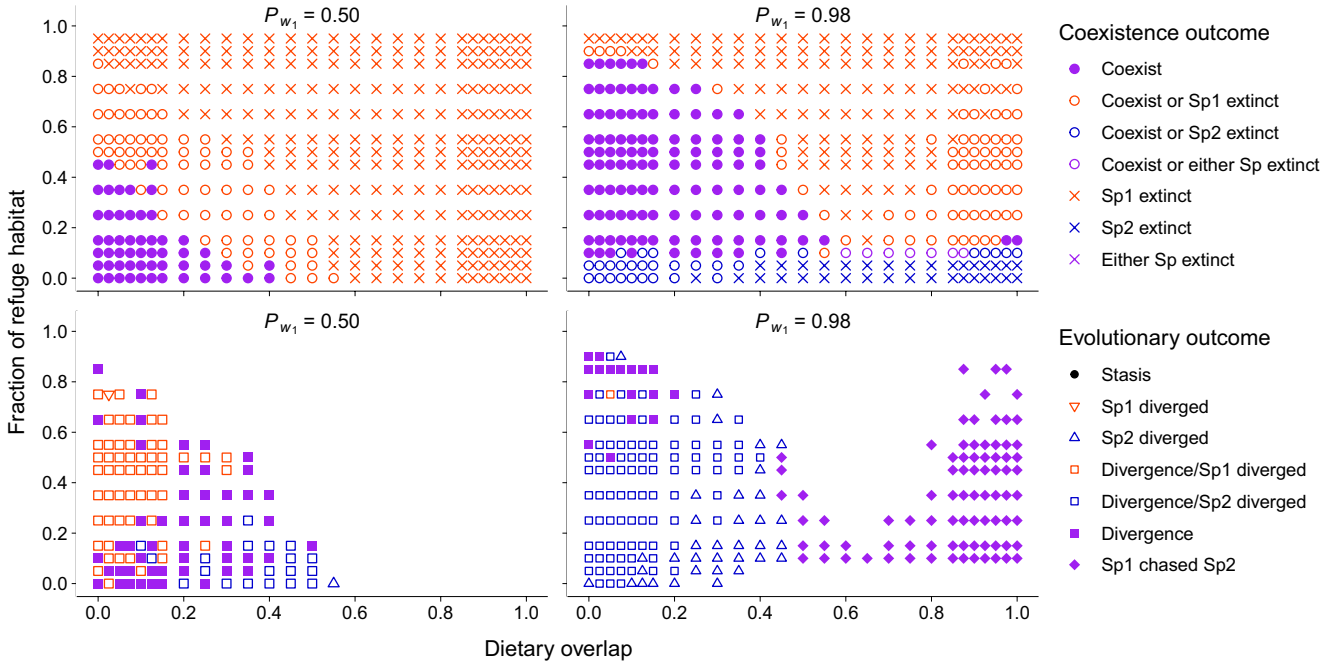

FIGURE 1 Coexistence and evolutionary outcomes in relation to dietary overlap, the fraction of the habitat where species 2 could breed without interference from species 1, and the probability of species 1 winning interspecific fights (Pw_1, based on the species difference in fighting ability). Each point represents a unique parameter set. In the top panels, symbols correspond to the observed coexistence outcomes (see legend). For example, 'Coexist or Sp1 extinct' means that the species coexisted to the end or species 1 went extinct, in different simulation runs. In the lower panels, symbols correspond to the evolutionary outcomes when both species persisted to the end (see legend): 'Stasis', neither species' mean values of z and μ changed significantly; 'Sp2 diverged', species 2 shifted away from species 1 and species 1 exhibited stasis; 'divergence', both species shifted away from the other; 'Sp1 chased Sp2', species 1 converged and species 2 diverged; 'divergence/Sp2 diverged', both outcomes occurred in different simulation runs; etc. This figure summarises a subset of the simulations in which the initial mean difference between the species in traits z and μ was 1. Figures S9–S12 summarise all of the simulations.

switched from divergence to chasing progressively decreased (Figures S11 and S12).

Unexpectedly, the relationship between the probability of coexistence and dietary overlap was U-shaped when the species differed in fighting ability (Figures 2; Figure S15). The rarity of coexistence at intermediate levels of dietary overlap arose from the high rate of extinction of the superior interference competitor (Figure S17), except at the lowest fractions of refuge habitat, where the superior exploitative competitor was at greater risk of extinction (Figure S19). To clarify why coexistence occurred more often at high than intermediate levels of dietary overlap, we examined all cases in which both species persisted for at least 1000 years after contact. This revealed that extinction at intermediate levels of dietary overlap usually occurred whilst the superior interference competitor was chasing the superior exploitative competitor (Figure S13; for examples, see Figures S5 and S6). Evidently, selection on the superior interference competitor to recognise the superior exploitative competitor was not strong enough at intermediate levels of dietary overlap to maintain interspecific territoriality and forestall competitive exclusion.

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

Indeed, when the dietary overlap was high, the probability of coexistence was strongly, and positively affected by whether heterospecifics recognised each other as competitors in the last years of contact during the simulations (Figure 3). When the superior interference competitor failed to converge rapidly enough to maintain a high probability of heterospecific recognition, it usually went extinct. The heterospecific recognition probability required to prevent competitive exclusion of the superior interference competitor

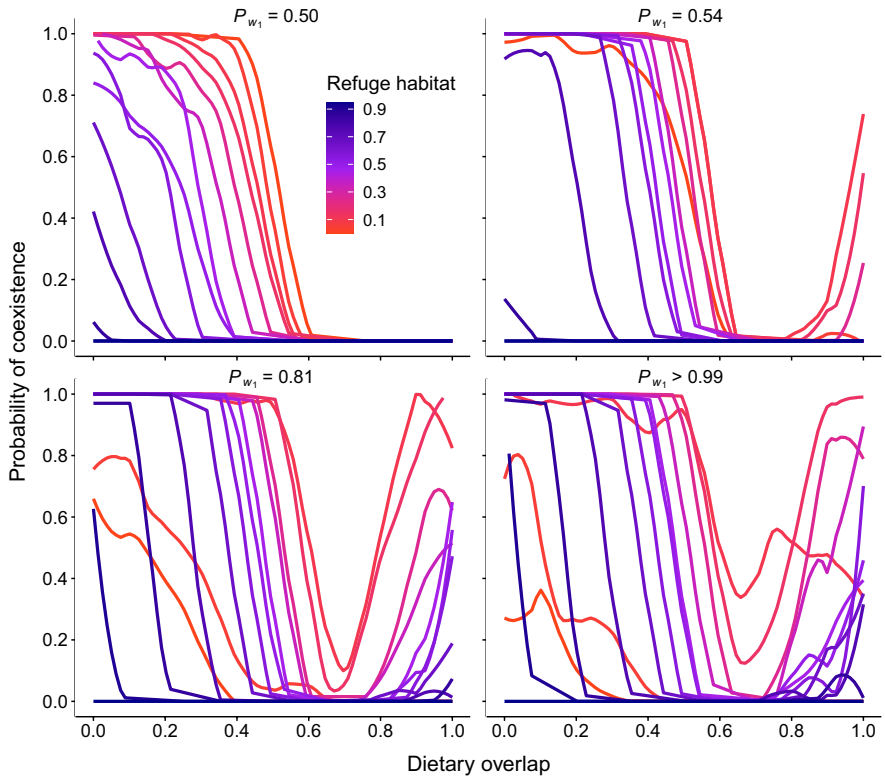

FIGURE 2 Probability of coexistence in relation to dietary overlap, the fraction of the habitat where species 2 could breed without interference from species 1 (colour scale), and the probability of species 1 winning interspecific fights (Pw_1). The lines were generated by a non-parametric smoothing function bounded by 0 and 1 (geom_smooth in the R package ggplot2). Here, the initial mean difference between the species in traits z and μ was 1. Figure S15 shows results for two additional levels of Pw_1, and Figure S16 shows the probability of coexistence for simulations in which the initial mean difference was 2.

decreased as the fraction of refuge habitat decreased and as the species difference in fighting ability increased (Figure 3). However, at the lowest fraction of refuge habitat, the positive effect of heterospecific recognition on coexistence disappeared when the species differed greatly in fighting ability because in this situation the superior exploitative competitor was at risk of extinction (Figure 3, bottom panels).

DISCUSSION

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

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

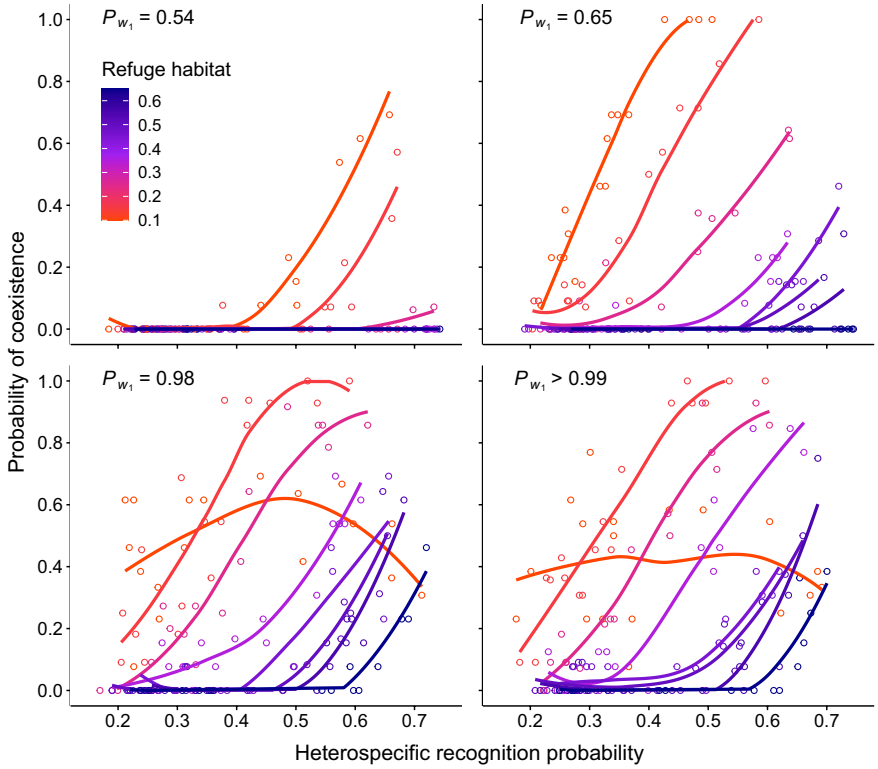

FIGURE 3 Probability of coexistence under high dietary overlap (≥0.75) in relation to the average probability of heterospecific males recognising each other as competitors in the final years of contact (i.e. just before one species went extinct or the simulation ended). Each point represents a unique parameter set. The colour scale indicates the fraction of the habitat where species 2 could breed without interference from species 1 (limited to the range shown in the legend). The lines were generated as in Figure 2. The initial mean difference between the species in traits z and μ was 1 or 2 in these simulations.

Our modelling approach applies to most, but not all, forms of interspecific territoriality. In our model, individuals have a single competitor recognition function that determines how they respond to both species. This is realistic for closely related species like *Ficedula* flycatchers (Nadachowska-Brzyska et al., 2013) because interspecific territorial aggression at the time of secondary contact would almost certainly result from homology in the phenotypic traits and neural templates used to recognise conspecifics (Grether, 2011). Most cases of interspecific territoriality in birds do involve phenotypically and genetically similar species, but there are some well-documented cases involving phenotypically distinct species from different families (Drury et al., 2020). Modelling heterospecific recognition between such distantly related species would probably require two separate competitor recognition functions (i.e., one for conspecifics and the other for heterospecifics). It would be unrealistic, however, to assume species possess recognition functions for other species they have yet to encounter. Innate recognition of phenotypically dissimilar species likely evolves in sympatry. Modelling the de novo evolution of heterospecific recognition may require integrating neural network models with explicitly genetic models of selection (Strand et al., 2002; Watson & Szathmáry, 2016).

We refer to the resource that individuals compete for exploitatively in our model as food, but the results likely hold for any depletable limiting resources to which territory holders have priority of access. In *Ficedula* flycatchers, nest sites may be the key limiting resource (Gustafsson, 1987; Slagsvold, 1978). Interspecific competition for food occurs during the nestling period in other cavity-nesting birds (reviewed by Dhondt, 2012), but *Ficedula* flycatchers have relatively small territories and frequently forage elsewhere (Rybinski et al., 2016; von Haartman, 1956). Whilst the most intensively studied *Ficedula* populations are provided with nest boxes, natural tree cavities vary in size and other characteristics that affect their suitability and accessibility to nest predators (Walankiewicz et al., 2007). Males with larger territories and more nest sites may have a higher probability of attracting a mate (or multiple mates; Alatalo et al., 1986; Dale & Slagsvold, 1996), and with more nest sites to choose from, a lower probability of nest failure. Thus, for this study system, the model parameter that determines the relative strength of interspecific exploitative competition could be called 'similarity in nest site requirements' instead of 'dietary overlap'. Pied and collared flycatchers evidently have very similar nest site requirements, and collared flycatchers are dominant over pied flycatchers (Qvarnström et al., 2010; Vallin et al., 2012), which

suggests this species pair's position in parameter space is the far-right side of the right-hand panels in Figure 1, where coexistence is precarious, which species is at risk of extinction depends on the availability of refuge habitat for pied flycatchers, and when the species do coexist, they are locked in a coevolutionary stalemate.

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

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

AUTHOR CONTRIBUTIONS

Gregory F. Grether conceived the project, Kenichi W. Okamoto wrote the code, and both authors contributed to model development and testing. Gregory F. Grether ran the simulations, processed and analysed the data, and wrote the manuscript. Kenichi W. Okamoto helped edit the manuscript and wrote the detailed model description.

ACKNOWLEDGEMENTS

We thank P.A. Amarasekare for comments at the proposal-writing stage, J.P. Drury for help with troubleshooting an early version of the model, and A.E. Finneran, J.N. Fischer, M.E. Zuercher and three anonymous reviewers for comments on manuscript drafts. We thank the National Science Foundation for funding to study real organisms and also to do theoretical work (cf. Van Valen, 1973). This work was supported by grants DEB-1020586, DEB-1457844, and DEB-NERC-2040883 to G.F.G.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.14091.

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SUPPORTING INFORMATION

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

How to cite this article: Grether, G.F. & Okamoto, K.W. (2022) Eco-evolutionary dynamics of interference competition. *Ecology Letters*, 25, 2167–2176. Available from: https://doi.org/10.1111/ele.14091