The Interaction Between Exploitative and Interference Competition: Limits to R^* Theory

Daniel J.B. Smith[1], Joanna Masel[1]

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA

Corresponding author: Joanna Masel, 1041 E Lowell St, Tucson AZ 85721, USA. masel@arizona.edu

Abstract

Most ecological theory emphasizes exploitative competition and ignores interference competition. Much corresponding theory centers around the R^* rule, which predicts that consumers who share a single limiting resource cannot coexist, because the superior exploitative competitor excludes the inferior. Here we model motile consumers that directly interfere during the resource handling stage, mechanistically capturing the dynamics of both exploitative and interference competition. We derive analytical coexistence conditions, which show that interference competition readily promotes coexistence. In contrast to previous theory, coexistence does not require intra-specific inference propensities to exceed inter-specific interference, nor for interference behaviors to carry a direct (rather than merely an opportunity) cost. R^* theory holds only within a narrow parameter value regime, given interference competition. The parameters that affect exploitative competitive ability also strongly modulate interference competition, and the latter rather than the former are sometimes responsible for competitive exclusion. When coexistence does occur, the underlying mechanisms often resemble either the competition-colonization trade-off or the Hawk-Dove game, canonical models from community ecology and evolutionary game theory, respectively. Our model therefore provides a tractable and more generalized framework to understand resource competition that synthesizes previous disparate models into a single framework.

Keywords: coexistence theory, consumer-resource model, Hawk-Dove game, Grime's triangle, Grime-Tilman debate, game theory, evolution of aggression

Introduction

The R^* rule (Armstrong and McGehee 1980, Tilman 1981, Tilman 1982) has been extraordinarily influential as a fundamental building block of community ecology and coexistence theory. Briefly, R^* theory equates the competitive ability of a focal species or genotype with its ability to deplete a limiting resource. Consider a consumer grown in monoculture with a single limiting resource. The consumer population will increase until resource consumption drives the resource concentration (R) down to a level (the consumer's R^*) at which consumer population growth stops. R^* theory emphasizes that a consumer with a lower R^* has a competitive advantage of those with a higher R^*. In a multi-species or polymorphic context, the species or genotype with the lowest R^* is predicted to exclude all others because it drives the resource level too low for others to persist – this is referred to as the R^* Rule.

R^* theory and the R^* Rule thus focus on *exploitative competition*, in which consumers compete indirectly through shared use of a depletable resource (either biotic or abiotic). This emphasis on theories of exploitative competition has often ignored *interference competition*. Interference competition refers to direct interactions between individuals at the same trophic level (e.g., direct conflicts for resource acquisition, territoriality, allelopathy); this is common in natural communities in a large variety of taxa (Schoener 1983, Ziv, Abramsky et al. 1993, Ziv and Kotler 2003, DeLong and Vasseur 2011, Inderjit, Wardle et al. 2011, Drury, Cowen and Grether 2020) but assumed negligible in most ecological theory, and absent in R^* theory.

Here we better integrate interference competition into mechanistic consumer-resource models, and explore its connections with R^* and coexistence theory. Most past ecological models of interference competition do not mechanistically consider resource dynamics (Case and Gilpin 1974, Schoener 1976, Schoener 1978, Hsu 1982, Vance 1984) and are therefore incommensurable with R^* theory. While Amarasekare (2002) explicitly considers resource dynamics, she still models interference phenomenologically to argue that (1) costly interference (e.g., aggression, territoriality) cannot maintain coexistence, and (2) interference competition does not maintain coexistence unless one consumer species eats or parasitizes the other. This supports the claim that interference competition over territory or food items cannot maintain coexistence.

In contrast, evolutionary game theory demonstrates that interference competition can facilitate the coexistence of different strategies. This is readily seen in the Hawk-Dove game (Maynard Smith and Price 1973, Maynard Smith 1974, Maynard Smith 1982), which considers two strategies competing for a shared, implicitly modeled resource: a “Dove” that abstains from, and a

"Hawk" that participates in interference competition. Obtaining resources yields benefit b and losing contests yields cost C. Coexistence is maintained if the cost of Hawk-Hawk conflicts generates sufficiently strong negative frequency dependence in the Hawk population, which occurs when $C < b$. However, these ideas have not been formally integrated into R^* theory.

The competition-colonization trade-off is a related, classic coexistence mechanism (Skellam 1951, Horn and MacArthur 1972, Hastings 1980, Tilman 1994). Species are subject to a trade-off between their ability to access resources (by rapidly colonizing a patch or resource pulse) and their competitive ability (to displace heterospecifics from patches). Inferior competitors can persist if they colonize patches sufficiently rapidly to escape superior competitors; inferior colonizers can persist by displacing superior colonizers from patches. Locally superior competitive ability is often implicitly assumed to be exploitative in nature, but it could just as easily be interference, which is how we interpret it here. Interpreted in this way, the competition-colonization trade-off constitutes a mechanism in which interference plays the key role in maintaining coexistence.

Here we develop a model of motile consumers that incorporates mechanistic descriptions of both exploitative and interference competition, connecting to both the Hawk-Dove game and the competition-colonization trade-off. We demonstrate that interference competition can readily allow the coexistence of consumer species that differ in R^* values, making the R^* of a species (or genotype) an unreliable qualitative metric of competitive outcomes.

Methods

Model

We extend a typical consumer-resource model to incorporate interference competition between the consumers for a single shared resource. Similar to (Galanthay, Křivan et al. 2023), we consider the following set of differential equations:

$$\frac{dS_i}{dt} = (1/\tau_i)(1+e)H_i + C_{ii}\beta_i + \frac{1}{2}\sum_{j\neq i} C_{ij}\beta_i - mS_i - \sum_{j=1}^{N} a_i S_i H_j - a_i S_i R$$

$$\frac{dH_i}{dt} = a_i S_i R + C_i(\beta_i + m_i + m_{Ci}) + \frac{1}{2}\sum_{j\neq i} C_{ij}(\beta_j + m_i + m_{Ci}) - m_i H_i - (1/\tau_i)H_i - \sum_{j=1}^{N} a_j S_j H_i$$

$$\frac{dC_{ii}}{dt} = 2a_i S_i H_i - 2C_{ii}(\beta_i + m_i + m_{Ci}) \qquad (1)$$

$$\frac{dC_{ij}}{dt} = 2(a_j S_j H_i + a_i S_i H_j) - C_{ij}\left(\beta_i + \beta_j + m_i + m_j + m_{Ci} + m_{Cj}\right)$$

$$\frac{dR}{dt} = f(R) - \sum_{j=1}^{N} a_j S_j R + \sum_{j=1}^{N} m_j H_j$$

While seemingly complex, these differential equations represent a relatively simple biological scenario (Fig. 1). S_i represents the number of *Searching* individuals of consumers of type i, and H_i represents the number of consumers in the process of *Handling* a resource. These discrete numbers are approximated using continuous differential equations, that can also be interpreted as densities. The consumer types could either be different species, or different variants of a single polymorphic species. R is resource density, which grows according to a saturating function $f(R)$. For simplicity, we assume $f(R) = r(K - R)$, representing a spontaneously regenerating consumable resource. We do this instead of assuming a biological resource that exhibits logistic growth (i.e. $f(R) = rR(1 - R/K)$) because it avoids complications such as limit cycles (see Galanthay et al., 2023).

Searching consumers of type i find resources at rate a_i and begin to handle them once encountered. Handling consumers utilize resources at rate $1/\tau_i$. Note that we refrain from referring to τ as "handling time" because, mathematically, it differs from the transformed handling time (h or T_h) traditionally used in ecological models (Real 1977). Consumers reproduce at a rate proportional to their utilization of resources $e_i \tau_i H_i$, with e_i as a conversion factor.

When a searching consumer encounters a handling consumer, this initiates a conflict. C_{ii} represents the total number of individuals of type i engaged in within-type contests, and C_{ij} ($j \neq i$) represents the number of individuals engaged in between-type contests. Conflicts resolve either by a consumer of type i giving up at rate β_i, or dying. During contests, mortality rate increases by $m_C \geq 0$, on top of a basal mortality rate of m. Importantly, consumers do not differentiate between opponents: consumers of type i initiate contests with types i and j at identical rates. Similarly, giving up rates are intrinsic: consumers of type i always give up at the same rate β_i irrespective of their opponent. We do so to avoid assuming, for example, intra-type interference propensity exceeds inter-type interference, which unsurprisingly, easily produces coexistence (Vance 1984). Nor do we need to invoke co-evolutionary dynamics to allow interference competition to play a role in coexistence (Grether and Okamoto 2022).

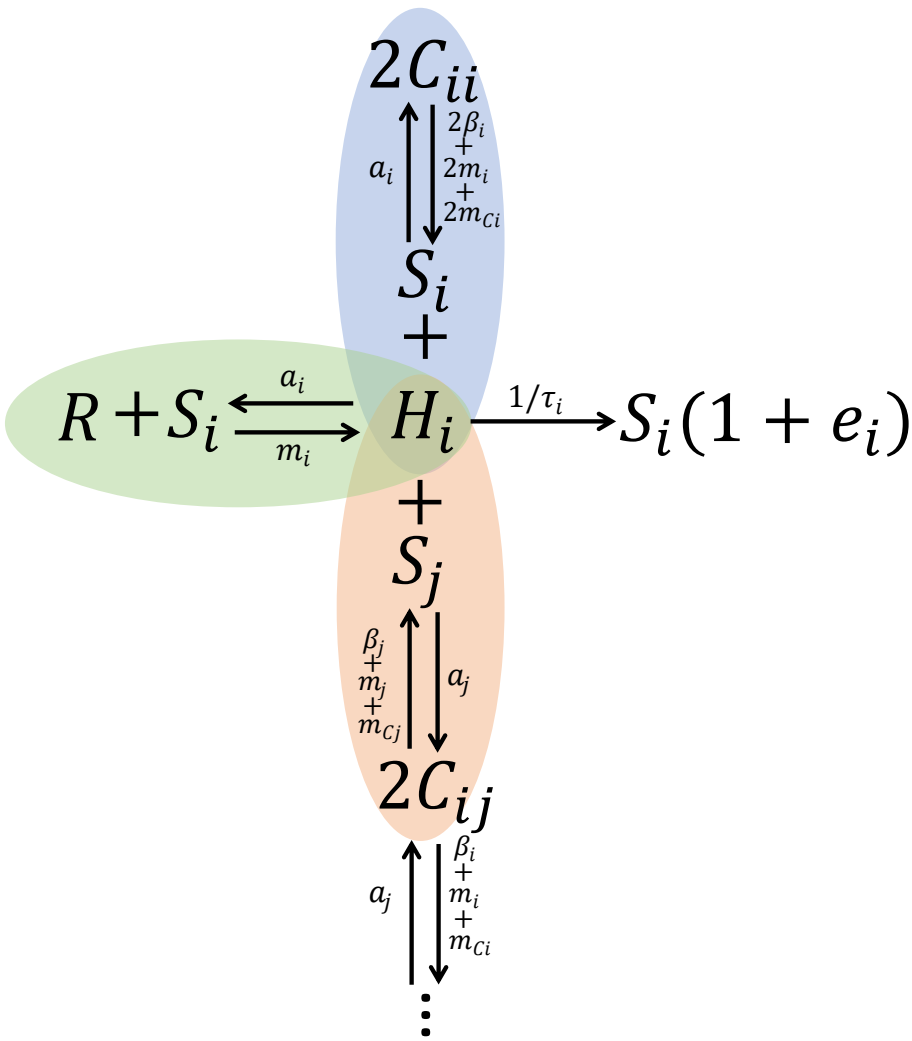

Fig. 1: Schematic representation of the model described by Equations 1. Full dynamics of species i are shown; those of consumer j are symmetric and truncated for simplicity from the lower portion of the figure. Colored ovals clarify which parties are engaged in transformation at which rates. Resources and Searching-consumers of type i ($R + S_i$) combine to form a Handling-consumer-i (H_i). Handling-consumers of type i combine with Searching consumers of types i or j (S_i or S_j) to form C_{ii} or C_{ij} Contest interaction complexes, respectively. Search rate is denoted a, mortality m, giving up on contests β, and handling $1/\tau$. Contest complexes contain 2's because conflicts always contain two consumers.

Analysis

In the Supplementary Notebooks, we perform invasion analysis (Turelli 1978) for the two-consumer one-resource system described by equation (1) when $N = 2$. To do so, we first solve the non-trivial equilibrium for each one-consumer one-resource system, yielding $S_i^*, H_i^*, C_{ii}^*,$ and R_i^*. We then derive the 4×4 Jacobian matrix for the variables S_j, H_j, C_{jj}, and C_{ij} where $j \neq i$. We then compute the eigenvalues of the Jacobian matrix at the point where consumer i is at its non-trivial equilibrium

and consumer j is a rare invader: $[S_i^*, H_i^*, C_{ii}^*, R_i^*, S_j = 0, H_j = 0, C_{jj} = 0, C_{ij} = 0]$. We perform analyses both analytically and numerically using Mathematica version 13.2. Consumer j will increase in abundance (invade) when rare if and only if at least one eigenvalue is positive. Coexistence is inferred from mutual invasibility. From this, we derive analytical conditions for consumer invasion and coexistence.

RESULTS

No Interference Competition

To remove interference competition as a thought experiment, without changing resource competition (fast handling $\tau_i \to 0$ would also change the latter), we take the limit of the giving up rate $\beta_i \to \infty$. Let $R_{i,E}^*$ denote the equilibrium resource abundance set by species i in isolation when only *exploitative* competition occurs. Assuming $R_{i,E}^* > 0$,

$$R_{i,E}^* = \frac{m_i(m_i\tau_i + 1)}{a_i(e_i - m_i\tau_i)} \tag{2}$$

(see Supplementary Notebook A section 1). We refer to $R_{i,E}^*$ as the *exploitative competitive ability* of consumer i. Similarly, we consider its ratio of between types, $R_{i,E}^*/R_{j,E}^*$, as the *relative exploitative competitive ability* of consumers i and j (if $R_{i,E}^*/R_{j,E}^* < 1$, type i is favored; if $R_{i,E}^*/R_{j,E}^* > 1$, type j is favored). $R_{i,E}^*$ additionally represents the minimum resource requirement for consumer i. In Supplementary Notebook A (sections 2-4), we derive that coexistence requires:

$$1 < \frac{R_{i,E}^*}{R_{j,E}^*} < 1 \tag{3}$$

which cannot be fulfilled. Mutual invisibility is therefore impossible, and the consumers cannot coexist -- this is the R^* Rule (Tilman 1982).

Interference competition by only one type

Interference competition ($\beta_i < \infty$) enables the resource density (R^*) to grow to a higher equilibrium (Fig. 2). We denote the equilibrium resource density set by species i as $R_{i,I}^* \geq R_{i,E}^*$, with equality for infinite β_i. We refer to $R_{i,I}^*$ as consumer $i's$ interference R^*. $R_{i,I}^*$ and $R_{i,E}^*$ differ because conflicts incur an opportunity cost – time spent in conflict is not available for searching for resources, allowing resources to increase in density.

As consumer density rises, interference events increase in frequency per capita. The resulting negative density-dependence decreases consumer abundance and increases resource density. Increased mortality during conflicts ($m_C > 0$) modifies $R^*_{i,I}$ quantitatively but not qualitatively (Fig 2A). Thus, interference competition does not need to be directly costly for it to influence the resource level; opportunity cost alone is sufficient. The more interference competition there this, the closer $R^*_{i,I}$ approaches the carrying capacity K (Fig. 2B).

We first consider a simplified model that bears some resemblance both to the Hawk-Dove game and the competition-colonization trade-off. Let i and j represent "Hawk" and "Dove" strategies. β_{Hawk} is finite while $\beta_{\text{Dove}} = \infty$, meaning the Hawk always contests resources while the Dove immediately gives up. Because $\beta_{\text{Dove}} = \infty$, $R^*_{\text{Dove},I} = R^*_{\text{Dove},E} = R^*_{\text{Dove}}$, whereas $R^*_{\text{Hawk},I} > R^*_{\text{Hawk},E}$. In Supplementary Notebook B section 4, we show that Doves can invade a community of Hawks if:

$$R^*_{\text{Dove}} < R^*_{\text{Hawk},I} \times P_{\text{Dove}} \tag{4}$$

Where $P_{\text{Dove}} = \frac{1/\tau_{\text{Dove}} + m}{1/\tau_{\text{Dove}} + m + a_{\text{Hawk}} S^*_{\text{Hawk}}}$ gives the probability that a Dove does not experience Hawk interference while utilizing the resource (see Supplemental Notebook B, section 5 for the interpretation of P_{Dove}). Verbally, Doves must be able to persist at a minimal resource density (R^*_{Dove}) not just below the resource density set by the Hawks ($R^*_{\text{Hawk},I}$), but below a lower level that takes into account the inability to benefit from resources that they relinquish to Hawks (P_{Dove}). Hawk interference generates both a benefit ($\Delta R^*_{\text{Hawk},I} - R^*_{\text{Hawk},E}$) and a cost ($P_{\text{Dove}}$) to Dove invasion.

Conversely, the Hawk can invade a resident Dove population if:

$$R^*_{\text{Hawk},E} < R^*_{\text{Dove}} + H^*_{\text{Dove}} \tag{5}$$

(see Supplementary Notebook B section 4). Verbally, the Hawk must be able to persist ($R^*_{\text{Hawk},E}$; Hawk-Hawk interference is negligible when Hawks are rare) on resources that include both those currently unclaimed by Doves (R^*_{Dove}) and those currently held by Doves that Hawks can readily steal (H^*_{Dove}).

Connection to the Classic Hawk-Dove Game

If we further assume that Hawks and Doves have identical exploitative competitive ability ($R^*_{\text{Hawk},E} = R^*_{\text{Dove}}$, as is implicit in the traditional Hawk-Dove game), the Dove invades when:

$$\frac{R^*_{\text{Hawk,I}}}{R^*_{\text{Hawk,E}}} P_{\text{Dove}} > 1. \tag{6}$$

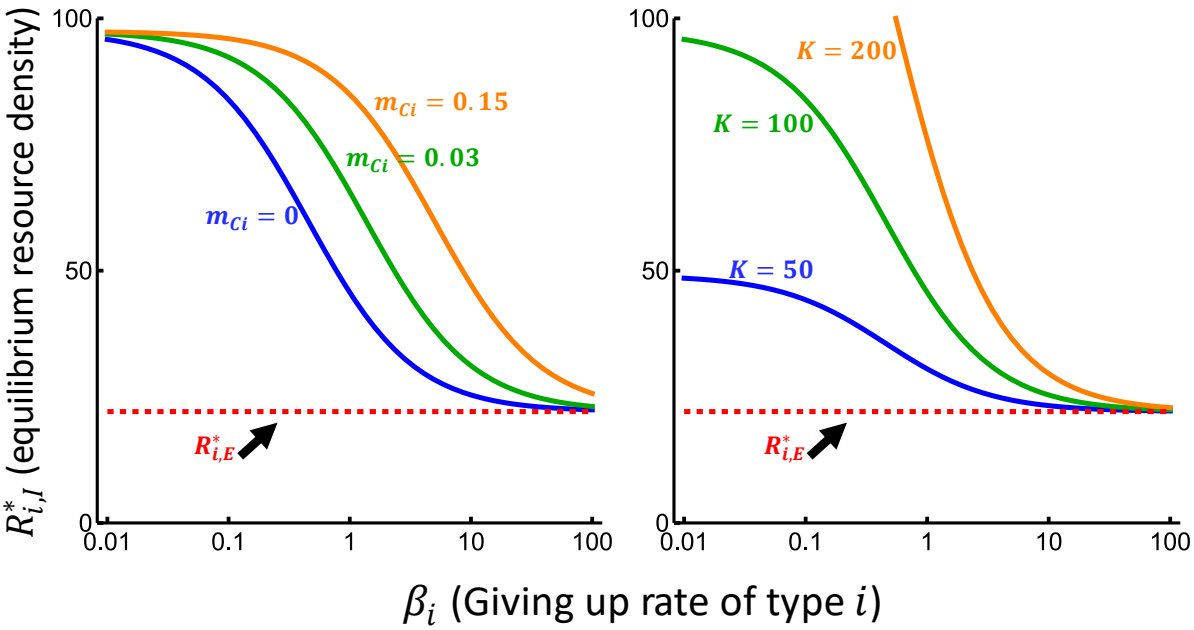

Fig. 2: Interference competition reduces equilibrium resource density. The y-axis $R^*_{i,I}$ shows the equilibrium resource abundance set by a consumer that engages in interference competition, and the x-axis shows β_i the "giving-up rate" of the consumer (note the log-scale). As β_i becomes large, $R^*_{i,I}$ converges to $R^*_{i,E}$ (red dashed line), representing a fully "Dove" strategy. Slower giving up rates yield an increase in $R^*_{i,I}$ relative to $R^*_{i,E}$ (ΔR^*_i becomes larger). (A) A higher mortality rate of consumers m_{Ci} during a conflict (higher curves) elevates $R^*_{i,I}$ with less interference competition (faster giving up rates), but does not qualitatively affect trends. With very slow giving up, $R^*_{i,I}$ is just as elevated, even when interference competition incurs no additional mortality. (B) The asymptote for slow giving up is $R^*_{i,I} \to K$; the resource reaches its capacity when consumers are always engaged in fighting rather than foraging.

$\frac{R^*_{\text{Hawk,I}}}{R^*_{\text{Hawk,E}}} P_{\text{Dove}} > 1$See Supplemental Notebook B, Section 6 for details. Satisfying equation (6) implies coexistence because the Hawk always invades when $R^*_{\text{Hawk},E} = R^*_{\text{Dove}}$ (equation (5)). As in the traditional Hawk-Dove game, coexistence depends on whether interference within a pure Hawk population yields an advantage to a rare Dove invader. The left-hand side of equation (6) is the product of the proportional increase in resource availability due to Hawk-Hawk interference ($R^*_{\text{Hawk,I}}/R^*_{\text{Hawk,E}}$) and the probability the Dove does not experience interference while handling a resource (P_{Dove}). Thus, the Dove invades if Hawk interference results in a net gain for Dove resource utilization (successful handling). Coexistence is possible due to an interference-interference trade-off: Hawks invade by stealing resources from Doves; Doves invade by benefitting from the increase in resource density from Hawk-Hawk interference.

Connection to the Competition-Colonization Trade-off

When $R^*_{\text{Hawk},I} \approx R^*_{\text{Hawk},E}$ (Hawk-Hawk interference does not meaningfully increase equilibrium resource density, which occurs when $0 \ll \beta_{\text{Hawk}} < \infty$), coexistence requires:

$$R^*_{\text{Hawk},E} - H^*_{\text{Dove}} < R^*_{\text{Dove}} < R^*_{\text{Hawk},E} P_{\text{Dove}} \tag{7}$$

where the left inequality permits Hawk invasion and the right permits Dove invasion. Recalling that $P_{\text{Dove}} < 1$, the Dove needs to be a superior exploitative competitor ($R^*_{\text{Dove}} < R^*_{\text{Hawk},E}$) to outweigh this interference. The Hawk can invade if there are enough Doves handling resources (H^*_{Dove}) that can be stolen to compensate for lower exploitative ability. This scenario resembles classic competition-colonization trade-off models, when competition is interpreted as interference competition. In particular, when the Dove's superior exploitation comes from a higher search rate (a), Doves invade when $a_{\text{Dove}} > a_{\text{Hawk}}/P_{\text{Dove}}$, mathematically similar to the 2-species coexistence condition from classical models (Hastings 1980, Tilman 1994; see Supplemental Notebook B, Section 7). Coexistence requires a trade-off between their abilities to find new resources vs. displace competitors from resources –an exploitative-interference trade-off.

Interference competition by both types

Interference competition adds two mechanisms that threaten the R^* Rule: increased resource availability due to intra-type interference, and resource theft, quantified by P_{Dove} and H^*_{Dove}, respectively. Next, we investigate how both $R^*$and these two additional mechanisms shape outcomes when both β_1 and $\beta_2 < \infty$. We call the consumer with the smaller β the Hawk and that with the larger the Dove, based on their propensities to engage in interference contests, although both are on a spectrum of Hawkishness. The two types might also differ in other ways.

Generalizing equations (4) and (5), consumer j can invade a community of type i if and only if:

$$R^*_{j,E} < P_j\left(R^*_{i,I} + \omega_j H^*_i\right). \tag{8}$$

See Supplemental Notebook C sections 1-4 for details of its derivation. If $\beta_i \to \infty$ and $\beta_j < \infty$, then equation (8) reduces to equation (5), the case of a Hawk invading a population of Doves. Conversely, if $\beta_j \to \infty$ and $\beta_i < \infty$, equation (8) reduces to equation (4), the case of the Dove invading a population of Hawks.

P_j is a generalization of P_{Dove}, quantifying the negative impacts of interference competition on invasion of type j ($0 \leq P_j \leq 1$). P_j accounts both for the costs invader j experiences from

interference from resident i, and for the opportunity cost the invader experiences due to interfering with residents. See Supplemental Notebook C, section 3 for more details. P_j is multiplied by terms describing the positive influences on invasion. $R^*_{i,I}$ is the equilibrium resource level of the resident i, including its elevation from interference competition. ω_j is the probability that invader j wins a contest against resident i: $\omega_j = (\beta_i + m)/(\beta_j + \beta_i + 2m)$ (see Supplemental Notebook C, sections 4-5). $\omega_j H_i^*$ therefore represents the additional resources that invader j can access by taking them from handling residents i (the benefit j experiences from its own Hawkish behavior).

Rearranging Equation (8) for each consumer type (1 and 2), we derive criteria for coexistence in terms of interference and exploitative competition:

$$\underbrace{\frac{1}{P_2\left(\frac{H_1^*}{R_{1,E}^*}\omega_2 + \frac{R_{1,I}^*}{R_{1,E}^*}\right)}}_{\substack{\text{Net impact of}\\ \text{interference on the}\\ \text{invasion of type 2}\\ (I_2)}} < \underbrace{\frac{R_{1,E}^*}{R_{2,E}^*}}_{\substack{\text{Relative}\\ \text{exploitative}\\ \text{competition}\\ \text{abiliity}\\ (E_{12})}} < \underbrace{P_1\left(\frac{H_2^*}{R_{2,E}^*}\omega_1 + \frac{R_{2,I}^*}{R_{2,E}^*}\right)}_{\substack{\text{Net impact of}\\ \text{interference on the}\\ \text{invasion of type 1}\\ (I_1)}} \tag{9}$$

where I_j represents the net impact of interference on invasion of consumer j ($j = 1,2$) and E_{12} represents the relative exploitative competition ability of the consumer 1 relative to consumer 2. In the absence of interference (when $\beta_1 = \beta_2 = \infty$), $I_1 = I_2 = 1$ and the expression collapses to the R^* Rule (equation (3)). Without loss of generality, we assume $\beta_1 < \beta_2$, and denote $\beta_H = \beta_1$ and $\beta_D = \beta_2$. The relative importance of exploitative and interference competition can be quantified according to the magnitudes of $|\log I_{\mathrm{H}}|$, $|\log E_{HD}|$, and $|\log I_{\mathrm{D}}|$.

Five distinct scenarios are possible (see Table 1 and Fig. 3). In scenarios 1-3, one consumer is competitively excluded, while coexistence occurs in scenarios 4-5 when $1/I_{\mathrm{D}} < E_{HD} < I_{\mathrm{H}}$. We find that $1/I_{\mathrm{D}} > E_{HD} > I_{\mathrm{H}}$ cannot be fulfilled (priority effects do not occur). Competitive exclusion can be due either to differences in exploitation (scenario 1, reminiscent of the R^* Rule; Fig. 3, red shading), or to differences in interference (Fig. 3, blue shading). In scenario 2, Hawk interference is too costly to Doves, while in scenario 3, the Hawk's opportunity cost from interference is too large. Unlike for the simplified case of $\beta_{\mathrm{D}} = \infty$, the Hawk may be excluded even if the Dove is not superior at exploitative competition.

Coexistence in scenario 4 stems from an interference-interference trade-off similar to the classic Hawk-Dove game (Fig. 3, purple shading, middle region). Interference considerations dominate both invasion directions, when $|\log E_{HD}| < |\log I_{\mathrm{D}}|$ and $|\log E_{HD}| < |\log I_{\mathrm{H}}|$. In contrast, coexistence in scenario 5 occurs via a trade-off between exploitative and interference competition abilities (Fig. 3, purple shading, top and bottom regions). In scenario 5a, Doves invade primarily due

Scenario	Definition	Condition
(1) R^* Rule	Exclusion on the basis of inferior exploitative ability.	$\lvert\log E_{HD}\rvert > \lvert\log I_H\rvert$ OR $\lvert\log E_{HD}\rvert > \lvert\log I_D\rvert$
(2) Hawk wins	Dove is excluded due to interference from the Hawk.	$\lvert\log E_{HD}\rvert < \lvert\log I_D\rvert$
(3) Dove wins	Hawk is excluded due to opportunity cost from slow giving up rate.	$\lvert\log E_{HD}\rvert < \lvert\log I_H\rvert$
(4) Interference-interference trade-off	Invasion of both Hawk and Dove is predominantly facilitated by the impact of interference competition.	$\lvert\log E_{HD}\rvert < \lvert\log I_H\rvert$, $\lvert\log E_{HD}\rvert < \lvert\log I_D\rvert$,
(5a) Interference-exploitation trade-off (Competition-colonization)	Dove invades due to superior exploitation, Hawk invades due to superior interference.	$\lvert\log E_{HD}\rvert > \lvert\log I_D\rvert$ $\lvert\log E_{HD}\rvert < \lvert\log I_H\rvert$
(5b) Interference-exploitation trade-off	Hawk invades due to superior exploitation, Dove invades due to superior interference.	$\lvert\log E_{HD}\rvert < \lvert\log I_D\rvert$ $\lvert\log E_{HD}\rvert > \lvert\log I_H\rvert$

Table 1: Summary of the five different scenarios, their definitions, and the condition under which they occur. Scenarios 1-3 depict competitive exclusion (equation 9 is not fulfilled; either $1/I_{\mathrm{D}} > E_{HD}$ or $E_{HD} > I_{\mathrm{H}}$). Scenarios 4-5b depict coexistence (equation 9 is fulfilled; $1/I_{\mathrm{D}} < E_{HD} < I_{\mathrm{H}}$).

to superior exploitative ability ($|\log E_{HD}| > |\log I_{\mathrm{D}}|$), while Hawks invade primarily by stealing resources from Doves ($|\log E_{HD}| < |\log I_{\mathrm{H}}|$). This resembles the competition-colonization trade-off, particularly when $a_2 > a_1$. In scenario 5b, Doves invade due to the negative density-dependence induced by Hawk-Hawk interference ($|\log E_{HD}| < |\log I_{\mathrm{D}}|$), while Hawks invade primarily due to superior exploitative competitive ability ($|\log E_{HD}| > |\log I_{\mathrm{H}}|$). By putting them on orthogonal axes, Fig. 3 illustrates I_j and E_{ij} as though they were independent, but they are far from it. Instead, changes to a single model parameter (e.g., a or τ) alter multiple key properties ($R^*_{i,E}, R^*_{i,I}, \omega_i H^*_j, P_i$). We next dig deeper into the causal effects of mechanistic parameters.

First, consider the relatively simple case in which consumers are equal in exploitative competitive ability (i.e. in all traits except giving up rate, β). Coexistence occurs if and only if β_1 and β_2 are on either side of a central value (henceforth β_0; Fig. 4A, green star). β_0 is a complicated (though analytically tractable) expression that depends on every parameter of the model (See Supplemental Notebook C, Section 6). The only possible outcomes (Fig. 4B) are Hawk victory (Scenario 2), Dove victory (Scenario 3), or an interference-interference trade-off (Scenario 4). Interestingly, coexistence does not require a qualitative trade-off between the key metrics

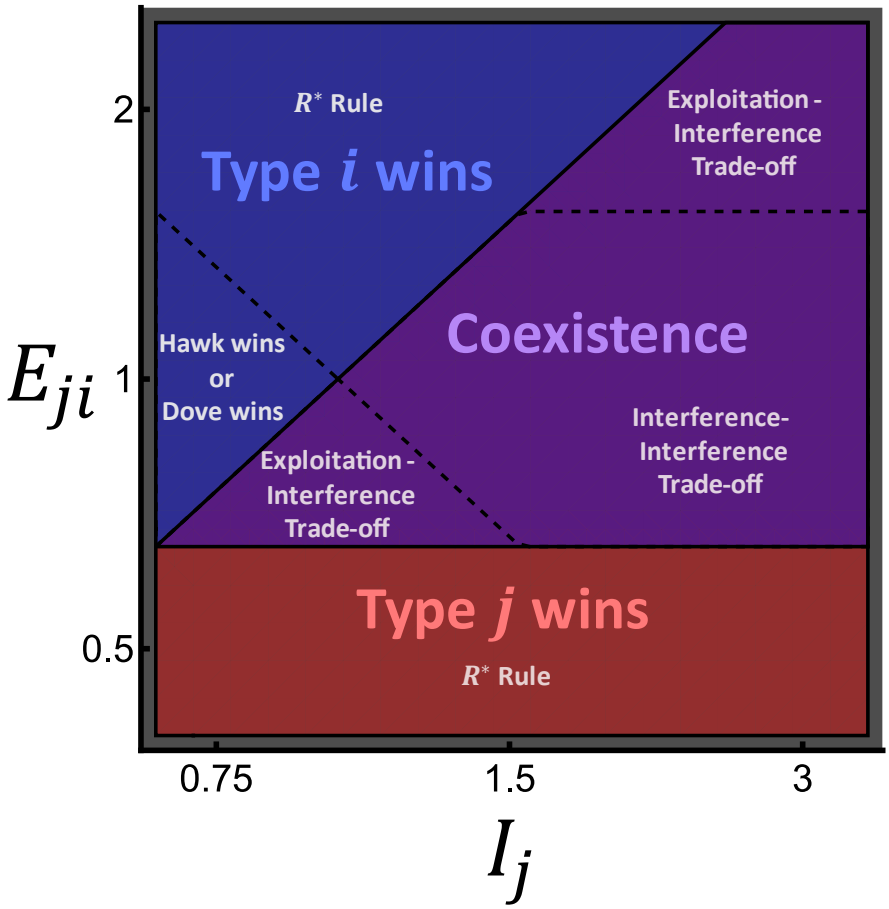

Fig. 3: Interference I_j and exploitative E_{ji} forms of competition combine to shape outcomes. Colors indicate outcome, dashed lines delineate five mechanisms by which they are achieved. Three outcomes are depicted: j excludes i (red), i excludes j (blue), and coexistence (purple). Coexistence can be produced either when interference ability trades off with exploitation, or due to trade-offs embedded within the coexistence possibilities of the Hawk-Dove game. Similarly, competitive exclusion can either follow the R* rule, or be driven by Hawk-Dove interference dynamics. Within the latter region, Hawk victory occurs if $\beta_j > \beta_i$ and Dove victory occurs if $\beta_j < \beta_i$. $I_i = 0.65$ throughout.

associated with Doveish and Hawkish benefits ($R^*_{i,I} - R^*_{i,E}$, and $\omega_j H^*_i$, respectively). I.e., coexistence can occur when $\omega_1 H^*_2 > R^*_{1,I} - R^*_{i,E}$ and $\omega_2 H^*_1 > R^*_{2,I} - R^*_{2,E}$ (both consumers predominantly benefit from resource theft), and also when $\omega_1 H^*_2 < R^*_{1,I} - R^*_{1,E}$ and $\omega_2 H^*_1 < R^*_{2,I} - R^*_{2,E}$ (both consumers benefit predominantly from resources made available by their competitor's intra-type interference).

The equilibrium ratio of resource abundances set by consumers ($R^*_{2,I}/R^*_{1,I}$) does not determine the competitive outcome in the manner predicted by R^* theory, which predicts exclusion of the consumer with the higher R^*. Indeed, coexistence predominantly occurs when the equilibrium

resource abundance R_I^* differs by a larger factor depending on which type is the resident (Fig. 4C, top-left and bottom right corners).

When consumers also differ in exploitative competitive ability ($R_{1,E}^*/R_{2,E}^* \neq 1$), the region of coexistence changes, sometimes dramatically (Fig. 5). The parameters that affect exploitative ability also impact interference. E.g., faster search a slightly increases opportunities to interfere with others, while faster resource use $1/\tau$ more dramatically decreases vulnerability to interference by others. Which trait underlies a difference in exploitative competitive ability can therefore strongly impact outcomes.

When different search rates are responsible for a moderate difference in exploitative competitive ability (e.g., $R_{1,E}^*/R_{2,E}^* = 1.2$ because $a_2 > a_1$; Fig 4A, 4F), outcomes are similar (compare Figs. 4A and 5A; e.g. a little more coexistence instead of wins by the worse exploiter, type 1). However, the mechanism behind the same outcome may be different (compare Figs. 4B and 5F). When giving up rates (β) are similar, the R^* Rule now operates, and coexistence can now stem from interference-exploitation as well interference-interference trade-offs. Even with larger differences in exploitative ability (e.g., $R_{1,E}^*/R_{2,E}^* = 1.75$ because $a_2 > a_1$; Fig 5B), coexistence remains possible for a wide region of parameter space, largely via exploitation-interference trade-offs (Fig. 5G).

When differences in the resource use time τ drive the same advantage in exploitative competitive ability, coexistence becomes less likely ($R_{1,E}^*/R_{2,E}^* = 1.2$ in Fig. 5C), at some point largely evaporating ($R_{1,E}^*/R_{2,E}^* = 1.75$ in Fig. 5D). Hawk or Dove victories (Scenarios 2 or 3) encapsulate most of the parameter space in which competitive exclusion occurs, rather than the R^* Rule (Figs. 5H, 5I).

$R_{1,E}^*/R_{2,E}^*$ rarely explains competitive outcomes. Indeed, a "superior" resource competitor can be excluded via interference by a type that searches more slowly but uses resources faster (e.g., Fig. 5E, 5J; $R_{1,E}^*/R_{2,E}^* = 0.5$ with $a_2 > a_1$ and $\tau_1 > \tau_2$). This occurs even though both $R_{1,E}^*/R_{2,E}^* < 1$ and $R_{1,I}^*/R_{2,I}^* < 1$ for much of the parameter space.

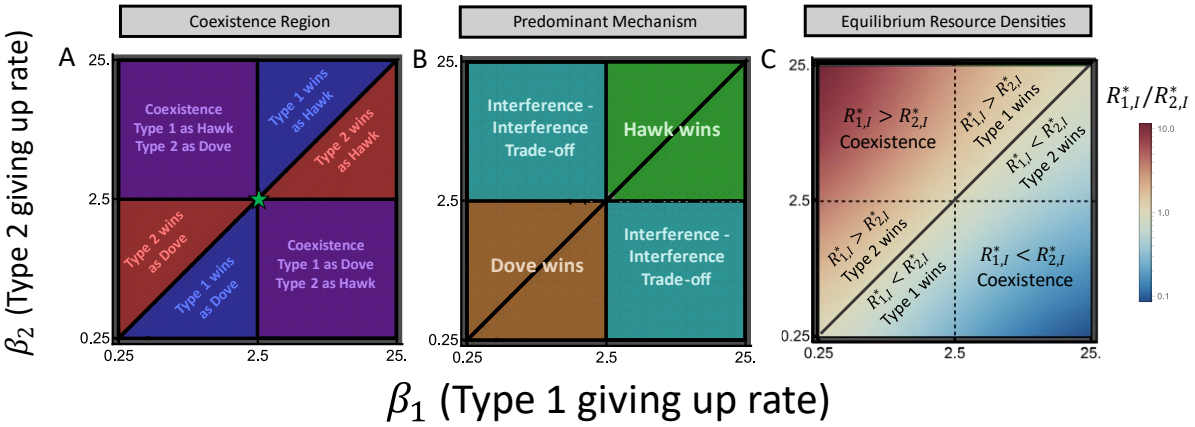

Fig. 4: Given identical exploitative competitive abilities ($R^*_{1,E} = R^*_{2,E}$), coexistence behavior revolves around the relationships between β_1 and β_2 with a central giving up rate β_0 (green star in A). Panel A: coexistence is possible when $\beta_1 < \beta_0 < \beta_2$ where β_0 is the value indicated at the green star and $i \neq j$. Panel B: coexistence (when it occurs) is mediated via an interference-interference trade-off (Scenario 4); competitive exclusion occurs via Dove or Hawk victory. The absence of exploitative differences ($E_{12} = 1$) prohibits the operation of the R^* Rule (Scenario 1) or exploitation-interference trade-offs (Scenario 5). Panel C: β_1 and β_2 strongly modify $R^*_{1,I}/R^*_{2,I}$. The dashed lines separate regions of coexistence and the solid diagonal line represents when $R^*_{1,I} = R^*_{2,I}$. Coexistence in panel A occur in the upper-left and bottom-right corners, regions of parameter space in which $R^*_{1,I}/R^*_{2,I}$ is the farthest from unity (1). Each consumer can be excluded when it has a lower R^*_I (upper-right corner) or a higher R^*_I (bottom-left corner). Note the log scale for color in Panel C. Throughout, parameters are: $\tau_i = 1, a_i = 0.1, m = 0.015, e = 0.035, m_{C1} = m_{C2} = 0, r = 0.25, K = 250$ ($i = 1,2$).

DISCUSSION

Resource competition is the foundation of much ecological theory, in the form of R^* theory (Tilman 1982), but its co-occurrence with interference competition remains understudied. Here, we analyze a mechanistic framework in which consumers can be interrupted by interference competitors while handling a resource, and time invested in contesting a resource incurs an opportunity cost of not searching for uncontested resources. Outcomes rarely follow R^* theory, whether R^* is interpreted as the equilibrium resource level, or as the hypothetical equilibrium resource level in the absence of interference / minimum resource level required for persistence. Both exploitation-interference and interference-interference trade-offs can lead to co-existence. The former is sometimes analogous to the competition-colonization trade-off, while the latter is analogous to the Hawk-Dove game.

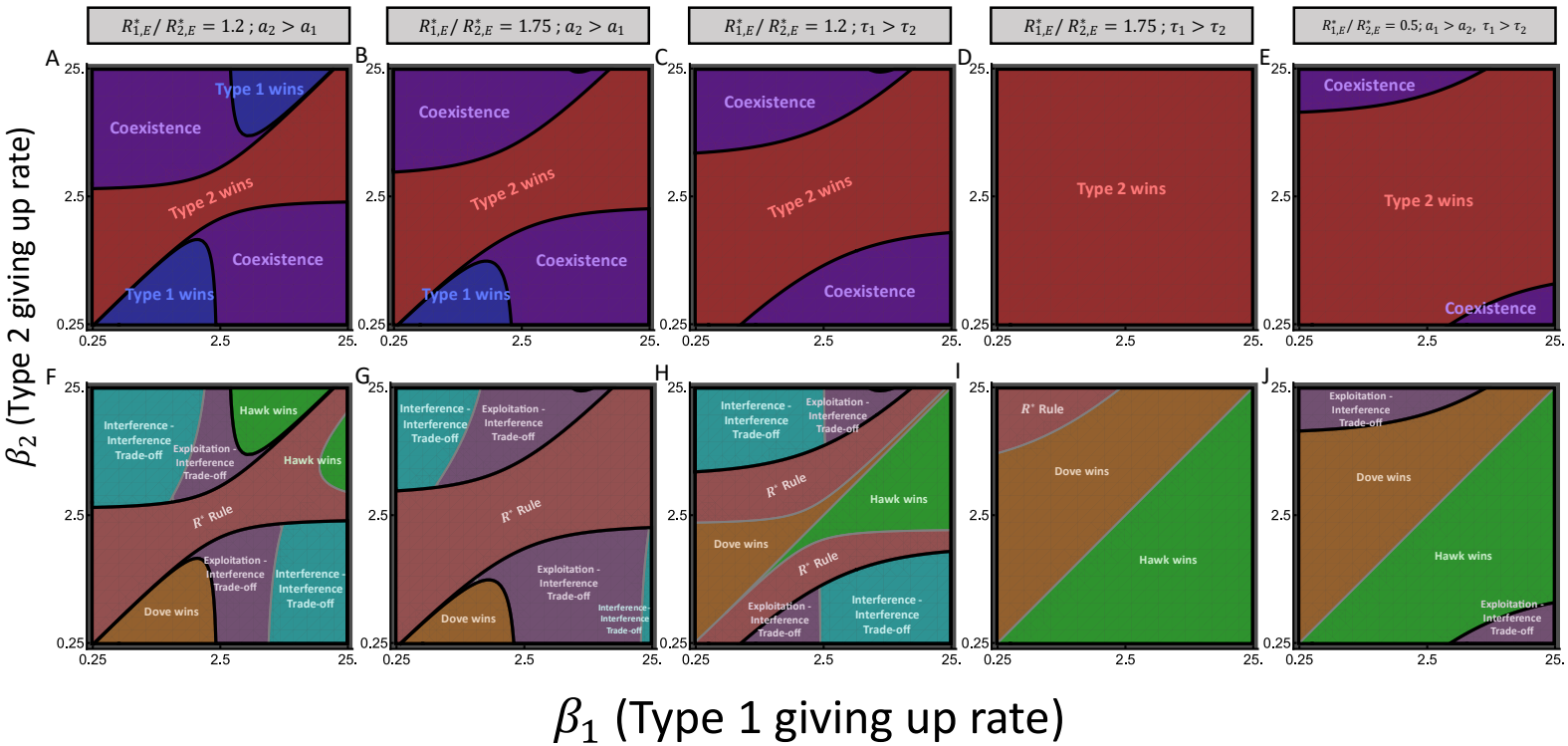

Fig 5: The impact of different giving-up rates (β_1 and β_2) on outcomes and mechanisms by which they occur, when consumers differ in exploitative ability ($R^*_{1,E}/R^*_{2,E} \neq 1$). Row 1 (Panels A-E) depicts outcome and row 2 (Panels F-J) depicts the corresponding dominant mechanism as defined by Table 2. The first two columns describe consumers that differ in search rate (a). The third and fourth columns describe consumers that differ in resouce use rate (τ), and the rightmost column shows consumers who differ in both. Columns 1 and 3 depict relatively small differences in exploitative competitive ability ($R^*_{1,E}/R^*_{2,E} = 1.2$ via $a_1 = 0.1, a_2 = 0.12$ or $\tau_1 = 1, \tau_2 = 1/1.35$) while columns 2 and 4 depict relatively larger differences ($R^*_{1,E}/R^*_{2,E} = 1.75$ via $a_1 = 0.1, a_2 = 0.175$ or $\tau_1 = 1, \tau_2 = 1/30$). In column 5, consumer 1 is superior at exploitation ($R^*_{1,E}/R^*_{2,E} = 0.5$) because it is a more efficient searcher ($0.35 = a_1 > a_2 = 0.01$), but consumer 2 generally wins because it utilizes resources considerably faster ($1/5.19 = \tau_2 < \tau_1 = 1$). When not specified above, $a_i = 0.1, \tau_i = 1, m = 0.015, e = 0.035, m_{C1} = m_{C2} = 0, r = 0.25, K = 250$.

Interference Competition and R^* Theory

R^* theory breaks down for two basic reasons. Firstly, interference allows the equilibrium resource density to rise, and thus outcomes are not always determined by which consumer tolerates the lowest resource density. Within R^* theory, the minimum tolerated resource density R_E^* is equal to the equilibrium resource density R_I^*. With interference competition, this is no longer true.

Secondly, an invading consumer may steal resources from its competitor. Invader growth rates are therefore higher than expected from the equilibrium density of free resources. Thus, in contrast to traditional R^* theory, the ability of type j to invade depends not only on the equilibrium resource density set by resident i ($R_{i,I}^*$) but also on the density of residents currently handling resources (H_i^*; see equation 4).

Key traits (e.g., search rate a, resource use rate, $1/\tau$) that are traditionally associated with exploitative competitive ability have diverse implications for interference competition. Specifically, genotypes or species that achieve low R_E^* due to faster resource utilization ($1/\tau$) gain more via protection from interference competition than genotypes that achieve the same low R_E^* through faster search (a) gain via increased ability to interfere with others. Although many previous models used a handling time h (analogous to our τ) in consumers' functional responses (i.e. to make consumption a saturating function of resource density), they do not emphasize h except as it pertains to intrinsically driven consumer-resource oscillation (Rosenzweig 1971, Johnson and Amarasekare 2015) and to relative non-linearity in functional responses (Armstrong and McGehee 1980). This is driven by the assumption that h influences competitive outcomes only via its effect on R^*, which we show here to be unfounded.

We do find support for traditional R^* theory within some regions of parameter space (Figs. 3, 5). Thus, whether R^* theory explains particular competitive outcomes is an empirical question. However, while R^* theory is supported by a substantial number of experimental studies (Wilson, Spijkerman and Huisman 2007), they generally involve microorganisms within well-mixed chemostats. This experimental design minimizes the impact of interference competition. Outside the laboratory, however, spatial structure is ubiquitous. Interference competition is widespread; perhaps most obviously in animals (Schoener 1983, Drury, Cowen and Grether 2020), but also among plants via the soil interactions and allelopathy (Inderjit et al. 2011, Meiners et al. 2012, Rice 2012) and microbe-microbe interactions through mechanisms such as stabbing (Böck et al. 2017, Ghoul and Mitri 2016, García-Bayona and Comstock 2018, Boynton 2019).

Furthermore, when the same consumer is favored by both exploitative and interference competition, measuring outcomes plus exploitative ability provides insufficient evidence in favor of the R^* Rule (compare Figs. 5G and 5I). Ideally, experiments and models should be tailored to the mechanistic biology of the organisms in question. As a more general strategy, comparing R_E^* (as measured by the mean trait values of a, m, e, and τ) to R_I^* (as measured by the equilibrium resource abundance set by a consumer population) will likely provide insights into the strength of negative density-dependence driven by interference. Analyses of the functional responses of consumer species to resource and consumer densities can also offer a means of detecting interference competition, given a phenomenological form (Beddington 1975, DeAngelis, Goldstein and O'Neill 1975, Arditi and Akçakaya 1990, DeLong and Vasseur 2011, Novak, Wolf et al. 2017).

Toward a Synthesis of Resource-Competition Mechanisms

A synthesis of previously disparate mechanisms of competition emerges organically from our mechanistic framework. We classify mechanisms by asking whether competitive exclusion can be attributed primarily to exploitation vs. to interference, and whether coexistence can be attributed primarily to an interference-exploitation trade-off vs. an interference-interference trade-off. The R^* rule describes competitive exclusion due to exploitation, and the fact that exploitative competition over a single resource cannot produce coexistence. The Hawk-Dove game describes both competitive exclusion due to interference, and coexistence due to an interference-interference trade-off. Our interpretation of the competition-colonization trade-off describes coexistence due to an interference-exploitation trade-off. Which scenario occurs is a complex outcome of parameter value combinations, with many mechanistic parameters affecting both exploitative and interference competition abilities (e.g., a and τ). The R^* rule occurs when differences in exploitative abilities ($R_{j,E}^*/R_{i,E}^*$) are large in magnitude relative to differences from interference . The R^* Rule applies most often occurs when consumers are similar in interference-specific traits (similar β) and exhibit considerable differences in exploitative competitive ability via a parameter such as search rate (a; Fig. 5G) that has only a modest impact on interference competition.

The fitness benefits and costs of Hawkishness and Doveishness are emergent properties of underlying density-dependent interactions. This differentiates our model from recent advances that hold a payoff matrix fixed given a resource level, and consider eco-evolutionary fluctuations derived from self-renewing and/or decaying resources (Tilman, Plotkin and Akçay 2020). In our analysis, we partition the impacts of interference competition on invasion into three key terms: the increase in resource abundance due to intra-type interference ($R_I^* - R_E^*$), resource theft (ωH^*), and costs due

429 to interference (P). This allows for precise descriptions of how (or if) interference competition
430 permits coexistence.

431 Our underlying model is similar to recent work incorporating density-dependence into game
432 theory models, to position Hawk-Dove dynamics within more ecologically realistic scenarios (Křivan,
433 Galanthay and Cressman 2018, Křivan and Cressman 2022, Galanthay, Křivan et al. 2023). Our work
434 formally connects this underlying model to R^* theory for the first time.

435 Our model reproduces dynamics analogous to the competition-colonization trade-off, where
436 competition is interpreted as interference. In addition, a second and perhaps counterintuitive form
437 of exploitation-interference trade-off also arises in our model. In this case, it is the Hawk who is
438 favored by exploitative competition, and the Dove who is favored by interference competition
439 (Scenario 5b). I.e., a Hawk, who is more likely to displace its competitor, is also superior at
440 exploitative competition, but the Dove can nevertheless invade because of the resources freed up by
441 Hawk-Hawk contests. This novel coexistence mechanism complicates empirical efforts to detect and
442 interpret trade-offs in interference and exploitative competitive abilities.

443 Importantly, interference-exploitation trade-offs and interference-interference trade-offs
444 are not mutually exclusive. While we qualitatively differentiate each mechanism in our analyses by
445 highlighting which has the dominant effect on invasion (Fig. 5), both may operate simultaneously
446 and play an important role in coexistence. Except in limiting cases (see equations (6-7)), their joint
447 operation is almost assured. Future theoretical and empirical studies focused on the competition-
448 colonization trade-off should also examine the possibility of interference-interference trade-offs
449 (particularly in motile organisms). For example, Mordecai et al. (2016) find evidence for the
450 prerequisites of the competition colonization trade-off in a trematode community, but conclude it is
451 insufficient to explain coexistence. A precise mechanistic understanding of the dynamics
452 underpinning interference competition, that allows assessment of the interference-interference
453 trade-off, may offer deeper insights into the role of interference competition plays in maintaining
454 the diversity of this and similar communities.

455 *Connections to Previous Models of Interference Competition*

456 Most previous models of interference competition use phenomenological terms to summarize the
457 strengths of intra-specific (or intra-type) and inter-specific (or inter-type) interference. Such models
458 are extensions of traditional Lotka-Volterra equations, in which resources are either modeled
459 implicitly or non-dynamically (Case and Gilpin 1974, Schoener 1976, Schoener 1978, Hsu 1982,
460 Vance 1984). A typical finding is that two consumers that differ in exploitative competitive ability can

coexist only when they both self-limit resource acquisition considerably more than they limit each other's (Vance 1984). In such models, *why* intraspecific interference might exceed interspecific interference is unclear. Importantly, our model does not presuppose that intra-consumer interference propensities are greater than inter-consumer interference propensities. I.e., consumers in our model do not modify either the initiation or the termination of interference behavior based on the identity of the competitor they interact with.

We nevertheless derive coexistence, largely because interference competition interrupts consumption and thus increases resource density ($R_I^* > R_E^*$; Fig. 2). McPeek (2012) previously used a phenomenological term to generate intra-specific density-dependence, increasing the resource level set by a resident, and thus allowing multi-consumer coexistence on a single resource. We show that interference competition for a single limiting resource alone can yield this pattern. This provides a mechanism by which such density-dependence likely occurs.

Amarasekare (2002), analyzing a model similar to our own, assumes no intraspecific interference (implying $R_E = R_I^*$) and concludes that (1) mutually costly forms of interspecific interference (e.g., aggression, territoriality) cannot maintain coexistence, and (2) interference-exploitation trade-offs can facilitate coexistence when interference is beneficial to the inferior exploiter. While Amarasekare (2002) argues this scenario reflects intraguild predation or parasitism, it has the same form as our competition-colonization trade-off limiting case (equation (7); Scenario 5a). An alternative exploitation-interference trade-off (Scenario 5b) and interference-interference trade-offs (Scenario 4) make up a large portion of potential coexistence space (which are not examined in Amarasekare, 2002), suggesting that the range of conditions under which costly interference competition maintains coexistence is greatly underappreciated.

Caveats, Future Directions, and Conclusion

In this study, we analyzed a simple ecological scenario: two consumers competing for a single limiting resource. It remains an open question precisely how much diversity can be maintained when interfering consumers compete for multiple resources.

Our model considers a spontaneously generated, consumable resource, rather than a biotic resource that undergoes a replicative form of growth from a starting population. The same general principles likely apply for other resource types. However, there is an interesting caveat. Because our model introduces resource handling (quantified by τ), we add non-linearity to the consumer functional response (Holling 1965). For a replicating rather than a spontaneously generated resource, this allows the possibility of stable limit cycles. When different non-linear function

493 responses (for example, when $\tau_1 \neq \tau_2$) result in a trade-off between fitness in low-resource
494 environments (gleaners) and high-resource environments (opportunists), resource oscillations may
495 contribute to species coexistence (Armstrong and McGehee 1980, Yamamichi and Letten 2022). The
496 interplay of this effect with interference competition is beyond the scope of our study.

497 Our modeling of interference competition as a delay before a motile organism "gives up" is
498 not an obvious fit to sessile plants, although it is, following precedent in classic game theory
499 (Maynard Smith and Price, 1973), a good fit for motile animals (Stanton, Palmer and Young 2002,
500 Rodríguez, Jansson and Andrén 2007, Ferzoco and McCauley 2023). Specifically, temporal
501 investment in interference incurs an opportunity cost to foraging, facilitating coexistence. Plants also
502 invest in local interference strategies, e.g., root competition, overgrowth, undercutting, and
503 allelopathy, likely incurring an opportunity cost to reproduction and resource acquisition, rather
504 than foraging. Such trade-offs are likely ubiquitous, and other process-based models of interference
505 may yield results similar to our study.

506 Our model considers a consumable resource. Bertram and Masel (2019) considered
507 competition for a durable resource such as territory, via three traits within a variable-density lottery
508 model: the rate b that adults give birth to and disperse juveniles, juveniles' ability c to contest each
509 other to take possession of an unoccupied territory and thus become and adult, and adult survival
510 $1/d$. Our searching term a is somewhat analogous to b, our persistence in interference competition
511 $1/\beta$ is somewhat analogous to c, and our mortality m is directly analogous to d.

512 These similarities perhaps reveal profound patterns. Grime (1977, 1988, 2006) hypothesized
513 that trade-offs shaped species into three types of specialization – "ruderals" tolerate low resource
514 levels, "competitors" excel at interference competition, and "colonizers" rapidly disperse to
515 ephemeral resources. Grime's three-dimensional scheme has been the subject of an extensive
516 debate in the competition literature, often contrasted with more traditional models of competition
517 mediated by resource consumption (the "Grime-Tilman debate"; Aerts 1999; Craine 2005; Jabot and
518 Pottier 2012). A major obstacle to synthesis (and empirical testing) has been the lack of explicit
519 mathematical models of the different selective pressures proposed by Grime (Tilman 2007, Jabot
520 and Pottier 2012). Our framework mathematically unites ideas of Grime with ideas of Tilman. The
521 essence of their dispute was that Grime imagined low density environments in which intraspecific
522 competition was weak and ruderals would prevail, whereas Tilman's view was that organisms in
523 apparently low density environments simply had larger territories, with resource levels still set by
524 consumption down to the lowest tolerated level. Our work provides loose support for Grime's view,
525 by showing that resource levels need not be set by exploitation alone.

In our model, aggressive behavior (as defined by β) is likely to co-evolve with other critical parameters (e.g. m, a, τ). Concerted trait combinations seem likely, including traits not considered by our model. E.g., consumers may differ in intrinsic fighting abilities, as reflecting in the death rate of their opponent. Physiological constraints might impose trade-offs, e.g., between fighting, reducing vulnerability to interference τ, dispersing a, and persisting at low resource levels m and e. Multidimensional adaptive dynamic models (Dieckmann, Heino and Parvinen 2006, Leimar 2009) may provide a means of understanding how the combination of exploitative factors and life history tradeoffs lead to the evolution of aggression in motile organisms such as animals and the propensity for such trade-offs to promote or inhibit species coexistence and/or polymorphisms.

CODE AVAILABILITY

All computation was conducted within Mathematica notebooks, available as Supplementary Files.

AUTHOR CONTRIBUTIONS

DS and JM conceived the project, DS constructed the model and conducted its analysis, DS wrote the first draft of the manuscript, DS and JM substantially revised the manuscript for both content and presentation.

ACKNOWLEDGEMENTS

We thank Jason Bertram for early conceptual work in this area, and the John Templeton Foundation (62220) for funding.

REFERENCES

Aerts, R. (1999). "Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks." Journal of experimental botany **50**(330): 29-37.

Amarasekare, P. (2002). "Interference competition and species coexistence." Proceedings of the Royal Society of London. Series B: Biological Sciences **269**(1509): 2541-2550.

Arditi, R. and H. Akçakaya (1990). "Underestimation of mutual interference of predators." Oecologia **83**: 358-361.

Armstrong, R. A. and R. McGehee (1980). "Competitive exclusion." The American Naturalist **115**(2): 151-170.

Beddington, J. R. (1975). "Mutual interference between parasites or predators and its effect on searching efficiency." The Journal of Animal Ecology: 331-340.

Bertram, J. and J. Masel (2019). "Density-dependent selection and the limits of relative fitness." Theoretical population biology **129**: 81-92.

Böck, D., et al. (2017). "In situ architecture, function, and evolution of a contractile injection system." Science **357**(6352): 713-717.

Boynton, P. J. (2019). "The ecology of killer yeasts: Interference competition in natural habitats." Yeast **36**(8): 473-485.

Case, T. J. and M. E. Gilpin (1974). "Interference Competition and Niche Theory." Proceedings of the National Academy of Sciences **71**(8): 3073-3077.

Craine, J. M. (2005). "Reconciling plant strategy theories of Grime and Tilman." Journal of ecology **93**(6): 1041-1052.

DeAngelis, D. L., R. Goldstein and R. V. O'Neill (1975). "A model for tropic interaction." Ecology **56**(4): 881-892.

DeLong, J. P. and D. A. Vasseur (2011). "Mutual interference is common and mostly intermediate in magnitude." BMC ecology **11**: 1-8.

Dieckmann, U., M. Heino and K. Parvinen (2006). "The adaptive dynamics of function-valued traits." Journal of Theoretical Biology **241**(2): 370-389.

Drury, J. P., M. C. Cowen and G. F. Grether (2020). "Competition and hybridization drive interspecific territoriality in birds." Proceedings of the National Academy of Sciences **117**(23): 12923-12930.

Ferzoco, I. M. C. and S. J. McCauley (2023). "Breaking down the components of the competition-colonization trade-off: New insights into its role in diverse systems." Journal of Animal Ecology **92**(2): 352-366.

Galanthay, T. E., et al. (2023). "Evolution of Aggression in Consumer-Resource Models." Dynamic Games and Applications: 1-17.

García-Bayona, L. and L. Comstock (2018). Bacterial antagonism in host-associated microbial communities. Science 361: eaat2456.

Ghoul, M. and S. Mitri (2016). "The ecology and evolution of microbial competition." Trends in microbiology **24**(10): 833-845.

Grether, G. F. and K. W. Okamoto (2022). "Eco-evolutionary dynamics of interference competition." Ecology Letters **25**(10): 2167-2176.

Grime, J. P. (1977). "Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory." The American Naturalist **111**(982): 1169-1194.

Grime, J. P. (1988). The CSR model of primary plant strategies—origins, implications and tests. Plant evolutionary biology, Springer**:** 371-393.

Grime, J. P. (2006). Plant strategies, vegetation processes, and ecosystem properties, John Wiley & Sons.

Hastings, A. (1980). "Disturbance, coexistence, history, and competition for space." Theoretical population biology **18**(3): 363-373.

Holling, C. S. (1965). "The functional response of predators to prey density and its role in mimicry and population regulation." The Memoirs of the Entomological Society of Canada **97**(S45): 5-60.

Horn, H. S. and R. H. MacArthur (1972). "Competition among fugitive species in a harlequin environment." Ecology **53**(4): 749-752.

Hsu, S.-B. (1982). "On a resource based ecological competition model with interference." Journal of Mathematical Biology **12**: 45-52.

Inderjit, et al. (2011). "The ecosystem and evolutionary contexts of allelopathy." Trends in ecology & evolution **26**(12): 655-662.

Jabot, F. and J. Pottier (2012). "A general modelling framework for resource-ratio and CSR theories of plant community dynamics." Journal of ecology **100**(6): 1296-1302.

Johnson, C. A. and P. Amarasekare (2015). "A metric for quantifying the oscillatory tendency of consumer-resource interactions." The American Naturalist **185**(1): 87-99.

Křivan, V. and R. Cressman (2022). "The asymmetric Hawk-Dove game with costs measured as time lost." Journal of Theoretical Biology **547**: 111162.

Křivan, V., T. E. Galanthay and R. Cressman (2018). "Beyond replicator dynamics: From frequency to density dependent models of evolutionary games." Journal of Theoretical Biology **455**: 232-248.

Leimar, O. (2009). "Multidimensional convergence stability." Evolutionary Ecology Research **11**(2): 191-208.

Maynard Smith, J. (1974). "The theory of games and the evolution of animal conflicts." Journal of Theoretical Biology **47**(1): 209-221.

Maynard Smith, J. (1982). Evolution and the Theory of Games, Cambridge University Press.

Maynard Smith, J. and G. R. Price (1973). "The logic of animal conflict." Nature **246**(5427): 15-18.

McPeek, M. A. (2012). "Intraspecific density dependence and a guild of consumers coexisting on one resource." Ecology **93**(12): 2728-2735.

Meiners, S. J., et al. (2012). "Developing an ecological context for allelopathy." Plant Ecology **213**: 1221-1227.

Mordecai, E. A., et al. (2016). "The role of competition–colonization tradeoffs and spatial heterogeneity in promoting trematode coexistence." Ecology **97**(6): 1484-1496.

Novak, M., et al. (2017). "Quantifying predator dependence in the functional response of generalist predators." Ecology Letters **20**(6): 761-769.

Real, L. A. (1977). "The kinetics of functional response." The American Naturalist **111**(978): 289-300.

Rice, E. L. (2012). "Allelopathy."

Rodríguez, A., G. Jansson and H. Andrén (2007). "Composition of an avian guild in spatially structured habitats supports a competition–colonization trade-off." Proceedings of the Royal Society B: Biological Sciences **274**(1616): 1403-1411.

Rosenzweig, M. L. (1971). "Paradox of enrichment: destabilization of exploitation ecosystems in ecological time." Science **171**(3969): 385-387.

Schoener, T. W. (1976). "Alternatives to Lotka-Volterra competition: models of intermediate complexity." Theoretical population biology **10**(3): 309-333.

Schoener, T. W. (1978). "Effects of density-restricted food encounter on some single-level competition models." Theoretical population biology **13**(3): 365-381.

Schoener, T. W. (1983). "Field experiments on interspecific competition." The American Naturalist **122**(2): 240-285.

Skellam, J. G. (1951). "Random dispersal in theoretical populations." Biometrika **38**(1/2): 196-218.

Stanton, M., T. Palmer and T. Young (2002). "Competition–colonization trade-offs in a guild of African acacia-ants." Ecological Monographs **72**(3): 347-363.

Tilman, A. R., J. B. Plotkin and E. Akçay (2020). "Evolutionary games with environmental feedbacks." Nature communications **11**(1): 915.

Tilman, D. (1981). "Tests of resource competition theory using four species of Lake Michigan algae." Ecology **62**(3): 802-815.

Tilman, D. (1982). Resource competition and community structure, Princeton university press.

Tilman, D. (1994). "Competition and biodiversity in spatially structured habitats." Ecology **75**(1): 2-16.

Tilman, D. (2007). "Resource competition and plant traits: a response to Craine et al. 2005." Journal of ecology: 231-234.

Turelli, M. (1978). "Does environmental variability limit niche overlap?" Proceedings of the National Academy of Sciences **75**(10): 5085-5089.

Vance, R. R. (1984). "Interference Competition and the Coexistence of Two Competitors on a Single Limiting Resource." Ecology **65**(5): 1349-1357.

Wilson, J. B., E. Spijkerman and J. Huisman (2007). "Is there really insufficient support for Tilman's R* concept? A comment on Miller et al." The American Naturalist **169**(5): 700-706.

Yamamichi, M. and A. D. Letten (2022). "Extending the gleaner–opportunist trade-off." Journal of Animal Ecology **91**(11): 2163-2170.

Ziv, Y., et al. (1993). "Interference competition and temporal and habitat partitioning in two gerbil species." Oikos: 237-246.

Ziv, Y. and B. P. Kotler (2003). "Giving-up densities of foraging gerbils: the effect of interspecific competition on patch use." Evolutionary Ecology **17**: 333-347.