



SPECIAL FEATURE REVIEW

Sex and Biological Communities

Frequency-dependent community dynamics driven by sexual interactions

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Abstract

Research in community ecology has tended to focus on trophic interactions (e.g., predation, resource competition) as driving forces of community dynamics, and sexual interactions have often been overlooked. Here we discuss how sexual interactions can affect community dynamics, especially focusing on frequency-dependent dynamics of horizontal communities (i.e., communities of competing species in a single ecological guild). By combining mechanistic and phenomenological models of competition, we place sexual reproduction into the framework of modern coexistence theory. First, we review how population dynamics of two species competing for two resources can be represented by the Lotka–Volterra competition model as well as frequency dynamics, and how niche differentiation and overlap produce negative and positive frequency-dependence (i.e., stable coexistence and priority effect), respectively. Then, we explore two situations where sexual interactions change the frequency-dependence in community dynamics: (1) reproductive interference, that is, negative interspecific interactions due to incomplete species recognition in mating trials, can promote positive frequency-dependence and (2) density-dependent intraspecific adaptation load, that is, reduced population growth rates due to adaptation to intraspecific sexual (or social) interactions, produces negative frequency-dependence. We show how reproductive interference and density-dependent intraspecific adaptation load can decrease and increase niche differences in the framework of modern coexistence theory, respectively. Finally, we discuss future empirical and theoretical approaches for studying how sexual interactions and related phenomena (e.g., reproductive interference, intraspecific adaptation load, and sexual dimorphism) driven by sexual selection and conflict can affect community dynamics.

KEYWORDS

coexistence theory, competition, eco-evolutionary dynamics, intraspecific adaptation load, reproductive interference

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1 | INTRODUCTION

Traditionally ecologists have focused on trophic interactions such as predation, parasitism, and resource competition as fundamental driving forces of community dynamics (Chase et al., 2002; Chesson, 2000; Connell, 1971; Gause, 1934; Holt, 1977; Hutchinson, 1961; Janzen, 1970; MacArthur & Levins, 1967; May, 1972; Paine, 1966). While recent studies have revealed the importance of mutualistic interactions in community dynamics (Bascompte & Jordano, 2013; Mougi & Kondoh, 2012; Valdovinos, 2019), sexual interactions and the presence of male individuals are often ignored in research on population and community dynamics (Rankin & Kokko, 2007). For example, two standard textbooks of community ecology, Morin (2011) and Mittelbach and McGill (2019), used terms that contain “sex” (e.g., sexual reproduction, sexual selection) only four times in 424 pages and nine times in 409 pages, respectively. On the other hand, some recent studies have suggested that sexual interactions can affect community dynamics (Gómez-Llano et al., 2021) through various processes (Burdfield-Steel & Shuker, 2011; De Lisle et al., 2022; Gröning & Hochkirch, 2008; Kyogoku, 2015; Tsuji & Fukami, 2020; Yamamichi et al., 2020) and can cause eco-evolutionary feedbacks (Giery & Layman, 2019; Svensson, 2019). While the importance of sexual interactions is still unclear in microbial communities, sexual interactions should be incorporated into the theory of community dynamics in plants and animals.

Here we demonstrate the effects of sexual interactions on coexistence of species competing for shared resources through the lens of modern coexistence theory by combining mechanistic and phenomenological models of competition. First, we review how frequency-dependence arises in horizontal communities as an important and fundamental concept for understanding competitive exclusion and stable coexistence of competing species. While frequency-dependence has often been studied in evolutionary biology for understanding the maintenance of genetic variation (Ayala & Campbell, 1974; Heino et al., 1998), it has only more recently been considered in community ecology (Svensson et al., 2018; Vellend, 2016). Negative frequency-dependence (i.e., minority advantage) promotes stable species coexistence (Adler et al., 2007) whereas positive frequency-dependence (i.e., minority disadvantage) results in alternative stable states and priority effects (Ke & Letten, 2018).

Then, we explain the effects of sexual interaction on interspecific and intraspecific competition and the resultant negative or positive frequency-dependence in community dynamics. Interspecific sexual interactions can

result in negative interactions called reproductive interference due to incomplete species recognition in mating processes (Burdfield-Steel & Shuker, 2011; Gröning & Hochkirch, 2008; Kyogoku, 2015). Species recognition is sometimes incomplete in mating trials of animals and male individuals can be so aggressive that their mating attempts are harmful to heterospecific females. Flowering plant species often share pollinators and pollen transferred from one species to another species can cause deleterious effects because of pollen loss and stigma clogging. Because rare species suffer more from heterospecific mating trials by (or pollen transfer from) common species, this results in positive frequency-dependence in community dynamics (Iritani & Noriyuki, 2021; Kishi & Nakazawa, 2013; Kuno, 1992; Schreiber et al., 2019; Yoshimura & Clark, 1994). On the other hand, intraspecific sexual interactions may promote negative frequency-dependence in community dynamics by density-dependent intraspecific adaptation load, which is a reduction of population growth due to adaptation to intraspecific sexual and social interactions (Iritani, 2020; Kobayashi, 2017, 2019; Tsuji, 2013; Yamamichi et al., 2020). Organisms tend to try to increase individual-level relative fitness at the expense of population-level absolute fitness (population growth) via, for example, production of male offspring, male mating harassment, and infanticide. This process tends to be density-dependent because higher conspecific densities result in more intense intraspecific competition for reproduction opportunities (e.g., the frequency of male offspring of parasitic wasps increases with the population size in a patch due to local mate competition) (Yamamichi et al., 2020).

By connecting the mechanistic consumer-resource models and phenomenological Lotka–Volterra competition models, we can consider such community dynamics with sexual reproduction via the framework of modern coexistence theory where niche and competitive ability differences determine the outcome of competition (Barabás et al., 2018; Chesson, 2000, 2018). By deriving niche and competitive ability differences from mechanistic models, we show reproductive interference decreases niche difference (i.e., promotes positive frequency-dependence) whereas density-dependent intraspecific adaptation load increases niche differences (i.e., promotes negative frequency-dependence). This kind of approach will be valuable to understand how low-level process parameters (*sensu* Vellend, 2016) map to high-level processes in competition dynamics. Finally, we discuss future perspectives on theoretical and empirical

approaches in this research area, including the effects of sexual dimorphism on species diversity (De Lisle et al., 2022; Tsuji & Fukami, 2020).

2 | FREQUENCY-DEPENDENCE IN COMMUNITY DYNAMICS

The Lotka–Volterra competition model has been used for understanding the effects of strengths of intraspecific and interspecific competition on coexistence of two species (Mittelbach & McGill, 2019; Morin, 2011). When their population densities are N_1 and N_2 , dynamics are represented by

$$\begin{aligned} \frac{1}{N_1} \frac{dN_1}{dt} &= r_1(1 - \alpha_{11}N_1 - \alpha_{12}N_2), \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2(1 - \alpha_{21}N_1 - \alpha_{22}N_2), \end{aligned} \quad (1)$$

where r_i is the intrinsic growth rate, α_{ii} is the intraspecific competition coefficient, and α_{ij} is the interspecific competition coefficient where $i, j = 1, 2$ (see also Table 1; Lotka, 1932; Volterra, 1926). Coexistence is possible if rare species can increase its density when the other resident species is at the carrying capacity: $dN_i/dt > 0$ when $N_j = 1/\alpha_{ij}$, and this condition can be written as $1 - \alpha_{ij}/\alpha_{jj} > 0$ ($i, j = 1, 2$). Thus, stable coexistence with mutual invasibility occurs when interspecific competition is weaker than intraspecific competition, or $\alpha_{21} < \alpha_{11}$ and $\alpha_{12} < \alpha_{22}$.

The Lotka–Volterra competition model in Equation (1) can be derived from a more mechanistic model with two consumers and two resources where consumers have the Holling type I (linear) functional responses (Holling, 1959) and resources show logistic growth (Chesson, 1990; MacArthur, 1970; Spaak & De Laender, 2020) by assuming time-scale separation (Figure 1a,b):

$$\begin{aligned} \frac{1}{N_i} \frac{dN_i}{dt} &= \sum_{j=1}^2 c_{ij} a_{ij} R_j - d_i, \\ \varepsilon \frac{1}{R_i} \frac{dR_i}{dt} &= l_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^2 a_{ji} N_j, \end{aligned} \quad (2)$$

where N_i and R_i are the consumer density and resource abundance, respectively, c_{ij} and a_{ij} are the conversion efficiency and consumption rate of consumer i on resource j , respectively, d_i is the consumer mortality rate, and l_i and K_i are the intrinsic growth rate and carrying capacity, respectively ($i, j = 1, 2$). Here ε is a small positive parameter representing the difference in time-scales between

TABLE 1 Variables and parameters used in the models.

Variable	Description
N_i	Population density of competitor i
R_i	Abundance of resource i
F_i	Frequency of competitor i
N_T	Total density of competitors
P_i	Population density of predator i
Parameter	Description
r_i, l_i	Intrinsic growth rate
α_{ij}	Competition coefficient of species j on species i
c_{ij}	Conversion efficiency of consumer i on resource j
a_{ij}	Consumption rate of consumer i on resource j
d_i, m_i	Mortality rate
ε	Positive constant for time-scale separation
K_i	Carrying capacity
ρ	Niche overlap (Equation 6)
κ_1/κ_2	Competitive ability ratio (Equation 6)
ND	Niche difference ($= -\ln(\rho)$)
FD	Competitive ability difference ($= \ln(\kappa_1/\kappa_2)$)
b_i	Strength of reproductive interference on competitor i
h_{ij}	Handling time of consumer i on resource j
p	Fraction of reproduction not affected by reproductive interference
e_i	Coefficient for density-dependent intraspecific adaptation load
w_i	Frequency of female offspring ($1/2 \leq w_i < 1$)
k_i	Half saturation constant for w_i

consumers and resources (e.g., Cortez & Ellner, 2010). When we assume that resource dynamics are much faster than consumer dynamics, we can solve $dR_j/dt = 0$ and obtain two equations for dynamics of N_i by plugging $R_i = K_i \left(1 - \sum_{j=1}^2 a_{ji} N_j / l_i \right)$ into Equation (2) (Morin, 2011):

$$\begin{aligned} \frac{1}{N_i} \frac{dN_i}{dt} &= \underbrace{\sum_{k=1}^2 c_{ik} a_{ik} K_k}_{r_i} - \underbrace{\sum_{k=1}^2 \frac{c_{ik} a_{ik}^2 K_k}{l_k}}_{r_i \alpha_{ii}} N_i \\ &\quad - \underbrace{\sum_{k=1}^2 \frac{c_{ik} a_{ik} a_{jk} K_k}{l_k}}_{r_i \alpha_{ij}} N_j, \end{aligned} \quad (3)$$

where $i, j = 1, 2$. Although the phenomenological Lotka–Volterra competition model is useful, recent studies have underlined the potential importance of mechanistic

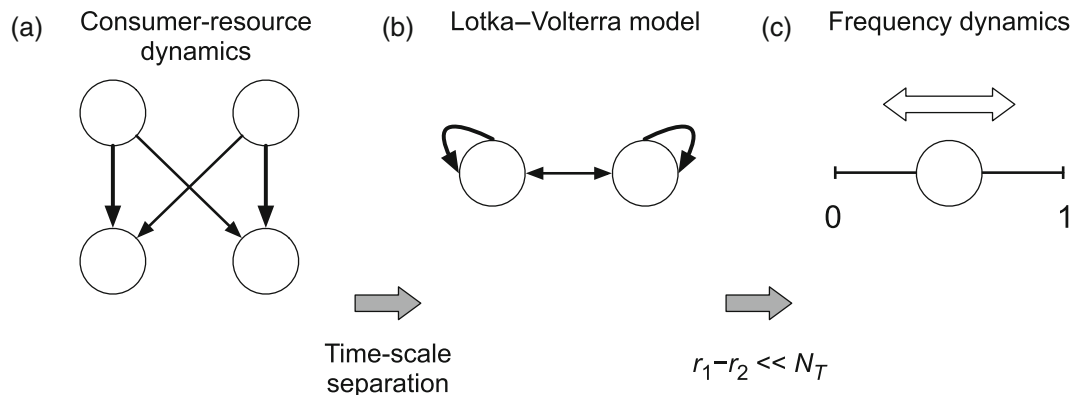


FIGURE 1 Simplified community dynamics. (a) Consumer-resource dynamics with four variables in Equation (2). Arrows represent resource consumption. (b) Lotka–Volterra competition model with two variables in Equation (1). When we assume resource dynamics are much faster than consumer dynamics in (a) (i.e., time-scale separation), we obtain (b). A two-headed arrow represents interspecific competition whereas one-headed arrows indicate intraspecific competition (i.e., self-regulation). (c) Frequency dynamics with a single variable between zero and one in Equation (4). When the condition $r_1 - r_2 \ll N_T$ is satisfied in (b), we can approximate (b) to obtain (c) where r_i is the intrinsic growth rate of species i ($i = 1, 2$) and N_T is the total density of the two species.

models for connecting empirical data and theoretical models as well as for understanding complex dynamics (Abrams, 2022; Mittelbach & McGill, 2019).

On the other hand, it will also be meaningful to consider a simplified dynamics with a single variable based on the Lotka–Volterra model (Figure 1b,c). When we define the frequency of species 1 as $F_1 = N_1/(N_1 + N_2)$, we can re-write the Lotka–Volterra model according to the quotient rule as follows (Hofbauer & Sigmund, 1998):

$$\begin{aligned} \frac{dF_1}{dt} &= F_1(1 - F_1) \left(\frac{1}{N_1} \frac{dN_1}{dt} - \frac{1}{N_2} \frac{dN_2}{dt} \right) \\ &= N_T F_1(1 - F_1) \left[\frac{r_1 - r_2}{N_T} - (r_1 \alpha_{11} - r_2 \alpha_{21}) F_1 \right. \\ &\quad \left. - (r_1 \alpha_{12} - r_2 \alpha_{22})(1 - F_1) \right], \end{aligned} \quad (4)$$

where N_T is the total population density ($N_1 + N_2$). Because $N_T F_1(1 - F_1)$ is always positive as $0 \leq F_1 \leq 1$, the frequency of species 1 increases if the square bracket is positive. When $(r_1 - r_2)/N_T$ is very small (i.e., $r_1 - r_2 \ll N_T$) due to the similar intrinsic growth rates ($r_1 \approx r_2$) and/or very large total population density, the square bracket can be approximated to depend only on the frequency (and not on the total density).

We show an example where stable coexistence is possible in the mechanistic consumer-resource model, Lotka–Volterra model, and frequency dynamics model (Figure 2a–c). In this parameterization, stable coexistence arises due to resource partitioning: the species 1 (2) mainly

consumes the resource 1 (2) and does not consume the resource 2 (1) so much (Figure 2a). This pattern in the consumer-resource model can be represented as an excess of intraspecific competition than interspecific competition in the Lotka–Volterra model (Figure 2b). On the other hand, this results in a phenomenological negative frequency-dependence in the frequency dynamics model (Figure 1c).

These patterns can be understood through the lens of contemporary niche theory and modern coexistence theory (Adler et al., 2007; Chase & Leibold, 2003; Chesson, 2000; Letten et al., 2017). The consumer-resource model can be represented by zero net growth isoclines (ZNGIs) and impact vectors (Chase & Leibold, 2003; Rothhaupt, 1988; Tilman, 1982). ZNGIs represent the resource abundances where the population growth rates become zero and impact vectors show the consumers' influences on resources. Here population growth of the consumer species 1 (2) is constrained by the resource 1 (2) (as shown by ZNGIs) whereas the species 1 (2) mainly consumes resource 1 (2) (as shown by impact vectors). Thus, consumers regulate their population growth rates (Figure 1d) and this self-regulation enables stable coexistence.

In the framework of modern coexistence theory (Barabás et al., 2018; Chesson, 2000, 2018), this can be stated that coexistence is possible when niche overlap, ρ , is sufficiently small and the competitive ability ratio, κ_1/κ_2 , is close to one, or

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho}, \quad (5)$$

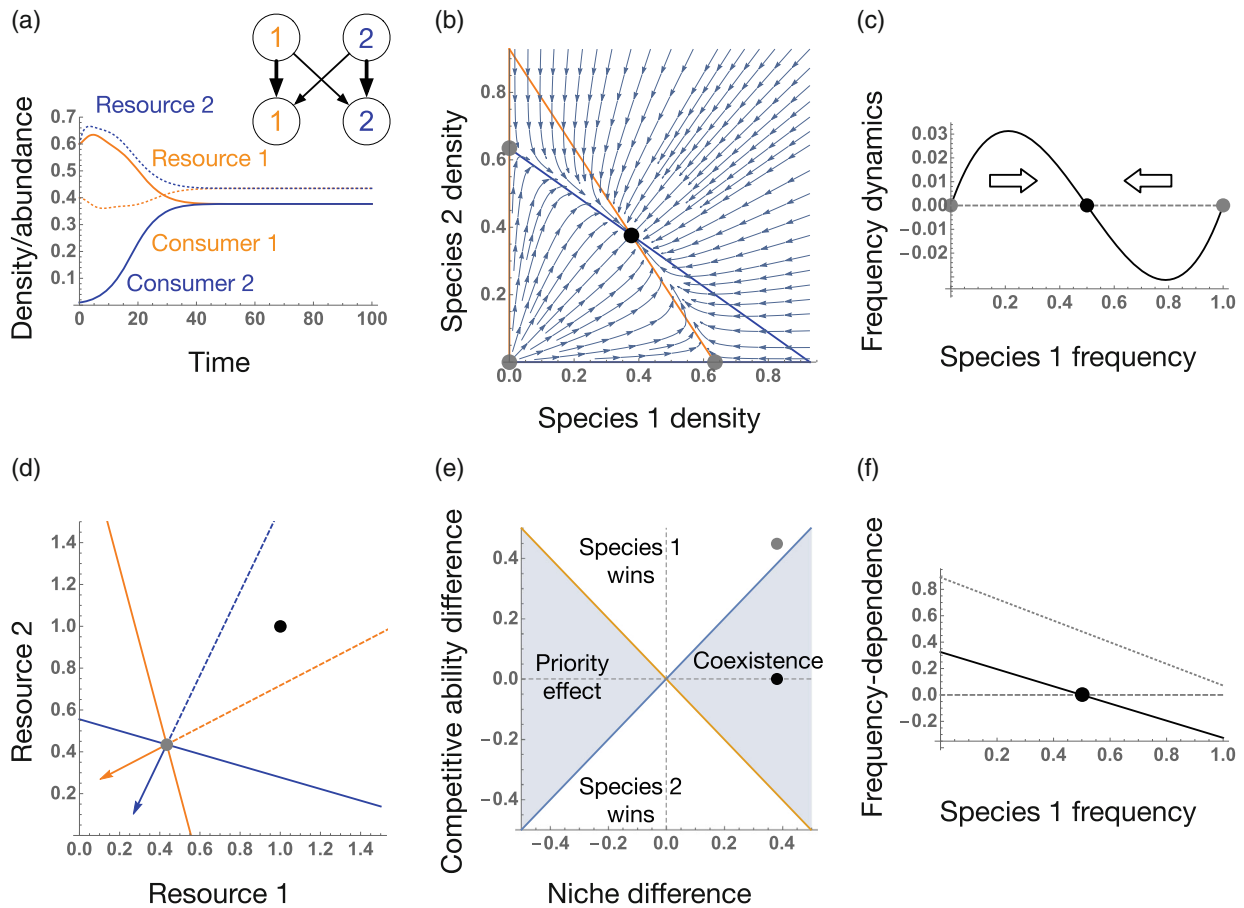


FIGURE 2 Negative frequency-dependence in community dynamics. (a) Stable coexistence due to resource partitioning in the mechanistic consumer-resource model. Solid orange and blue lines represent consumer species 1 and 2, respectively, whereas dotted orange and blue lines are resource 1 and 2, respectively. (b) Stable coexistence due to strong intraspecific competition in the Lotka–Volterra model. Orange and blue lines represent isoclines of the consumer species 1 and 2, respectively. Black and gray points represent locally stable and unstable equilibria, respectively. (c) Negative frequency-dependence in the frequency model. Here Y-axis is $dF_1/dt/N_T$ in Equation (4). (d) Zero net growth isoclines (ZNGIs: solid lines) and impact vectors (arrows) in the consumer-resource model (a). A black point indicates the abundance of resources in the absence of the consumers. (e) Niche difference (ND), $-\ln(\rho)$, and competitive ability difference (FD), $\ln(\kappa_1/\kappa_2)$, in the Lotka–Volterra model (b). A black point indicates the parameterization in (b). (f) Negative frequency-dependence in (c) where Y-axis is $dF_1/dt/[N_T F_1(1 - F_1)]$. Parameter values are $l_i = K_i = a_{ii} = 1$, $a_{ij} = c_{ij} = d_i = 0.5$, and $c_{ii} = 0.9$ ($i, j = 1, 2$). Therefore, $r_i = 0.65$, $\alpha_{ii} \approx 1.58$, and $\alpha_{ij} \approx 1.08$. In the gray point in (e) and the gray dotted line in (f), $\alpha_{11} = 1.01$ and $\alpha_{12} = 0.69$. [Color figure can be viewed at wileyonlinelibrary.com]

where

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}, \quad (6)$$

$$\frac{\kappa_1}{\kappa_2} = \sqrt{\frac{\alpha_{21}\alpha_{22}}{\alpha_{11}\alpha_{12}}}.$$

When we define niche difference, $ND = -\ln(\rho)$, and the competitive ability difference, $FD = \ln(\kappa_1/\kappa_2)$, coexistence occurs if $-ND < FD < ND$ (Figure 2e: Yamamichi et al., 2022), and the parameterization considered in Figure 2a–d results in this coexistence region (the black point in Figure 2e). Based on Equations (3) and (6), the niche overlap and competitive ability ratio in the mechanistic consumer-resource model can be represented by:

$$\rho = \sqrt{\frac{\sum_{j=1}^2 \frac{c_{1j}a_{1j}a_{2j}K_j}{l_j} \sum_{j=1}^2 \frac{c_{2j}a_{1j}a_{2j}K_j}{l_j}}{\sum_{j=1}^2 \frac{c_{1j}a_{1j}^2K_j}{l_j} \sum_{j=1}^2 \frac{c_{2j}a_{2j}^2K_j}{l_j}}}, \quad (7)$$

$$\frac{\kappa_1}{\kappa_2} = \frac{\sum_{j=1}^2 c_{1j}a_{1j}K_j - d_1 \sqrt{\frac{\sum_{j=1}^2 \frac{c_{2j}a_{2j}^2K_j}{l_j} \sum_{j=1}^2 \frac{c_{2j}a_{1j}a_{2j}K_j}{l_j}}{\sum_{j=1}^2 \frac{c_{1j}a_{1j}^2K_j}{l_j} \sum_{j=1}^2 \frac{c_{1j}a_{1j}a_{2j}K_j}{l_j}}}}{\sum_{j=1}^2 c_{2j}a_{2j}K_j - d_2 \sqrt{\frac{\sum_{j=1}^2 \frac{c_{2j}a_{2j}^2K_j}{l_j} \sum_{j=1}^2 \frac{c_{2j}a_{1j}a_{2j}K_j}{l_j}}{\sum_{j=1}^2 \frac{c_{1j}a_{1j}^2K_j}{l_j} \sum_{j=1}^2 \frac{c_{1j}a_{1j}a_{2j}K_j}{l_j}}}}.$$

From these equations, it is evident that, while the parameter d affects the competitive ability ratio only, both niche overlap and competitive ability ratio depend

on the parameters, c , a , l , and K and thus the two indices are not independent (Song et al., 2019). We note that it is also possible to obtain the Lotka–Volterra competition model and define niche overlap and

competitive ability ratio from a model with apparent competition assuming that exploiter dynamics are faster than victim dynamics (Box 1; Holt, 1977; Holt & Bonsall, 2017).

BOX 1 Apparent competition model

Just as like the model for resource competition between consumers, we can derive the Lotka–Volterra competition model from a model for apparent competition where generalist exploiters, P_i , produce a negative correlation between densities of two victim species, N_i (Holt, 1977; Holt & Bonsall, 2017):

$$\begin{aligned} \varepsilon \frac{1}{P_i} \frac{dP_i}{dt} &= \sum_{j=1}^2 c_{ij} a_{ij} N_j - m_i P_i, \\ \frac{1}{N_i} \frac{dN_i}{dt} &= l_i \left(1 - \frac{N_i}{K_i} \right) - \sum_{j=1}^2 a_{ji} P_j. \end{aligned} \quad (1.I)$$

Here we assume that the exploiter mortality rate is density-dependent ($d_i = m_i P_i$) and population dynamics of the exploiters are much faster than population dynamics of the victims (e.g., when exploiters are parasites and victims are hosts). The density-dependent mortality rate can stabilize population dynamics. We can obtain two equations for dynamics of N_i by plugging $P_i = \sum_{j=1}^2 c_{ij} a_{ij} N_j / m_i$ into Equation (1.I):

$$\begin{aligned} \frac{1}{N_1} \frac{dN_1}{dt} &= \underbrace{l_1}_{r_1} - \underbrace{\left(\frac{l_1}{K_1} + \sum_{j=1}^2 \frac{c_{j1} a_{j1}^2}{m_j} \right)}_{r_1 \alpha_{11}} N_1 - \underbrace{\sum_{j=1}^2 \frac{c_{j2} a_{j1} a_{j2}}{m_j}}_{r_1 \alpha_{12}} N_2, \\ \frac{1}{N_2} \frac{dN_2}{dt} &= \underbrace{l_2}_{r_2} - \underbrace{\sum_{j=1}^2 \frac{c_{j1} a_{j1} a_{j2}}{m_j}}_{r_2 \alpha_{21}} N_1 - \underbrace{\left(\frac{l_2}{K_2} + \sum_{j=1}^2 \frac{c_{j2} a_{j2}^2}{m_j} \right)}_{r_2 \alpha_{22}} N_2, \end{aligned} \quad (1.II)$$

and hence, the niche overlap and competitive ability ratio are represented by:

$$\begin{aligned} \rho &= \sqrt{\frac{\sum_{j=1}^2 \frac{c_{j1} a_{j1} a_{j2}}{m_j} \sum_{j=1}^2 \frac{c_{j2} a_{j1} a_{j2}}{m_j}}{\left(\frac{l_1}{K_1} + \sum_{j=1}^2 \frac{c_{j1} a_{j1}^2}{m_j} \right) \left(\frac{l_2}{K_2} + \sum_{j=1}^2 \frac{c_{j2} a_{j2}^2}{m_j} \right)}}, \\ \frac{\kappa_1}{\kappa_2} &= \frac{l_1}{l_2} \sqrt{\frac{\sum_{j=1}^2 \frac{c_{j1} a_{j1} a_{j2}}{m_j} \left(\frac{l_2}{K_2} + \sum_{j=1}^2 \frac{c_{j2} a_{j2}^2}{m_j} \right)}{\sum_{j=1}^2 \frac{c_{j2} a_{j1} a_{j2}}{m_j} \left(\frac{l_1}{K_1} + \sum_{j=1}^2 \frac{c_{j1} a_{j1}^2}{m_j} \right)}}. \end{aligned} \quad (1.III)$$

From this result, again, we can see that the two indices are not independent: changing parameters l , K , c , a , and m results in changing both indices as is shown in the main text for another model (Song et al., 2019).

In the phenomenological frequency dynamics model, we can show negative frequency-dependence as a linear relationship between the frequency of species 1 and its growth rate divided by $N_T F_1(1 - F_1)$ (Figure 2f; Adler et al., 2007). In Figure 2f, the niche overlap, ρ , affects the slope of frequency-dependence whereas the competitive ability ratio, κ_1/κ_2 , affects the intercept. Thus, the absence of niche difference and equivalence of competitive ability can result in neutral dynamics where the expected growth rate is always zero irrespective of the frequency (Adler et al., 2007). Also, the presence of niche differentiation is not enough for promoting stable coexistence. When the intercept is too large (the gray dotted line in Figure 2f) or too small due to large competitive ability differences

(the gray point in Figure 2e), there is no frequency where dF_1/dt becomes zero, and stable coexistence does not occur.

We can also consider a situation where coexistence is unstable due to niche overlap and dynamics show positive frequency-dependence (Figure 3). In this case, rare consumers cannot increase (Figure 3a) because conversion efficiencies of their main resources are so small: the consumer 1 (2) mainly consumes the resource 1 (2) which constrains growth of the consumer 2 (1) (Figure 3d). In the Lotka–Volterra model, alternative stable states arise (Figure 3b) when the inequalities in Equation (5) are flipped (Ke & Letten, 2018) and this can produce a priority effect in community dynamics (Figure 3e; Fukami, 2015). This positive

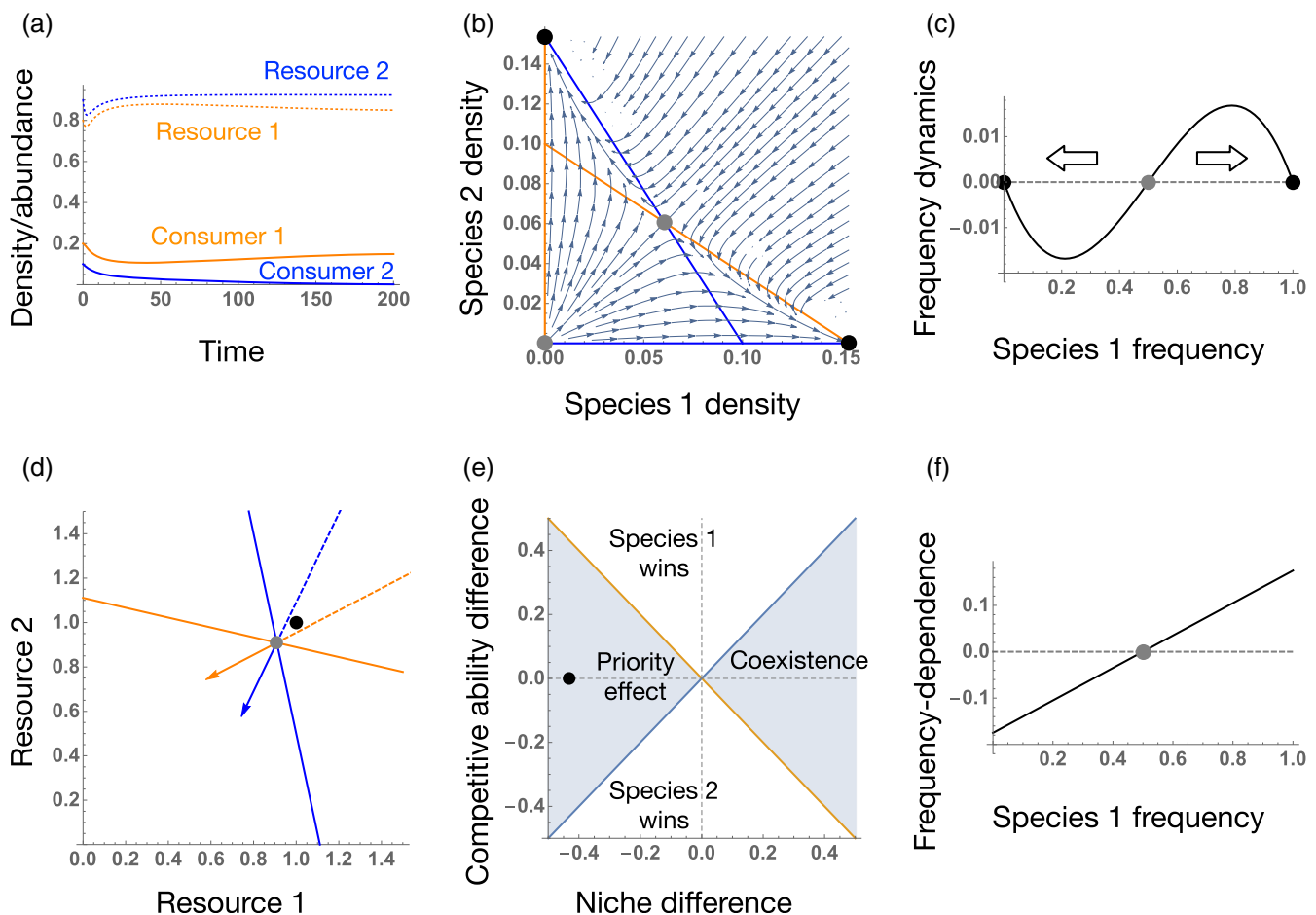


FIGURE 3 Positive frequency-dependence in community dynamics. (a) Priority effect due to resource overlap in the mechanistic consumer–resource model. Solid orange and blue lines represent consumer species 1 and 2, respectively, whereas dotted orange and blue lines are resource 1 and 2, respectively. (b) Alternative stable states due to strong interspecific competition in the Lotka–Volterra model. Orange and blue lines represent isoclines of the consumer species 1 and 2, respectively. Black and gray points represent locally stable and unstable equilibria, respectively. (c) Positive frequency-dependence in the frequency model. Here Y-axis is $dF_1/dt/N_T$ in Equation (4). (d) Zero net growth isoclines (ZNGIs; solid lines) and impact vectors (arrows) in the consumer–resource model (a). A black point indicates the abundance of resources in the absence of the consumers. (e) Niche difference (ND), $-\ln(\rho)$, and competitive ability difference (FD), $\ln(\kappa_1/\kappa_2)$, in the Lotka–Volterra model (b). A black point indicates the parameterization in (b). (f) Positive frequency-dependence in (c) when Y-axis is $dF_1/dt/[N_T F_1(1 - F_1)]$. Parameter values are $c_{ii} = 0.1$ and $c_{ij} = 0.9$ ($i, j = 1, 2$), and other parameter values are the same as Figure 2. Therefore, $r_1 = 0.05$, $\alpha_{ii} = 6.5$, and $\alpha_{ij} = 10$. [Color figure can be viewed at wileyonlinelibrary.com]

frequency-dependence is evident in frequency dynamics (Figure 3c) that shows minority disadvantage (Figure 3f).

How do sexual interactions affect the sign of frequency-dependence in community dynamics? In the following sections, we explore two topics: reproductive interference (arising from interspecific sexual interactions) and density-dependent intraspecific adaptation load (arising from intraspecific sexual interactions). The two topics can be connected as follows: evolution of female resistance against conspecific male mating trials would reduce an individual-level cost of male mating harassment but might impose a demographic cost on population growth (i.e., intraspecific adaptation load). In contrast, such selection pressures for heterospecific females would be weaker than for conspecific females (Kawatsu, 2013). Therefore, the effect of male mating harassment on heterospecific females (i.e., reproductive interference) would depend on the type of male behavior/trait, which may organize the case where sexual interactions result in positive/negative frequency-dependence in interspecific competition.

3 | EFFECTS ON INTERSPECIFIC INTERACTIONS: REPRODUCTIVE INTERFERENCE

Competitive exclusion in the Lotka–Volterra competition model due to positive frequency-dependence can be interpreted as a result of large niche overlap and small competitive ability difference in the modern coexistence theory framework (Figure 3). Here we demonstrate that

interspecific sexual interactions can also result in positive frequency-dependence, and this can also be interpreted as large niche overlap. In animals, some males are so aggressive that their mating attempts are harmful to heterospecific females. A form of interspecific interactions where male mating attempts on heterospecific females results in the negative influence is called reproductive interference (Burdfield-Steel & Shuker, 2011; Gröning & Hochkirch, 2008; Kyogoku, 2015). In the case of flowering plants, pollen is transferred from one species to the stigma of another when the plant species share pollinators. Such heterospecific pollen transfer may result in deleterious effects on both donor and recipient plant species due to pollen loss and stigma clogging (Morales & Traveset, 2008; Waser, 1978). Reproductive interference can promote positive frequency-dependence in community dynamics as females of rare species are more frequently harmed by males of dominant species.

Kishi and Nakazawa (2013) incorporated the positive frequency-dependence due to reproductive interference to the Lotka–Volterra competition model as following:

$$\begin{aligned} \frac{1}{N_1} \frac{dN_1}{dt} &= r_1 \left(\frac{N_1}{N_1 + b_1 N_2} - d_1 - \alpha_{11} N_1 - \alpha_{12} N_2 \right), \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2 \left(\frac{N_2}{b_2 N_1 + N_2} - d_2 - \alpha_{21} N_1 - \alpha_{22} N_2 \right), \end{aligned} \quad (8)$$

where b_i is the strength of reproductive interference and d_i is the scaled mortality rate ($i = 1, 2$). In this case, coexistence is possible with alternative stable states (Figure 4a). Here a coexistence equilibrium is locally

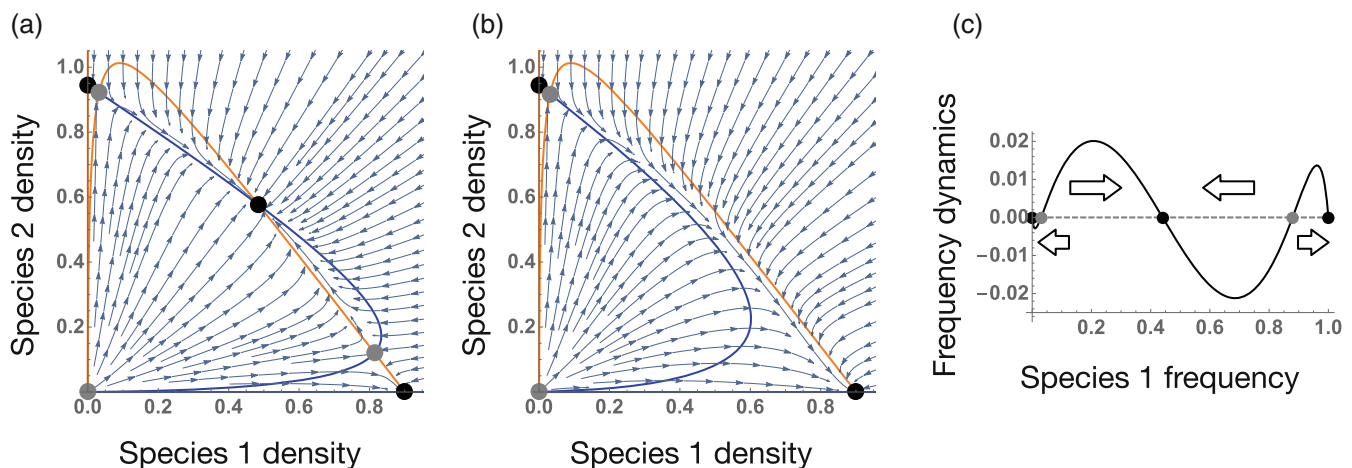


FIGURE 4 Positive frequency-dependence due to reproductive interference. (a) Coexistence is possible due to niche differentiation, but even in this case, a rare species goes extinct because of positive frequency-dependence of reproductive interference. (b) Increasing the reproductive interference parameter results in the loss of the coexistence equilibrium. Parameter values are $r_1 = 1.2$, $r_2 = 1.5$, $\alpha_{11} = 1$, $\alpha_{12} = 0.7$, $\alpha_{21} = 0.6$, $\alpha_{22} = 0.9$, $b_1 = 0.01$, $b_2 = 0.05$, $d_1 = 0.1$, and $d_2 = 0.15$ in (a) and $b_2 = 0.15$ in (b). (c) Positive and negative frequency-dependence in a frequency model based on Equation (8) (see also Equation 4). Here Y-axis is $dF_i/dt/N_T$ and we assumed that the total population density, $N_T = N_1 + N_2$, is constant ($N_T = 1$: cf., community-level regulation). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/1438-390X.12165)]

stable unlike the globally stable coexistence equilibrium in the Lotka–Volterra model (Figure 2b). The coexistence equilibrium is stable due to small interspecific competition coefficients, but a rare species goes extinct due to reproductive interference (Figure 4c). Increasing the strength of reproductive interference (b_i) can result in the loss of the coexistence equilibrium despite the niche differentiation (Figure 4b). This consequence of reproductive interference or satyr effect (Ribeiro & Spielman, 1986) is called sexual exclusion (Gröning & Hochkirch, 2008) or reproductive exclusion (Pfennig & Pfennig, 2009), and it has been often overlooked in community ecology unlike competitive exclusion (Gause, 1934; Hardin, 1960).

However, recent empirical studies have shown the potential importance of positive frequency-dependence due to reproductive interference in insects (Kawatsu & Kishi, 2018; Ohsaki et al., 2020), fish (Tsurui-Sato et al., 2019), and plants (Christie & Strauss, 2020; Johnson et al., 2022; Nishida et al., 2020) as well as other taxa. In parallel, theoretical models have been developed and analyzed for understanding the effects of frequency-dependent interference (Iritani & Noriyuki, 2021; Kishi & Nakazawa, 2013; Kuno, 1992; Paton & Bonsall, 2019; Schreiber et al., 2019; Yoshimura & Clark, 1994), density-dependent interference (Kyogoku & Sota, 2017; Yamamichi & Koizumi, 2020), and evolution for avoiding reproductive interference through reproductive character displacement (cf., reinforcement) (Goldberg & Lande, 2006; Irwin & Schluter, 2022; Konuma & Chiba, 2007; Kyogoku & Kokko, 2020; Kyogoku & Wheatcroft, 2020;

Kyogoku & Yamaguchi, 2023; Morita & Yamamichi, 2023; Pfennig & Pfennig, 2009; Yamaguchi & Iwasa, 2013) or through selfing (Katsuhara et al., 2021) on population persistence and community dynamics.

It will be interesting to consider competition models with resource dynamics (Abrams, 2022) for reproductive interference as well. This can show unique dynamics when consumers have the Holling type II (saturating) functional responses (Holling, 1959) as the system shows consumer–resource population cycles (note that we assumed Holling type I (linear) functional responses in Equation (2) for simplicity). If we assume that heterospecific mating trials affect reproduction, the system can be represented as:

$$\begin{aligned} \frac{1}{N_i} \frac{dN_i}{dt} &= \frac{N_i}{N_i + b_i N_j} \sum_{j=1}^2 \frac{c_{ij} a_{ij} R_j}{1 + \sum_{k=1}^2 a_{ik} h_{ik} R_k} - d_i, \\ \frac{1}{R_i} \frac{dR_i}{dt} &= l_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^2 \frac{a_{ji} N_j}{1 + \sum_{k=1}^2 a_{jk} h_{jk} R_k}, \end{aligned} \quad (9)$$

where h_{ij} is the handling time of consumer i on resource j , and its dynamics may show positive frequency-dependence as well as persistent fluctuations (Figure 5a). In this example, there is a long transient: the dynamics show “apparently sustainable chaotic oscillations suddenly results in species extinction” (Hastings et al., 2018) just like a previous study that considered a discrete-time single-species model with overcompensating density-dependence and an Allee effect (Schreiber, 2003).

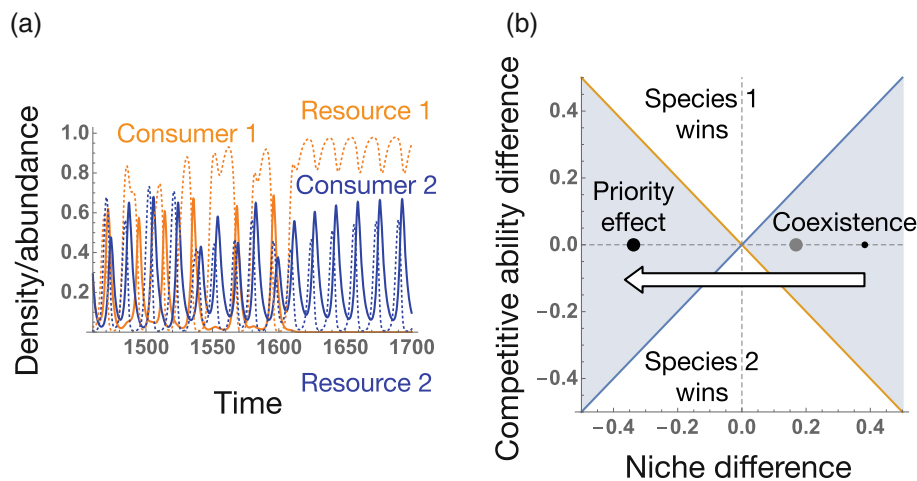


FIGURE 5 Consequences of reproductive interference. (a) Extinction of the consumer 1 occurs after a long transient in Equation (9). Solid orange and blue lines represent consumer species 1 and 2, respectively, whereas dotted orange and blue lines are resource 1 and 2, respectively. Note that the X-axis starts from 1460. Parameter values are $a_{ii} = 5$, $h_{ij} = 0.5$, $b_1 = 0.1$, and $b_2 = 0.01$. Other parameter values are the same as Figure 2. The initial condition is $N_1 = 0.1$, $N_2 = 0.4$, and $R_i = 1$ ($i = 1, 2$). (b) Reducing the effects of refuges from reproductive interference (i.e., reducing the parameter p) results in decreasing niche difference. Parameter values are $p = 1$ (a small black point), $p = 0.8$ (a gray point), and $p = 0.6$ (a large black point). Other parameter values are the same as (a). [Color figure can be viewed at wileyonlinelibrary.com]

Also, we can consider the mechanistic model of Equation (9) with the Holling type I functional response as follows:

$$\begin{aligned} \frac{1}{N_i} \frac{dN_i}{dt} &= \left[p + (1-p) \frac{N_i}{N_i + b_i N_j} \right] \sum_{j=1}^2 c_{ij} a_{ij} R_j - d_i, \\ \frac{1}{R_i} \frac{dR_i}{dt} &= l_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^2 a_{ji} N_j, \end{aligned} \quad (10)$$

where p indicates a fraction of reproduction that is not affected by reproductive interference (e.g., due to refuges). Then we can calculate the intra- and interspecific competition coefficients as like Equation (3) and investigate how reproductive interference affects niche and competitive ability differences. It should be noted that here the competition coefficients are calculated assuming one of the two competing species is dominant: namely, when we consider the invasibility of species 1, $dN_1/dt > 0$, competition coefficients α_{12} and α_{22} should be evaluated in the situation where the density of species 1 is zero and species 2 is at its equilibrium density (Box 2; Chesson, 2000; Yamamichi et al., 2022). In this case, competition coefficients for niche and competitive ability differences are no longer fixed parameters but depend on densities of competing species in a community. Based on this idea, we can see that increasing the effects of reproductive interference (i.e., decreasing the parameter p) results in larger niche overlap and eventually destabilizes coexistence (Figure 5b). This is interesting as p is not an ecological parameter for resource-consumer interactions, but larger p results in niche differentiation. It should be noted, however, that the system has an internal coexistence equilibrium even in the region of priority effect unlike the simple Lotka–Volterra model (Figure 3b,e). Typical studies of modern coexistence theory that acknowledge the priority effect (e.g., Ke & Letten, 2018) assume the Lotka–Volterra competition model, and the dynamics are either positive or negative frequency-dependent (Figures 2 and 3). But in a model that includes both reproductive interference and resource competition (or other negative frequency-dependence mechanism), both positive and negative frequency-dependence can be present, and their relative importance shifts depending on the frequencies of species (Figure 4c; Kishi & Nakazawa, 2013; Schreiber et al., 2019). This emphasizes that competition coefficients are phenomenological/aggregated parameters that include ecological and sexual interactions, and we need to carefully interpret their estimated values (Johnson et al., 2022).

4 | EFFECTS ON INTRASPECIFIC INTERACTIONS: INTRASPECIFIC ADAPTATION LOAD

Unlike reproductive interference, density-dependent intraspecific sexual interactions may promote negative frequency-dependence in community dynamics and lead to stable coexistence (Yamamichi et al., 2020). This is because adaptation (either by rapid evolution or phenotypic plasticity) to intraspecific sexual interaction sometimes reduce population growth through, for example, production of male offspring (Hamilton, 1967) or male mating harassment (Takahashi et al., 2014), and the resultant negative density-dependence in the population level can become negative frequency-dependence at the community level (Svensson et al., 2018). Probably the simplest way to incorporate the strong negative density-dependence is representing the intraspecific competition coefficient as an increasing function of its own population density:

$$\begin{aligned} \frac{1}{N_1} \frac{dN_1}{dt} &= r_1 [1 - \alpha_{11}(1 + e_1 N_1)N_1 - \alpha_{12}N_2], \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2 [1 - \alpha_{21}N_1 - \alpha_{22}(1 + e_2 N_2)N_2], \end{aligned} \quad (11)$$

where e_i is the coefficient for density-dependent intraspecific competition coefficient ($i = 1, 2$). This may be relevant to, for example, density-dependent male mating harassment where a higher conspecific density changes male behavior and the changed behavior results in more intense intraspecific competition of females (e.g., spatial aggregation of females to refuges from males or high density leads to more frequent male–female encounters, upon which females experience mating harassment). Thus, the phenomenological parameter e represents the effect of conspecific density on the intensity of intraspecific competition via sexual interactions. As previous studies have shown (e.g., Barabás et al., 2017), increasing the strength of intraspecific competition (i.e., self-regulation) promotes species coexistence (Figure 6).

Although this has been proposed sporadically in the past (Iritani, 2020; Kobayashi, 2017, 2019; Lee et al., 2012; Montero-Pau & Serra, 2011; Tsuji, 2013; Zhang & Hanski, 1998; Zhang & Jiang, 1995; Zhang et al., 2004), it has not been incorporated to community ecology theory (Yamamichi et al., 2020). However, recent studies suggest that evolution of sexual traits can be rapid enough to affect contemporary ecological dynamics (Giery & Layman, 2019; Hairston et al., 2005; Svensson, 2019) in addition to phenotypic plasticity. Therefore, integrating species coexistence and density-dependent evolution of sexual

BOX 2 Niche and competitive ability differences based on invasion growth

We can define niche and competitive ability differences in Equation (6) based on invasion growth rates even when competition coefficients are density-dependent (Chesson, 2000). Species i can increase when rare if $\alpha_{ij} < \alpha_{jj}$ ($i, j = 1, 2$) and these competition coefficients need to be evaluated at the resident equilibrium state in the absence of species i (Chesson, 2000; Yamamichi et al., 2022). When we define a competition coefficient when species i is absent and species j is at its equilibrium as $\alpha_{ij}|_j$ ($i, j = 1, 2$), the above condition and the density-dependent niche and competitive ability differences can be written as $\alpha_{ij}|_j < \alpha_{jj}|_j$ and

$$\begin{aligned} \rho|_{DD} &= \sqrt{\frac{\alpha_{12}|_2 \alpha_{21}|_1}{\alpha_{11}|_1 \alpha_{22}|_2}}, \\ \frac{\kappa_1}{\kappa_2}|_{DD} &= \sqrt{\frac{\alpha_{21}|_1 \alpha_{22}|_2}{\alpha_{11}|_1 \alpha_{12}|_2}}. \end{aligned} \tag{2.I}$$

In the case of reproductive interference in Equation (10), the residents' intraspecific competition coefficients are not affected as there is no heterospecific sexual interactions. The invaders' interspecific competition coefficients are, on the other hand, increased by reproductive interference compared to the case without reproductive interference as follows:

$$\alpha_{ij}|_j = \frac{p \sum_{k=1}^2 \frac{c_{ik} a_{ik} a_{jk} K_k}{l_k}}{p \sum_{k=1}^2 c_{ik} a_{ik} K_k - d_i}, \quad i, j = 1, 2. \tag{2.II}$$

The increased interspecific competition coefficients result in larger niche overlap (Figure 5b). On the other hand, with density-dependent intraspecific adaptation load in Equation (12), the residents' intraspecific competition coefficients are affected as their reproduction rates are reduced by production of males as follows:

$$\alpha_{ii}|_i = \frac{\frac{1}{2} \sum_{j=1}^2 \frac{c_{ij} a_{ij}^2 K_j}{l_j}}{\frac{1}{2} \sum_{j=1}^2 c_{ij} a_{ij} K_j - d_i}, \quad i = 1, 2. \tag{2.III}$$

The increased intraspecific competition coefficients compared to the case without intraspecific adaptation load reduce the carrying capacity and increase niche difference (Figure 7b).

traits with eco-evolutionary dynamics theory is an important next step of this field.

Again, it will be interesting to consider competition models with resource dynamics for understanding complex dynamics arising from density-dependent intraspecific adaptation load. The dynamics with consumers with local mate competition (i.e., rare species produces more female offspring; Hamilton, 1967; Yamamichi et al., 2020) can be represented as, for example:

$$\begin{aligned} \frac{1}{N_i} \frac{dN_i}{dt} &= w_i \sum_{j=1}^2 c_{ij} a_{ij} R_j - d_i, \\ \frac{1}{R_i} \frac{dR_i}{dt} &= l_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^2 a_{ji} N_j, \end{aligned} \tag{12}$$

where w_i is the frequency of female offspring and it is 1/2 when N_i is large and approaches to 1 when N_i is small. This density-dependent function can be phenomenologically

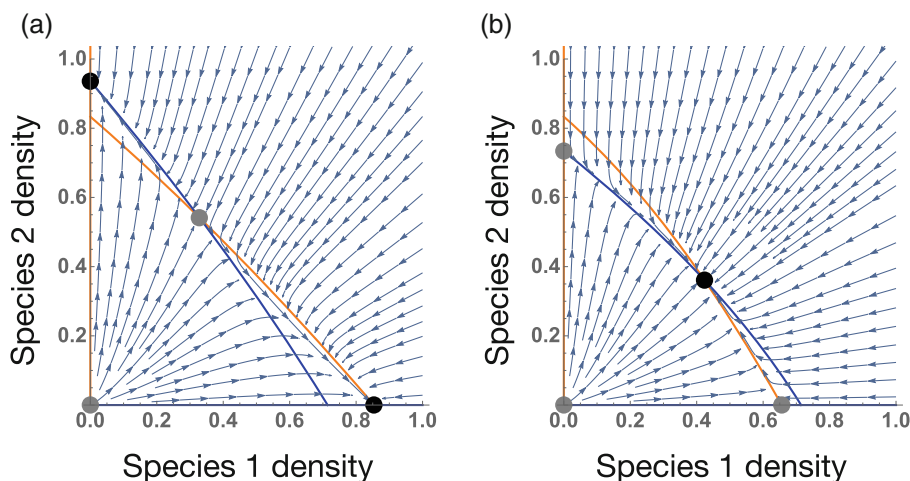
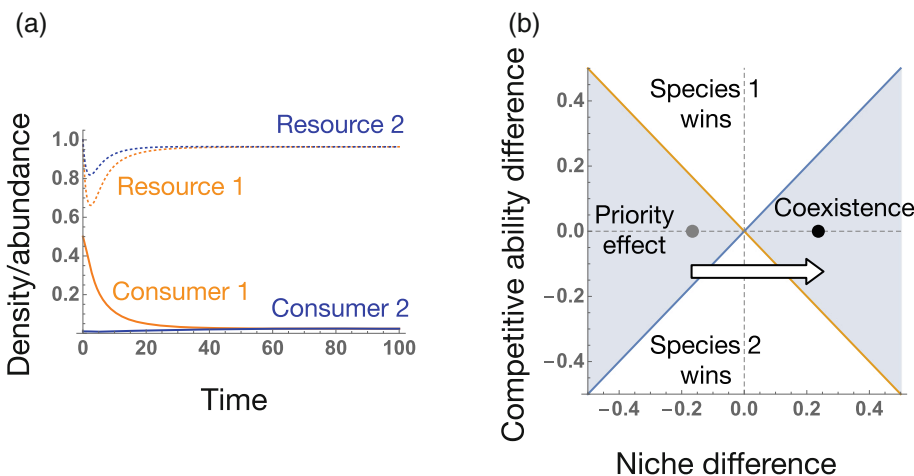


FIGURE 6 Density-dependent intraspecific adaptation load (intraspecific competition coefficient) promotes stable coexistence. (a) When the density-dependent intraspecific competition coefficient is small, coexistence is not possible as like Figure 3b. (b) Species coexistence is possible when the density-dependent intraspecific competition coefficient is large. Parameter values are $\alpha_{12} = 1.2$, $\alpha_{21} = 1.4$, and $e_i = 0.2$ ($i = 1, 2$) in (a) and $a_1 = 0.8$ and $a_2 = 0.7$ in (b). Other parameter values are the same as Figure 4. [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 7 Consequences of density-dependent intraspecific adaptation load. (a) Stable coexistence of competing two consumers due to intraspecific adaptation load. (b) Introducing intraspecific adaptation load results in increasing niche difference. The gray point shows the case when there is no intraspecific adaptation load (i.e., $w_i = 1$ irrespective of the population density). Parameter values are $c_{ii} = 0.3$, $c_{ij} = 1$, $k_i = 0.01$ ($i, j = 1, 2$) and other parameter values are the same as Figure 2. [Color figure can be viewed at wileyonlinelibrary.com]



represented as, for example, $w_i = 1 - N_i/[2(k_i + N_i)]$ where k_i is a half saturation constant. This density-dependent male production results in stable coexistence (Figure 7a) due to increased niche difference (Box 2; Figure 7b). Without density-dependent male production, the two species show alternative stable states in this parameterization (Figure 7b). Again, this result indicates that niche difference (i.e., negative frequency-dependence) can be greatly affected by sexual interactions.

5 | FUTURE DIRECTIONS

Recent studies have revealed that sexual interactions can be important drivers of community dynamics. However, there are several points to be addressed in

future studies: we need more empirical data as the topic is still theory heavy. Experimental studies using microcosm will be helpful for tracking dynamics of sexual traits and population densities in detail (Fussmann et al., 2003), but field experiments will be very valuable.

It is also important to integrate the perspectives in evolutionary ecology and community ecology. For example, we have so far focused on the effects of sexual traits on population dynamics, but there can be eco-evolutionary feedback, where interspecific competition that drives population dynamics affect the evolution of sexual traits (Rankin et al., 2007; Tsuji & Fukami, 2020). Through evolutionary processes, the interspecific competition could also change species diversity in the community (Tsuji & Fukami, 2020).

We considered horizontal communities with resource competition, but sexual traits may affect trophic and mutualistic interactions as well (Fryxell et al., 2019; Kawatsu, 2018). For example, sexual dimorphism in predators and producers can change the composition of prey communities (De Lisle et al., 2022; Fryxell et al., 2015) and that of herbivore communities (Petry et al., 2013; Tsuji & Sota, 2010, 2013), respectively. It is possible that males and females have distinct foraging preferences and such sexual niche divergence can affect prey community dynamics (De Lisle et al., 2022). An example that involves mutualistic interactions is when sexual differences in floral traits of monoecious or dioecious plants affect pollinator communities (Tsuji et al., 2020; Tsuji & Ohgushi, 2018), which can in turn drive the evolution of sexual dimorphism in flowers. Sexual differences in pollinator behaviors can also affect the strength of plant–pollinator mutualism (Smith et al., 2019).

Moreover, sexually dimorphic species can provide two different habitats that might affect frequency dependence that shapes communities in those habitats. For example, female and male flowers can contain microbial communities in nectar that differ in species composition and abundance due to sexual dimorphism in nectar chemistry and, consequently, interspecific interactions among nectar-colonizing microbial species (Tsuji & Fukami, 2018).

In this review, we introduced positive frequency-dependence due to interspecific sexual interactions and negative frequency-dependence due to intraspecific sexual interactions. It should be noted, however, that the link between sexual interactions and frequency-dependence may not be fixed. It may be possible to consider negative frequency-dependence due to interspecific sexual interactions (e.g., interspecific male mating attempts may promote spatial segregation and reduce interspecific competition coefficients) and positive frequency-dependence due to intraspecific sexual interactions (e.g., mate finding difficulty can cause an Allee effect). Also, it will be important to consider mechanistic models with apparent competition (Holt, 1977) as shown in Box 1 to understand complex feedbacks (Abrams, 2022). While previous studies tended to focus on the mechanistic exploitative competition model and the Lotka–Volterra competition model (Chesson, 1990; MacArthur, 1970; Morin, 2011), few studies have considered the equivalent phenomena in the apparent competition model (e.g., the gleaner–opportunist trade-off: Yamamichi & Letten, 2021, 2022). Thus, more theoretical studies are needed as well.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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