Complex community-wide consequences of consumer sexual dimorphism

Stephen P. De Lisle [1,2 *]

Sebastian J. Schrieber [3]

Daniel I. Bolnick [1]

[1] Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT 06269

[2] Present Address: Evolutionary Ecology Unit, Department of Biology, Lund University, Lund Sweden

[3] Department of Evolution and Ecology and Center for Population Biology, University of California, Davis, CA 95616

[*] email: stephen.de_lisle@biol.lu.se

Keywords: apparent competition, community assembly, competitive exclusion, ecological sexual dimorphism, resource competition

Statement of authorship: DB SD and SJS designed the study, SJS performed the mathematical analysis, SD performed the simulations and drafted the manuscript. All authors revised the manuscript.

Data accessibility statement: Complete R script is provided in the supplementary material

Abstract

Sexual dimorphism is a ubiquitous source of within-species variation, yet the community-level consequences of sex differences remain poorly understood. Here, we analyze a bitrophic model of two competing resource species and a sexually-reproducing consumer species. We show that consumer sex differences in resource acquisition can have striking consequences for consumer-resource coexistence, abundance, and dynamics. Under both direct interspecific competition and apparent competition between two resource species, sexual dimorphism in consumers' attack rates can mediate coexistence of the resource species, while in other cases can lead to exclusion when stable coexistence is typically expected. Slight sex differences in total resource acquisition also can reverse competitive outcomes and lead to density cycles. These effects are expected whenever both consumer sexes require different amounts or types of resources to reproduce. Our results suggest that consumer sexual dimorphism, which is commonplace, has wide-reaching implications for the assembly and dynamics of natural communities.

Introduction

Within-species variation is one key feature of natural populations that has emerged as a critical contributor to community ecology and species interactions (Hughes et al. 2008 , Bolnick et al. 2011, Des Roches et al. 2018). Even in the simplest scenario of a single-species community with a single optimum phenotype, within-population variation is expected to reduce population growth rate of a well-adapted population via effects on mean fitness (Haldane 1937). In more complex multi-species communities, phenotypic variation in consumers or their resources can either promote or constrain coexistence between competing species, under many circumstances yielding different conclusions than would be reached from models ignoring within species variation (Bolnick et al. 2011, Schreiber et al. 2011, Patel and Schreiber 2015, Cortez and Patel 2017). One emerging question (Bolnick et al. 2011) from this work is the degree to which understanding the specific source of phenotypic variation matters in community ecology.

Here, we explore the ecological consequences of sexual dimorphism, a central feature of metazoans and many plant populations that has not been fully incorporated into ecological theory. The gamete differences that define the sexes are expected to lead to divergence between males and females in a suite of life history traits (Trivers 1972, Shärer et al. 2012), and phenotypic traits. This divergence is iconically manifest as striking sexual dimorphism in sexually-selected traits such as body size or courtship displays (Darwin 1871, Andersson 1994). Although sexual selection and associated mate choice behaviors themselves may have relevance to interspecific ecological interactions (Gomez-Llano et al. 2018), the different life histories that define the sexes are often expected lead to different nutritional and resource requirements for males and females (Maklakov et al. 2008). As a specific example, in insects, differential contributions of longevity and fecundity to male and female lifetime reproductive success result

70 in different combinations of macronutrients that maximize male and female fitness (Maklakov et
71 al. 2008, Reddiex et al. 2013, Garlapow et al. 2015, Jensen et al. 2015, Camus et al. 2017).
72 Similarly, nutritional models of optimal foraging have been proposed to explain sex differences
73 in diets of moose (Belovksy 1978). Consequently, males and females of many species have
74 evolved divergent resource use, either as an indirect outcome of divergent reproductive roles or
75 through other forms of sex-specific natural selection, resulting in sex-differences in diet
76 composition and often in corresponding trophic morphology (Slatkin 1984, Temeles 1985, Shine
77 1989, Temeles et al. 2000, De Lisle and Rowe 2015a, De Lisle 2019).
78 Data suggest that these 'ecological' sexual dimorphisms can have substantial
79 consequences for community structure (Fryxell et al. 2015, Pincheira-Donoso et al. 2018, Start
80 and De Lisle 2018, Tsuji and Fukami 2018, 2020). More generally, sex differences may play an
81 important role in the relationship between ecological and evolutionary dynamics (Giery and
82 Layman 2019, Svensson 2019, Fryxell et al. 2019). Sexual dimorphism thus represents a key
83 source of ecologically-relevant variation within species. Within-species variation in resource
84 specialization is commonplace (Bolnick et al. 2003), with important consequences for species
85 interactions and community assembly (Hughes et al. 2008 , Bolnick et al. 2011, Des Roches et
86 al. 2018). Critically, as a source of intraspecific variation, sexual dimorphism may have different
87 consequences from other types of variation. Unlike most phenotypes, whose relative abundances
88 can evolve to reflect local ratios of alternative resources, the ratio of males to females (at birth) is
89 expected to be maintained at 1:1 (Darwin 1871, Fisher 1930), though their phenotypes and
90 demography may diverge to have differential ecological impacts. Thus, the rate at which males
91 are born (which determines predation pressure on males' prey), is strongly dependent on
92 females' foraging success. Perhaps to a lesser extent (depending on mating system), the rate of

female offspring production can depend on male foraging success. This coupling of the dynamics of two consumer phenotypes has unknown consequences for consumer-resource dynamics, consumer mediated coexistence of the resource species, and apparent competition between the resource species. Using a simple model of consumer-resource dynamics, we show that consumer sexual dimorphism can affect coexistence between resource species (competing directly or apparently), and species' abundance.

Materials and Methods

Our model represents a simple extension of a classic model of consumer-resource dynamics, in which a consumer species exploits two resources that themselves undergo density-dependent growth (Figure 1). Consumer growth rate is limited only by resource abundance. The original version of this model did not consider within-species phenotypic variation, and can lead to exclusion of one resource ('apparent competition'; (e.g. Holt 1977). More recently, (Schreiber et al. 2011) showed that quantitative trait variation in the predator, affecting attack rates on the two resources, can facilitate coexistence between the prey. Here, we instead allow for the possibility that male and female consumers differ in resource-specific attack rates. We can describe the population dynamics of two resources (with densities R_i, R_j) and consumer males (with density *M*) and females (with density *F*) using the system of ordinary differential equations:

$$\frac{dR_i}{dt} = r_i R_i\left(1 - \alpha_{ii}R_i - \alpha_{ij}R_j\right) - a_{M,i}R_i M - a_{F,i}R_i F \text{ for } j \neq i \qquad (1a)$$

$$\frac{dM}{dt} = \frac{1}{2}\, B(M, F, R_1, R_2) - d_M M \qquad (1b)$$

$$\frac{dF}{dt} = \frac{1}{2}\, B(M, F, R_1, R_2) \; - d_F F \qquad (1c)$$

Each resource undergoes density-dependent population growth with intrinsic per-capita growth rates *r*, with competition represented by competition coefficients α. Resources are also regulated by consumers depending on sex-specific attack rates by males a_M and by females a_F. Consumer dynamics are governed by females' birth rate *B* (half of the offspring being female), and limited by sex-specific intrinsic mortality rates d_M and d_F.

An appropriate function describing birth rates has been a point of debate for demographers, with the general conclusion being that any function describing birth rates should capture the negative effects of extreme sex ratio skew on birth rates, with the extreme being that birth rates should be zero when one sex is absent (Caswell and Weeks 1986), or unable to breed. Generally, treating birth rates proportional to the harmonic mean density of males and females is agreed as the best approach (Caswell and Weeks 1986, Lindstöm and Kokko 1998). Here, we extend this harmonic mean birth function to account for each sex's foraging success, on the logic that each sex must both be present and sufficiently well-fed to reproduce:

$$B\big(M, F, R_i, R_j\big) = \; 2\frac{MI_M * FI_F}{MI_M + FI_F} \qquad (2)$$

where *I* is the energy intake of a given sex:

$$I_{F=}\, b_F\big(a_{F,1}R_1 + \; a_{F,2}R_2\big) \text{ and } \; I_{M=}\, b_M\big(a_{M,1}R_1 + \; a_{M,2}R_2\big) \qquad (3)$$

which couples the dynamics of consumers and resources. In this model the rate of consumer births depends on not just the number of males and females but also on the abundance of both prey and the prey preference of each sex, where MI_M is the number of males weighted by their

energy to reproduce (similarly with females), b is a scaling constant reflecting the number of predator offspring created per prey eaten, and $a_{M,i}, a_{F,i}$ are the attack rates on the resource i.

Because we are specifically interested in understanding effects of sexual dimorphism in prey preference, we relate male and female resource-specific attack rates via the degree of sexual dimorphism, β, such that

$$a_{M,1} = a_{M,max}\left(\frac{1}{2}+\frac{\beta}{2}\right) \text{ and } a_{F,1} = a_{F,max}\left(\frac{1}{2}-\frac{\beta}{2}\right) \tag{4a}$$

$$a_{M,2} = a_{M,max}\left(\frac{1}{2}-\frac{\beta}{2}\right) \ and \ a_{F,2} = a_{F,max}\left(\frac{1}{2}+\frac{\beta}{2}\right) \tag{4b}$$

where β ranges from zero to one, with $\beta = 0$ representing complete sexual monomorphism if maximum attack rates are equal across the sexes (both sexes are generalists, attacking each prey at the rate, $a_{max}/2$; we explore both $a_{M,\,max} = a_{F,\,max} = a_{max}$ as well as $a_{M,\,max} \neq a_{F,\,max}$), and $\beta = 1$ representing complete sexual dimorphism such that males only attack R_1 and females only attack R_2.

By assuming that resource acquisition of males and females contributes to the consumer birth rate, we are not necessarily making any assumption about parental care or condition-dependent fecundity. Rather, this is an assumption that the fraction of each sex available for reproduction depends in part on resource acquisition, a realistic feature of many organisms. For instance, males' energetic costs of finding a mate, defending a territory, care for offspring, or expressing a sexually-selected trait are all expected to depend on the resource pool available to males (Rowe and Houle 1996). Females' ability to produce eggs, gestate, and provision young (e.g., lactation in mammals) similarly depends on their energy intake. Parental care and other

factors can also lead to associations between sex-specific resource abundance and consumer birth rates, beyond what would be expected beyond the costs of simply being available to mate.

We analyzed this model to find equilibria when both one or two resources are present, as well as invasion criteria for a resource into a two species community at equilibrium. Using the mathematical theory of permanence (Schreiber 2000, Patel & Schreiber 2018), we can use these invasion criteria to determine whether all three species coexist (in the sense of permanence), exhibit a bistability, or competitive exclusion occurs. In addition to presenting our analytical results below, we provide further mathematical detail in Supplement A. We also numerically explored the behavior of the model under a variety of scenarios using the packages deSolve v. 1.21 (Soetgart et al. 2010) and caTools v. 1.17.1.2 (Tuszynski 2019) in R v. 3.5.0 (R Core Team 2018). Importantly, using simulations allowed us to explore the behavior of our model for cases where 2-species consumer-resource equilibria do not exist. Because there are a large number of potential combinations of parameters that could be explored, we focused our simulations on three different biological scenarios: 1) completely symmetric male and female total attack rates and contributions to birth rate, 2) asymmetric total attack rates across the sexes, and 3) asymmetric contribution of male and female resource acquisition to consumer birth rates. The first scenario applies most readily to organisms with biparental care and similar total caloric requirements across the sexes. The second scenario likely applies to many organisms where total lifetime resource acquisition is higher for one sex, which is the case for many organisms where the sexes differ, for example, in body size. The third scenario is another realistic departure from the first, relevant for organisms where resource acquisition in one sex (e.g., females) has a greater influence on that sexes mating propensity, or cases with biased operational sex ratios due to polyandry or polygyny. For each scenario we explore the consequences of consumer ecological

sexual dimorphism (β) for consumer persistence and coexistence. For each set of parameter values, we simulated the model 1,000 time steps (to ensure the simulation reaches its equilibrium). For each run, we determined the equilibrium abundances of M, F, R_1 and R_2 at t = 1,000. We also calculated the standard deviation of species' abundances in the last 50 time-steps. Although we present solutions simulated on the scale of α_{ii} = 0.1, we obtained qualitatively equivalent conclusions rescaling under a wide range values of competition coefficients (see Table S1B, Supplement B). The R script to generate all figures and results presented is available in the supplementary material.

Results

Analytical results

Our analysis begins by considering a subsystem of a single resource species, say species i, and the consumer species. These two species can coexist if

$$H_i \frac{1}{\alpha_{ii}} > 2 \tag{5}$$

where $H_i := 2\frac{\frac{b_M a_{i,M}}{d_M}\frac{b_F a_{i,F}}{d_F}}{\frac{b_M a_{i,M}}{d_M}+\frac{b_F a_{i,F}}{d_F}}$ is the harmonic mean of the lifetime per-capita resource contributions of each sex to reproduction, and $\frac{1}{\alpha_{ii}}$ corresponds to the carrying capacity of resource species i. Intuitively, $H_i \frac{1}{\alpha_{ii}}$ corresponds to the average number of offspring produced by a mating pair during their lifetime when the resource species is at its carrying capacity. These harmonic means decrease to zero with the degree of sexual dimorphism (i.e. H_i is a decreasing function of β and H_i=0 when $\beta = 1$), there always is critical degree of sexual dimorphism above which the consumer cannot persist on a single resource species. Intuitively, this arises when one of the sexes specializes too much on the other (absent) resource species and, consequently, contributes

too little to reproduction. When the coexistence condition holds, the consumer-resource species pair coexist at the following equilibrium densities:

$$R_i^* = 2/H_i$$

$$F_i^* = \frac{r_i\left(1-{}^{2\alpha_{ii}}/_{H_i}\right)}{a_{i,F}+\frac{a_{i,M}d_F}{d_M}} \tag{6}$$

$$M_i^* = \frac{d_F}{d_M}F_i^*$$

At these densities of the consumer and resource *i*, the second (rare) resource species *j* can invade if its per capita growth rate

$$I_j = r_j\left(1-\frac{2\alpha_{ji}}{H_i}\right) - A_jF_i^* \tag{7}$$

is positive. Here, $A_j = a_{F,j} + a_{M,j}d_F/d_M$ is the average attack rate on resource *j* when the males and females are at an equilibrium. Provided the consumer species can persist on each of the resource species individually, the invasion growth rates I_1 and I_2 determine the ecological outcomes. If both invasion growth rates are positive (mutual invasibility), all three species coexist. If both invasion rates are negative, there is a priority effect in which both single resource-consumer equilibria are stable. If one invasion growth rate is positive and the other is negative, this suggests (as confirmed by numerical simulations) that the resource species with the positive invasion growth rate excludes the other resource species. In the supplementary material (Supplement A), we provide more details about this analysis and describe the invasion conditions for these outcomes or when the consumer only persists in the presence of both resource species.

As a step toward understanding the general conditions for coexistence and exclusion, we first examine two special cases corresponding to (i) resource competitive symmetry whereby $\alpha_{11} = \alpha_{12} = \alpha_{21} = \alpha_{22}$ and (ii) pure apparent competition whereby $\alpha_{12} = \alpha_{21} = 0$. When there is competitive symmetry, the resource species with the larger value of r_i/A_i excludes the other

resource species. The quantity r_i/A_i corresponds to the consumer density supported by resource species *i* when intraspecific competition is very weak i.e. $\alpha_{ii} = 0$. Hence, the resource species that supports the highest consumer equilibrium density (in the absence of self-limitation) excludes the other. This is an analog of the P^* rule (Holt 1977, Holt and Lawton 1993, Schreiber 2021). In this case, sexual dimorphism (as measured by β) influences outcomes only if there is an asymmetry in the maximal attack rates of the female and male (e.g., female masked boobies dive for prey more often than males; Weimerskirch et al. 2009). For example, if the female-preferred resource (R_1) has the higher intrinsic rate of growth ($r_1 > r_2$) and the female consumer has the higher maximal attack rate of the two sexes, then the female-preferred resource species excludes the other resource species when sexual dimorphism is low (i.e. A_1=A_2 when $\beta = 0$). However, as the average attack rate A_1 on the female-preferred resource increases with the magnitude β of the sexual dimorphism, sexual dimorphism reverses the outcome of apparent competition whenever $r_1/a_{F,max} < r_2/a_{M,max}$ and the self-limitation in the female-preferred resource is weak.

Next, we consider the case of pure apparent competition in which there is no direct competition between the resources, i.e. $\alpha_{12} = \alpha_{21} = 0$. Then, coexistence occurs when

$$\frac{1}{1-2\alpha_{ii}/H_i} > \frac{r_i/A_i}{r_j/A_j} \text{ for } i \neq j \tag{8}$$

The right-hand side of this condition determines the outcome of apparent competition in the case of competitive symmetry i.e. the species with larger r_i/A_i wins. The left-hand is always greater than one and increases to infinity as the sexual dimorphism increases. This has two implications: (i) when r_1/A_1 and r_2/A_2 are equal, the resource species coexist at any level of sexual dimorphism, and (ii) when r_1/A_1 and r_2/A_2 are unequal, sufficiently strong sexual dimorphisms (allowing the consumer to persist) will ensure coexistence of the two resource species by diluting

the strength of apparent competition.

Finally, the general coexistence condition is

$$\frac{1-2\alpha_{ji}/H_i}{1-2\alpha_{ii}/H_i} > \frac{r_i/A_i}{r_j/A_j} \text{ for } i \neq j \tag{9}$$

The effect of sexual dimorphism on the left-hand side term depends on the relative strengths of intra- and interspecific competition. When intraspecific competition is greater than interspecific competition (i.e. $\alpha_{ii} > \alpha_{ji}$), the left-hand side term increases to infinity with increasing sexual dimorphism. In contrast, when interspecific competition between resources is greater than intraspecific competition (i.e. $\alpha_{ji} > \alpha_{ii}$), the left-hand side term of the general coexistence condition decreases to zero with increasing levels of sexual dimorphism. The effect of sexual dimorphism on the right-hand side term of the general coexistence criterion is as discussed for the case of competitive symmetry. Together these observations imply that if resource 1 is the better direct competitor i.e. $\alpha_{21} > \alpha_{11}$ and $\alpha_{21} < \alpha_{22}$, then coexistence requires that resource 2 is the better apparent competitor i.e. $r_2/A_2 > r_1/A_1$. In which case, a sexual dimorphism can help consumer-mediated coexistence.

Numerical results: Symmetric resource acquisition across the sexes

Our numerical results generally matched conclusion from our analytical solutions and are summarized in Table 1. The effects of consumer sexual dimorphism on resource population dynamics are illustrated in Figure 2. Sexual dimorphism results in increased resource density (Fig 2B vs. 2D; Fig 3) and can facilitate persistence of a competitively inferior resource species (Fig 2A vs. 2B). When competition is purely apparent and resource acquisition by the consumer is symmetric across the sexes, increasing consumer sexual dimorphism increases the parameter

space under which resources can coexist (Fig. 2C vs 2D), consistent with our analytical results (Fig. 4A). In particular, as sexual dimorphism approaches the extreme (each sex uses a different resource exclusively), competitively inferior resource species can coexist with a superior competitor that is more susceptible to apparent competition (Figure 4).

When resources compete directly with symmetric intraspecific competition, resource acquisition is symmetric across the sexes and intrinsic per-capita growth rates are equal between resources, consumer sexual dimorphism has little effect on invasion of a resource into a consumer-single-resource community at equilibrium (S1A-C, S4A). Yet even in the absence of effects on coexistence consumer sexual dimorphism has strong effects equilibrium resource abundance, both under analytical solutions to a two species community and under simulations of three species communities (Fig 3). As predicted by our analytical conditions, when resource growth rates are unequal, sexual dimorphism changes expected regions of coexistence of both resources and the consumer, leading to invasion and persistence of competitively inferior resource that is a superior apparent competitor i.e. has a larger value of r_i/A_i (Figure 5B, Figure S4B, Figure S1).

Numerical results: Asymmetric total resource acquisition

Introducing asymmetric total resource acquisition, represented as sex differences in the maximal attack rates $a_{F,max}$ and $a_{M,max}$, has complex effects on both population dynamics and coexistence between competing resources. Introducing asymmetric attack rates can promote coexistence (as predicted by the analytical results) while simultaneously creating cyclical resource dynamics (Fig 2B). Under pure apparent competition and asymmetric attack rates, consumer sexual dimorphism has some similar effects to the case of symmetry, mediating

288 coexistence of resources that differ in intrinsic per-capita growth rates (Fig 4B).

289 Under direct interspecific competition, sexual dimorphism in resource specialization has
290 striking effects on resource persistence when the sexes differ in total resource acquisition,
291 expanding regions of coexistence (Figs 5A, B) and in some cases leading to persistence of a
292 competitively inferior resource (Figs 5C, D; Supplement B Figs S4B, C). Moreover, sex
293 differences in total resource acquisition can reverse competitive outcomes when resources differ
294 in their intrinsic per-capita growth rates and the degree of resource specialization is held constant
295 (Figs 5C, D). The effect of sex differences in total resource acquisition on patterns of prey
296 persistence can be as striking as the effects of resource specialization (Supplement B Figs S2,
297 S1).

298

299 *Asymmetric contribution of resource acquisition to birth rate*

300 Introducing asymmetries in the contribution of sex-specific resource acquisition to birth rate
301 (e.g., polygyny or polyandry, manifest as changes of the constant b_f), had little qualitative effect.
302 This similarity is illustrated in Supplement B figure S3 (compare to S1). Although changing
303 these constants results in shifts of absolute regions of coexistence, the influence of consumer sex
304 differences was similar. Lack of sensitivity in asymmetries in the contribution of resource
305 acquisition to birth rates is consistent with our analytical results (Supplement A) that apply to all
306 first-order homogenous mating functions including geometric and arithmetic contributions to
307 reproduction.

308

309 **Discussion**

310 Using a general model of consumer-resource dynamics we show that consumer sexual
311 dimorphism has substantial consequences for community assembly. Competitive exclusion via
312 apparent competition is expected and observed when males and females are monomorphic
313 generalists and resources differ substantially in their intrinsic per-capita growth rates. However,
314 when male and female consumers differ in their resource-specific attack rates, resource species
315 that differ substantially in their intrinsic per-capita growth rates can coexist. Similar effects of
316 consumer sexual dimorphism are observed when resources compete directly, with sexual
317 dimorphism in some cases permitting coexistence or persistence of a competitively inferior
318 resource (summarized in Table 1). However, for both direct and apparent competition, consumer
319 sexual dimorphism can also lead to competitive exclusion between resources that would typically
320 be expected to coexist. Thus, consumer sex differences result in fundamental changes in the
321 types of competing resources that can establish during community assembly. These results also
322 support conclusions from other food web models suggesting trophic position may impact the
323 observed ecological effects of sexual reproduction (Kawatsu 2018). Moreover, equilibrium
324 resource abundances and temporal dynamics are altered by consumer sexual dimorphism even
325 when long-term ecological outcomes are unaffected. We expect to observe these types of effects
326 whenever consumer mating propensity depends, in part, on resource acquisition, a biological
327 reality for many sexually-reproducing consumers (e.g. widespread evidence of developmental
328 thresholds for transitions to reproduction, reveiwed in Wilbur and Collins 1973, Day and Rowe
329 2002, and resource-dependent sexual displays, Bonduriansky 2007).
330 Although our results suggest that the effects of consumer sexual dimorphism on
331 community assembly can be complex, our analysis reveals some key predictions from our model.
332 First, consumer sex differences in resource-specific attack rates result in an increase in the

equilibrium density of each resource and a decrease in the abundance of the consumer species. Intuitively, sexual dimorphism can frequently lead to slightly suboptimal resource use of the species due to a mismatch between demand (restricted by a 50:50 sex ratio) and resource availability which can be more variable and dynamic. Second, consumer sexual dimorphism can promote coexistence when the more aggressively-feeding sex (higher total attack rates) specializes on and suppresses what would otherwise be the competitively superior resource. This later situation may be commonplace if sex-specific natural selection favors specialization, by the sex with higher resource requirements, on the most abundant resource. Finally, and related to the previous observation, the effects of consumer sexual dimorphism are most pronounced when resources either differ in intrinsic per-capita growth rates, or when consumer sexes differ in their total resource acquisition.

Our simulation models focused on a harmonic mean birth function, which is biologically realistic in that it captures severely reduced birth rates when any one sex is rare. Empirically evaluating alternative birth functions in real systems is difficult, requiring extreme variation in adult sex ratios rarely seen in many species. However, some empirical data exists and supports the harmonic mean as the best-fitting description of sexual birth rates (Miller and Inouye 2011). Nonetheless, our analytical results (see Supplement A for details) that our conclusions apply to any birth function that is first order homogenous i.e. $B(aMI_M, aFI_F) = aB(MI_M, FI_F)$ for any positive constant $a>0$. These functions include all functions typically considered candidate birth functions by demographers (Caswell and Weeks 1986, Miller and Inouye 2011). Our conclusions do depend on the assumption that male abundance makes some contribution to birth rate.

355 Although even moderate sex differences in attack rates can change the conditions under
356 which resources coexist, the strongest effects are observed when the consumer population
357 approaches complete sexual dimorphism in resource specific attack rates. Cases of such extreme
358 sex differences in diet preference exist (Temeles et al. 2000), although whether they occur with
359 any regularity is unclear. Diet divergence between the sexes, and sexual dimorphisms in trophic
360 morphology, are common (Shine 1989), although overlap in male and female diets can be
361 substantial even in the presence of ecological sex differences (e.g., Stamps et al. 1997, De Lisle
362 and Rowe 2015a). Yet overlap in diet content may be expected even in the case of large
363 differences in attack rates, as diet content is the product of both attack rate and resource
364 abundance. Further, males and females may fail to diverge in diet preference even when
365 optimum diet nutritional content differs across the sexes (Reddiex et al. 2013). These challenges
366 to understanding sex-specific resource acquisition highlight the need for further empirical studies
367 disentangling expressed diet preference, male and female nutritional optima, and the evolution of
368 ecological sexual dimorphism.
369 We have assumed a Fisherian sex ratio, where the primary sex ratio is maintained at a
370 stable 1:1 ratio (Fisher 1930), although our model allows for deviations from a 1:1 operational
371 sex ratio via sex-specific intrinsic mortality. Sex-specific mortality is commonplace in natural
372 populations and can occur for a variety of reasons, such as sex-specific costs of reproduction,
373 predation, or sexual conflict. In our model, sex-specific mortality, as well as variation in
374 consumer mating system (see Supplemental material) had predictable consequences for resource
375 abundance, leading to increases in the abundance of the resource favored by the sex with higher
376 intrinsic mortality. Nonetheless, the general effects of sexual dimorphism hold under sex-biased
377 mortality and departures from monogamy, indicating our general conclusions may also apply to

systems with diverse mating systems or where the primary sex ratio, or the operational sex ratio, deviates from 1:1.

Our analysis also assumes that the male and female trophic traits are constant. In nature, however, the degree and even direction of sexual selection can vary dramatically among closely related populations (e.g., Reimchen et al. 2016). Dimorphism clearly evolves rapidly in response to spatially varying sexual selection and resource availability. Future extensions to our strictly ecological model could add in eco-evolutionary dynamics of sexual dimorphism.

Male and female densities were reduced with increasing ecological sexual dimorphism, because consumer births are limited by resource acquisition in both sexes in our model. In the extreme case, where the consumer cannot persist on a single resource (for example, under complete sexual dimorphism), coexistence of the consumer depends on stable coexistence of the resource species (Supplement A). Our simulations suggest robust persistence of extremely dimorphic consumers in two-consumer communities, albeit at reduced density. Both of these results – reduced consumer density and dependence on the presence of both resource species in the community – suggest that sexually-dimorphic populations may face a higher risk of extinction due to demographic stochasticity. However, it is difficult from our purely deterministic ecological model to fully interpret the consequences of sexual dimorphism on extinction probability. Evolution of sexual dimorphism from a monomorphic ancestor that specializes on a single resource could lead to increased population mean fitness, by increasing the total resource pool available across both sexes (Rand 1952, Selander 1966, Slatkin 1984); such a process represents a form of within-species, between-sex ecological character displacement. More generally, evolution of sexual dimorphism is expected to be critical to population mean fitness whenever optima differ for males and females (Lande 1980), and

401 empirical data suggest sexual dimorphism can be associated with reduced extinction probability
402 at both the macroevolutionary scale and in extant populations (De Lisle and Rowe 2015b).
403 Nonetheless, our results suggest a full understanding of sexual dimorphism's role in population
404 persistence could require integrating theory and data from population/community ecology and
405 evolutionary genetics. This conclusion is complemented by recent theory (de Vries and Caswell
406 2019) indicating sexual dimorphism in demographic parameters can have important
407 consequences for maintaining genetic diversity.

408 Our model generally predicts that ecological sexual dimorphism may in some cases
409 promote, and in other cases reduce, diversity at lower trophic levels during community assembly.
410 Testing this prediction with correlative data (reviewed in Tsuji and Fukami 2020) would be
411 possible but challenging. An alternative and non-exclusive hypothesis, that dimorphic predators
412 are more likely to establish in communities with diverse prey assemblages, would also generate
413 patterns consistent with our results. Alternatively, experiments that manipulate the expressed
414 dimorphism of predators and track community dynamics at lower trophic levels are tractable in
415 some systems. Similar experiments have been performed (Fryxell et al. 2015, Start and De Lisle
416 2018), in which effects of predator sex ratio manipulation on prey communities are assessed in
417 mesocosm designs. Although the results of these experiments do suggest sex differences can
418 have important community consequences, no studies (to our knowledge) have compared
419 communities in which the magnitude of morphological sexual dimorphism is manipulated under
420 a stable sex ratio. Such designs are possible when distributions of male and female phenotypes
421 exhibit substantial variation, and would represent an ideal empirical test of the theoretical results
422 presented here.

Ecological sex differences are commonplace, although the details of their evolutionary drivers and ecological consequences are unclear. Emerging theory and data indicate ecological sex differences may have important consequences for the evolutionary genetics of adaptation (Zajitschek and Connallon 2017), the dynamics of diversification (Bolnick and Doebeli 2003, De Lisle and Rowe 2015b) and community assembly (Fryxell et al. 2015, Pincheira-Donoso et al. 2018, Start and De Lisle 2018). Our results add to this body of work, indicating that sexual dimorphism can have substantial effects on the structure, abundance, and dynamics of ecological communities, including changing conditions for coexistence between competing resource species.

Acknowledgements. We thank Tim Connallon and Miguel Gomez for comments on an early draft of this manuscript, as well as Gonzalo Hernando for assistance in the early stages of the project. This work was supported by funds from the University of Connecticut to DIB, an establishment grant from the Swedish Research Council to S.P.D. (2019-03706), and an U.S. National Science Foundation Grant DMS176803 to SJS.

References

Andersson, M. B. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Belovksy, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology **14**:105-134.

Bolnick, D. I., P. Amarasekare, M. S. Araujo, R. Burger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution **26**:183-192

Bolnick, D. I., and M. Doebeli. 2003. Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. Evolution **57**:2433-2449.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003 The Ecology of Individuals: Incidence and implications of individual specialization. The American Naturalist **161** 1-28.

Bonduriansky, R. 2007. The evolution of condition-dependent sexual dimorphism. The American Naturalist **169**:9-19.

Camus, M. F., K. Fowler, M. W. D. Piper, and M. Reuter. 2017 Sex and genotype effects on nutrient-dependent fitness landscapes in Drosophila melanogaster. Proceedings of the Royal Society of London Series B. **284**:20172237.

Caswell, H., and D. E. Weeks. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. American Naturalist **128**:707-735.

Cortez, M. H., and S. Patel. 2017. The effects of predator evolution and genetic variationon predator-prey population-level dynamics. Bulletin of Mathematical Biology **79**:1510-1538.

Darwin, C. 1871. The descent of man and selection in relation to sex. J. Murray, London.

Day, T., and L. Rowe. 2002. Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. The American Naturalist **159**:338-350.

De Lisle, S. P. 2019. Understanding the evolution of ecological sex differences: Integrating character displacement and the Darwin-Bateman paradigm. Evolution Letters **3**:444-447.

De Lisle, S. P., and L. Rowe. 2015a. Ecological character displacement between the sexes. The American Naturalist **186**:693-707.

469 De Lisle, S. P., and L. Rowe. 2015b. Independent evolution of the sexes promotes amphibian
470 diversification. Proceedings of the Royal Society B: Biological Sciences **282**:20142213.
471 de Vries, C., and H. Caswell. 2019. Selection in two-sex stage structured populations: Genetics,
472 demography, and ploymorphism. Theoretical Population Biology **130**:160-169.
473 Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison, J. A.
474 Schweitzer, and E. P. Palkovacs. 2018. The ecological importance of intraspecific
475 variation. Nature Ecology and Evolution **2**:57-64.
476 Fisher, R. 1930. The genetical theory of natural selection. Oxford University Press, Oxford, UK.
477 Fryxell, D. C., H. A. Arnett, T. M. Apgar, M. T. Kinnison, and E. P. Palkovacs. 2015. Sex ratio
478 variation shapes the ecological effects of a globally introduced freshwater fish.
479 Proceedings of the Royal Society of London Series B. **282**:20151970.
480 Fryxell, D. C., D. Weiler, M. Kinnison, and E. P. Palkovacs. 2019 Eco-evolutionary dynamics of
481 sexual dimorphism. Trends in Ecology and Evolution **in press**.
482 Garlapow, M. E., W. Huang, M. T. Yarboro, K. R. Peterson, and T. F. C. Mackay. 2015.
483 Quantitative genetics of food intake in Drosophila melanogaster. PloS OnE **10**:e0138129.
484 Giery, S. T., and C. G. Layman. 2019. Ecological consequences of sexually selected traits: An
485 eco-evolutionary perspective. The Quarterly Review of Biology **94**:29-74.
486 Gomez-Llano, M. A., H. M. Bensch, and E. I. Svensson. 2018. Sexual conflict and ecology:
487 species composition and male density interact to reduce male mating harassment and
488 increase female survival. Evolution **72**:906-915.
489 Haldane, J. B. S. 1937. The effect of variation on fitness. The American Naturalist **71**:337-349.
490 Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities.
491 Theoretical Population Biology **12**:197-229.

492 Holt, R. D., and J. H. Lawton. 1993. Apparent competition and enemy-free space in insect host-
493 parasitoid communities. The American Naturalist **142**:623-645.
494 Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008 Ecological
495 consequences of genetic diversity. Ecology Letters **11**:609-623.
496 Jensen, K., C. McClure, N. K. Priest, and J. Hunt. 2015. Sex-specific effects of protein and
497 carbohyfrate intake on reproduction but not lifespan in Drosophila melanogaster. Aging
498 Cell **14**:605-615.
499 Kawatsu, K. 2018. Ecological effects of sex differ with trophic positions in a simple food web.
500 Ecology and Evolution **8**:1239-1246.
501 Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters.
502 Evolution **34**:292-305.
503 Lindstöm, J., and H. Kokko. 1998. Sexual reproduction and population dynamics: the role of
504 polygony and demographic sex differences. Proceedings of the Royal Society of London
505 Series B. **265**:483-488.
506 Maklakov, A., S. J. Simpson, F. Zajitchek, M. D. Hall, J. Dessmann, F. Clissold, D.
507 Raubenheimer, R. Bonduriansky, and R. C. Brooks. 2008. Sex-specific effects of nutrient
508 intake on reproduciton and lifespan. Current Biology **18**:1062-1066.
509 Miller, T. E. X., and B. D. Inouye. 2011. Confronting two-sex demographic models with data.
510 Ecology **92**:2141-2151.
511 Patel, S., and S. J. Schreiber. 2015. Evolutionarily driven shifts in communities with intraguild
512 predation. The American Naturalist **186**:E98-E110.

513 Pincheira-Donoso, D., T. Tregenza, R. K. Butlin, and D. J. Hodgson. 2018. Sexes and species as
514 rival units of niche saturation during community assembly. Global Ecology and
515 Biogeography **27**:593-603.
516 R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for
517 Statistical Computing, Vienna, Austria.
518 Rand, A. L. 1952. Secondary sexual characters and ecological competition. Fieldiana-Zoology
519 **34**:65-70.
520 Reddiex, A. J., T. P. Gosden, R. Bonduriansky, and S. F. Chenoweth. 2013. Sex-specific fitness
521 consequences of nutrient intake and the evolvability of diet preferences. The American
522 Naturalist **182**:91-102.
523 Reimchen, T., D. Steeves, and C. A. Bergstrom. 2016. Sex matters for defence and trophic traits
524 of threespine stickleback. Evolutionary Ecology Research **17**:459-485.
525 Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition
526 dependent traits. Proceedings of the Royal Society of London Series B-Biological
527 Sciences **263**:1415-1421.
528 Schreiber, S. J. 2021. The P* rule in the stochastic Holt-Lawton model of apparent competition.
529 Discrete and Continuous Dynamical Systems-B **26**:633.
530 Schreiber, S. J., R. Burger, and D. I. Bolnick. 2011. The community effects of phenotypic and
531 genetic variation within a predator population. Ecology **92**:1582-1593.
532 Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. The Condor
533 **68**:113-151.
534 Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the
535 evidence. Quarterly Review of Biology **64**:419-461.

536 Shärer, L., L. Rowe, and G. Arnqvist. 2012 Anisogamy, chance and the evolution of the sex
537 roles. Trends in Ecology & Evolution **27**:260-264.
538 Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution **38**:622-630.
539 Soetgart, K., T. Petzoldt, and R. W. Setzer. 2010. Solving Differential Equations in R: Package
540 deSolve. Journal of Statisitcal Software **33**:1-25.
541 Stamps, J. A., J. B. Losos, and R. M. Andrews. 1997. A comparative study of population density
542 and sexual size dimorphism in lizards. American Naturalist **149**:64-90.
543 Start, D., and S. P. De Lisle. 2018. Sexual dimorphism in a top predator drives aquatic prey
544 community assembly. Proceedings of the Royal Society of London Series B. **2018**:1717.
545 Svensson, E. I. 2019. Eco-evolutionary dynamics of sexual selection and sexual conflict.
546 Functional Ecology **33**:60-72.
547 Temeles, E. J. 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey
548 vulnerability. The American Naturalist **125**:485-499.
549 Temeles, E. J., I. L. Pan, J. L. Brennan, and J. N. Horwitt. 2000. Evidence for ecological
550 causation of sexual dimorphism in a hummingbird. Science **289**:441-443.
551 Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 *in* B. Campbell,
552 editor. Sexual selection and the descent of man. Aladine, Chicago.
553 Tsuji, K., and T. Fukami. 2018. Community-wide consequences of sexual dimorphism: evidence
554 from nectar microbes in dioecious plants. Ecology **99**:2476-2484.
555 Tsuji, K., and T. Fukami. 2020. Sexual dimorphism and species diversity: from clades to sites.
556 Trends in Ecology and Evolution **35**:105-114.
557 Tuszynski, J. 2019. caTools: Tools: moving window statistics, GIF, Base64, ROC AUC, etc.. R
558 package version 1.17.1.2. https://CRAN.R-project.org/package=caTools.

Weimerskirch, H., M. Le Corre, H. Gadenne, D. Pinaud, A. Kato, Y. Ropert-Coudert, and C.-A. Bost. 2009. Relationship between reversed sexual dimorphism, breeding investment and forgaing ecology in a pelagic seabird, the masked booby. Oecologia **161**:637-649.

Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphbian metamorphosis. Science **182**:1305-1314.

Zajitschek, F., and T. Connallon. 2017. Partitioning of resources: the evolutionary genetics of sexual conlflict over resource acquisition and allocation. Journal of Evolutionary Biology **30**:826-838.

Table 1. Summary of effects of sex differences in resource use. Arrows indicate effects on mean species density and the range of parameter space under which resource coexistence is observed.

Density	Coexistence	
Consumer ↓	Apparent competition	↑
Resource ↑	Direct competition, equal resource growth rates, symmetric acquisition	0
	Direct competition, different resource growth rates, symmetric acquisition	↑
	Direct competition, asymmetric acquisition	↑↓

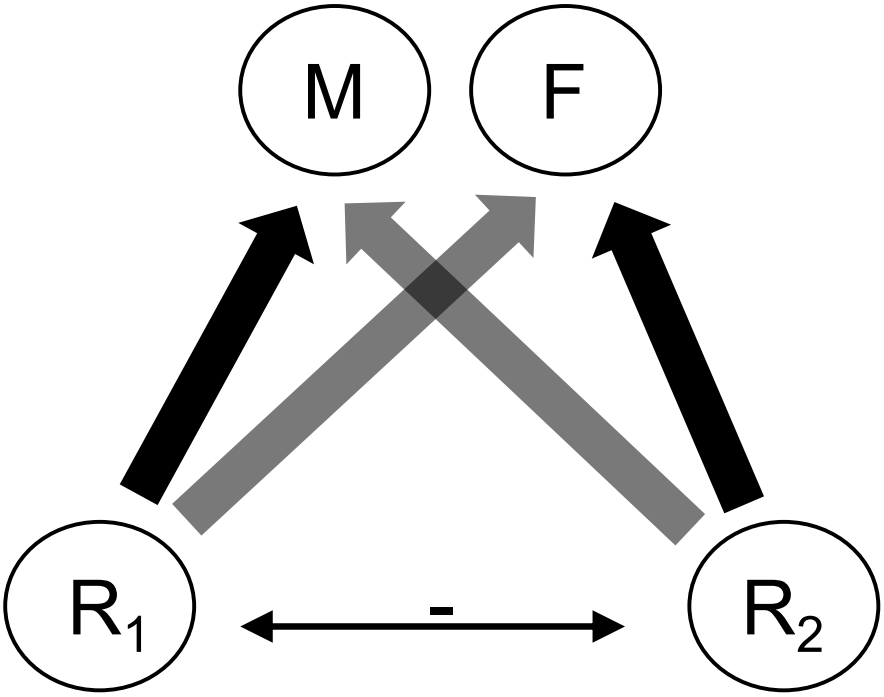


Figure 1. Illustration of the model structure. Males (*M*) and females (*F*) of a consumer species exploit two resources (R_1 and R_2) that may or may not also compete directly (double arrow). Sex-specific attack rates (black arrows) generate sex differences in ecological niche such that males and females preferentially attack R_1 and R_2, respectively, with varying degrees of overlap (grey arrows). Although males and females may consume different resources, fitness is equal across the sexes and so the dynamics of males, females, resource 1 and resource 2 are coupled.

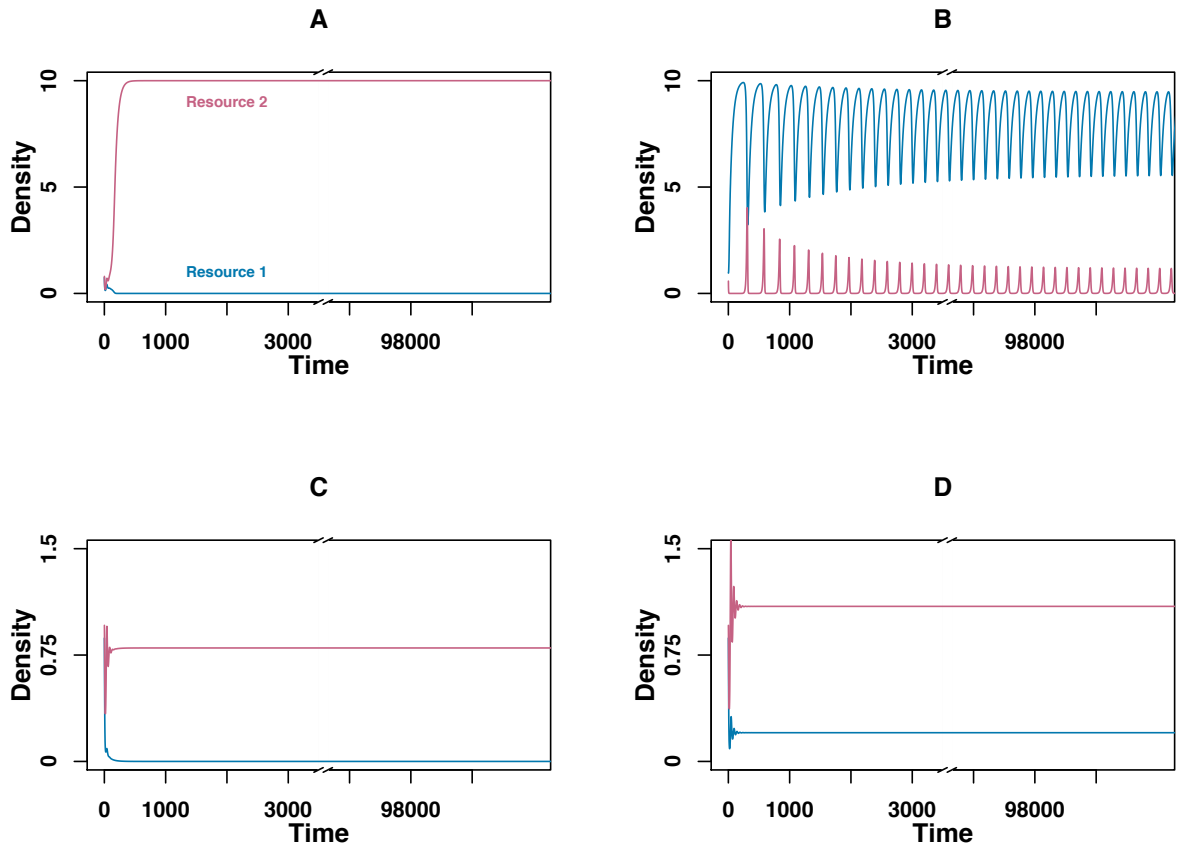


Figure 2. Coexistence mediated by sexual dimorphic consumers. In panel A, resource 2 (red) is a superior competitor to resource 1 (blue), leading to exclusion of resource 1 despite the presence of the consumer species. However, adding sex differences in total resource acquisition, under otherwise identical parameter values, leads to coexistence with cyclical dynamics (B). When competition is completely apparent (C, D), the resource with superior growth rate (red) excludes the inferior resource when consumers are sexually monomorphic (C). Under the same parameterization but with sexually dimorphic consumers (D), density of both resources is increased and they coexist. Parameter values: **A**, $\alpha_{11} = .1$, $\alpha_{12} = .12$, $\alpha_{22} = .1$, $\alpha_{21} = .09$, $\beta = 1$, $d_M = d_F = 0.02$, $b_M = b_F = .1$, $a_{M,\,max} = a_{F,\,max} = 1$, $r_1 = r_2 = 1$; **B** $\alpha_{11} = .1$, $\alpha_{12} = .12$, $\alpha_{22} = .1$, $\alpha_{21} = .09$, $\beta = 1$, $d_M = d_F = 0.02$, $b_M = b_F = .1$, $a_{M,\,max} = .8$, $a_{F,\,max} = 1.2$, $r_1 = 1$, $r_2 = 1$; **C** $\alpha_{11} = .1$, $\alpha_{12} =$

0, $\alpha = .1$, $\alpha_{21} = 0$, $\beta = 0$, $d_M = d_F = 0.02$, $b_M = b_F = .1$, $a_{M,\,max} = 1$, $a_{F,\,max} = 1$, $r_1 = 1$, $r_2 = 1.1$; **D** $\alpha_{11} = .1$, $\alpha_{12} = 0$, $\alpha_{22} = .1$, $\alpha_{21} = 0$, $\beta = 0.9$, $d_M = d_F = 0.02$, $b_M = b_F =$, $a_{M,\,max} = 1$, $a_{F,\,max} = 1$, $r_1 = 1$, $r_2 = 1.1$;

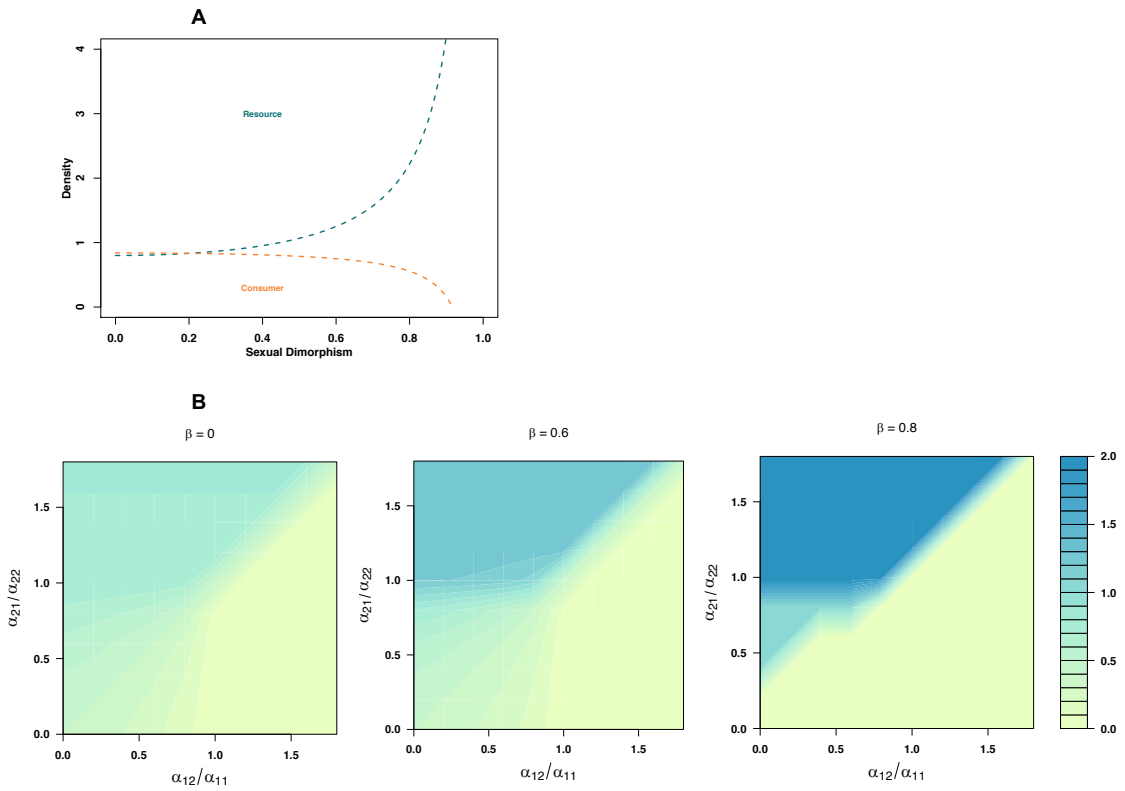
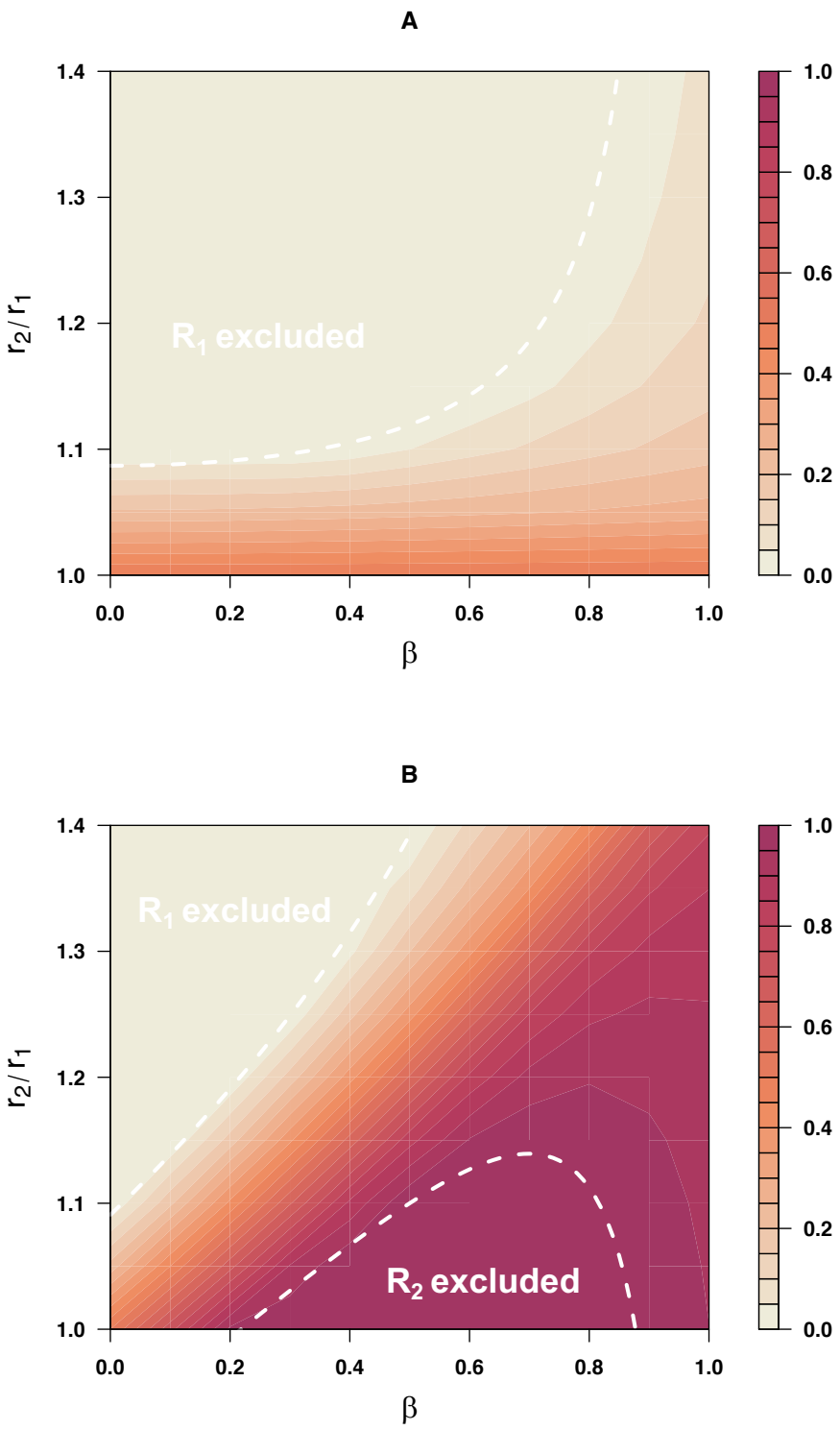
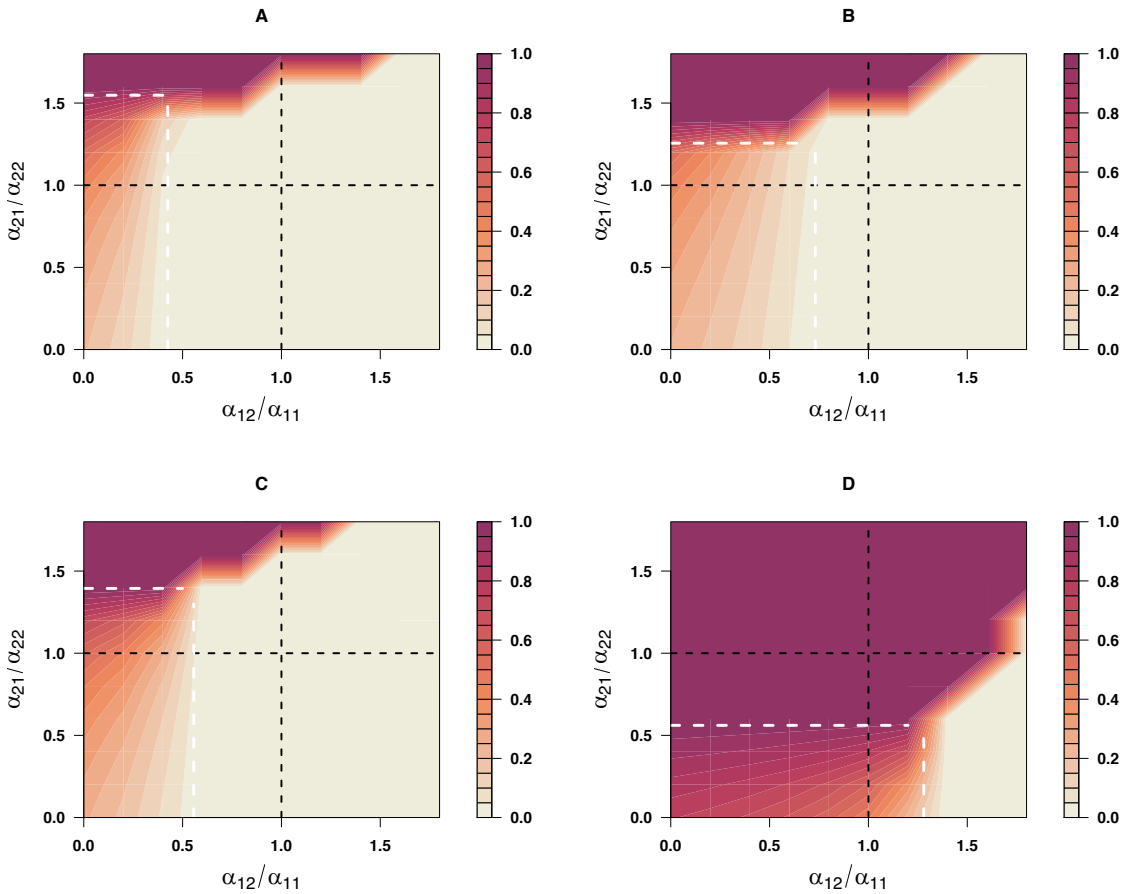


Figure 3. Consumer sexual dimorphism results in increased resource density and reduced consumer density in two and three species communities. Panel A: Equilibrium consumer female density decreases and resource 1 density increases with increased sexual dimorphism in a two species (consumer- 1 resource) community (equation 6). Panel B: these results hold in simulations in three species communities, where resource 1 density is plotted against competition coefficients in both resource species under three levels of sexual dimorphism, increasing from left to right. Assuming symmetric total attack rates across the sexes, symmetric contribution of resource acquisition to consumer birth rates, and equal growth rates across resources.


A
1.4
1.3
1.2
1.1
1.0
r2/ r1
R1 excluded
0.0
0.2
0.4
0.6
0.8
1.0
β
1.0
0.8
0.6
0.4
0.2
0.0
B
1.4
1.3
1.2
1.1
1.0
r2/ r1
R1 excluded
R2 excluded
0.0
0.2
0.4
0.6
0.8
1.0
β
1.0
0.8
0.6
0.4
0.2
0.0

638

Figure 4. Sexual dimorphism expands regions of coexistence between resources under apparent competition. Panels show relative density of resource 1 ($R_1/(R_1+R_2)$) from numerical simulations with starting conditions of $R_1 = R_2 = 1$ and $M = F = 1$. The top panel A shows the outcomes under symmetric maximal attack rates across the sexes ($a_{M,\,max} = a_{F,\,max} = 1$). Panel B shows the outcomes assuming sex differences in maximal attack rate ($a_{M,\,max} = .8$, $a_{F,\,max} = 1.2$). White dashed lines indicate analytical solutions (equation 8).



654

655 **Figure 5. Sexual dimorphism alters regions of coexistence of resource species.** Panels show
656 relative density of resource 1 ($R_1/(R_1 + R_2)$) from numerical simulations with starting conditions
657 of $R_1 = R_2 = 1$ and $M = F = 1$. Panel A shows outcomes under sexual monomorphism ($\beta = 0$),
658 unequal growth rates ($r_1 = 2$, $r_2 = 2.1$) across resources, and no sex differences in total attack rate
659 ($a_{M,\,max} = a_{F,\,max} = 1$). Panel B shows the outcome under the same parameter values but with
660 strong consumer sexual dimorphism ($\beta = 0.7$). Panels C and D show the effect of sexual niche
661 divergence when the sexes also differ in total attack rates (total resource acquisition), with C
662 showing the outcomes under unequal total attack rates ($a_{M,\,max} = .7$, $a_{F,\,max} = 1.3$), sexual
663 monomorphism in prey preference ($\beta = 0$), and differential resource growth rates ($r_1 = 1.6$, $r_2 =$
664 1.8), and D showing the outcome under the same parameter values but with moderate sexual

dimorphism in prey preference ($\beta = 0.4$). Black dashed lines demark equal inter and intraspecific competition coefficients. White dashed box demarks coexistence determined by analytical invasion criteria into a two-species community under equation 9.