

Asymmetric relationships and their effects on coexistence

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Abstract

Species coexistence attracts wide interest in ecology. Modern coexistence theory (MCT) identifies coexistence mechanisms, one of which, storage effects, hinges on relationships between fluctuations in environmental and competitive pressures. However, such relationships are typically measured using covariance, which does not account for the possibility that environment and competition may be more related to each other when they are strong than when weak, or vice versa. Recent work showed that such ‘asymmetric tail associations’ (ATAs) are common between ecological variables, and are important for extinction risk, ecosystem stability, and other phenomena. We extend the MCT, decomposing storage effects to show the influence of ATAs. Analysis of a simple model and an empirical example using diatoms illustrate that ATA influences can be comparable in magnitude to other mechanisms of coexistence, and that ATAs can make the difference between species coexistence and competitive exclusion. ATA influences are an important new mechanism of coexistence.

1 Introduction

At the core of ecology is the study of relationships - between organisms and between organisms and their environments. Ecologists may ask, for instance, how local environment relates to population growth rate. To study such relationships and to understand how two variables interact, ecologists very commonly use metrics such as correlation and covariance. But these standard measures of the strength and direction of association between variables often do not tell the whole story (Ghosh *et al.*, 2020a). To illustrate, the three pairs of variables in Fig. 1a-c all have the same Pearson correlation despite striking differences in association structure: Fig. 1b shows a symmetric type of association, while Fig. 1a,c exhibit what we have previously referred to as “asymmetric tail association” [ATA; Ghosh *et al.*, 2020a]. Metrics of association other than correlations and covariance are also often used (e.g., various forms of regression), but correlations are extremely common, and other common methods also reveal only a small portion of the information content of the relationship between variables (Nelsen, 2006). ATAs and related ideas had previously been seldom considered in ecology, but recently several insights have been gained by studying how features of associations beyond standard measures impact various ecological phenomena (de Valpine *et al.*, 2014; Anderson *et al.*, 2019; Popovic *et al.*, 2019; Ghosh *et al.*, 2020a,c,b, 2021). For instance, Ghosh *et al.* (2020a) show that ATAs are common in ecology and can influence Taylor’s law and Moran effects; Ghosh *et al.* (2020c) argue that extinction risks can become elevated when metapopulations are subject to ATAs; and Ghosh *et al.* (2021) show that ATAs can alter the stability of ecosystem functioning. Fig. 1d,e show contrasting examples of ATAs in nature using plankton population density time series. To our knowledge, the implications of ATAs for competition and coexistence have not yet been investigated. Doing so is the overarching goal of this study.

Competition, coexistence, and the maintenance of biodiversity are research topics at the core of modern ecology (MacArthur, 1958; Hutchinson, 1961; Schmidha & Ellner, 1984). The competitive exclusion principle states that two species competing for the same limiting resource cannot coexist at constant densities - one will instead outcompete the other and drive it extinct (Hardin, 1960). Modern coexistence theory [MCT; Chesson (1994, 2000); Barabas *et al.* (2018)] is a framework for understanding how species nevertheless coexist, and biodiversity is maintained, in real ecosystems, through the niche partitioning effects of environmental variation. MCT breaks down coexistence into the contributions of various mechanisms, with names such as “relative nonlinearity in competition” and “storage effects” (Chesson, 1994) which will be familiar to many readers. MCT has been applied to several systems, including annual (Angert *et al.*, 2009; Hallett *et al.*, 2019) and perennial plants (Adler *et al.*, 2006, 2010), tropical trees (Usinowicz *et al.*,

2012), plankton (Cáceres, 1997; Descamps-Julien & Gonzalez, 2005; Narawani *et al.*, 2013), and corals (Álvarez-Noriega *et al.*, 2020). Although MCT is somewhat mathematically complex, recent extensions make it more accessible (Ellner *et al.*, 2016, 2019).

It is possible to see, intuitively, why ATAs may influence one mechanism of coexistence in particular, storage effects. We review, conceptually, what storage effects are (Chesson, 1994; Chesson *et al.*, 2012; Ellner *et al.*, 2016; Barabas *et al.*, 2018), and explain why ATAs may be relevant to them. Storage effects allow competing species to fluctuate in abundance, without any going extinct, by providing a relative benefit to whichever species is currently rare (Chesson, 2000). Storage effects hinge on positive covariation between the fluctuating quality of the environment for a species (E) and the strength of competition (C) experienced by that species (called EC covariance); and on the assumption that optimal environmental conditions for distinct species are also distinct, so that no two species find the same conditions to be optimal. Then, good environmental conditions for a currently common species are paired with strong intraspecific competition, because of positive EC covariance and the commonness of the species. But good environmental conditions for a currently rare species are not as closely accompanied by strong competition because the rarity of the species limits competitive influence. The resulting asymmetry is what provides the relative benefit to the rare species. Storage effects can be quantified by measuring to what extent EC covariance contributes to differences between currently rare and currently common species growth rates (Chesson, 1994; Ellner *et al.*, 2016). ATAs may, in principle, influence storage effects simply because storage effects hinge on EC covariation, and ATAs, when they occur between environment and competition variables, can be an aspect of EC covariation.

To further demonstrate the plausibility of ATAs altering coexistence between species, we carried out simple simulations using a two-species model, the well-known lottery model. The simulations described in this paragraph are sufficient to demonstrate that ATAs influence coexistence in some manner; the precise nature of that influence is the subject of the rest of the paper. The lottery model, which was originally introduced as a model of coral reef fish competing for a set of N breeding territories, is as follows. Letting $N_i(t)$ denote the adult population density of species $i = 1, 2$ at time t , and defining $N = N_1(t) + N_2(t)$, model equations are

$$N_i(t+1) = (1 - \delta)N_i(t) + \delta N \frac{B_i(t)N_i(t)}{B_1(t)N_1(t) + B_2(t)N_2(t)} \quad (1)$$

for $i = 1, 2$. Here, δ is an adult mortality rate, and $B_i(t)$ is the fecundity of species i at time t . The model postulates that adults die at rate δ at each time step, and are replaced by juveniles in proportion to the reproductive outputs of the two species that year. Note that N is constant through time. Notation for the

whole paper is summarized in Table 1. We assume for simplicity that the random variables ($B_1(t), B_2(t)$) are independent and identically distributed (iid) through time. In three distinct simulations (Fig. 1f-h), B_1 and B_2 were, respectively, left- (Fig. 1a), right- (Fig. 1c) and symmetrically (Fig. 1b) tail associated, while the same marginal distributions for these fecundities were used in all simulations (see Methods for details). Thus, the model setup was identical in the three simulations except for different ATAs. ATAs substantially influenced aspects of species coexistence in these simulations (Fig. 1f-h).

We previously demonstrated that ATAs are common in nature can influence ecological phenomena (Ghosh *et al.*, 2020a,c,b, 2021); and our arguments above indicate that ATAs may influence species coexistence. Thus, we here seek to quantify the consequences of ATAs for competition, coexistence, and the maintenance of biodiversity, by means of the following specific goals. G1) We will augment MCT to show formally how ATAs play a role in coexistence. MCT decomposes a measure of coexistence into components due to each of several mechanisms. We address how ATAs contribute to these components. We examine mechanisms of coexistence that apply in models exhibiting solely temporal variation; spatial variation can be considered in future work. G2) We will explore, using the simple lottery model, the relative magnitudes of the contributions to coexistence that come from ATAs compared to other, previously known mechanisms of coexistence; and to determine whether species may sometimes coexist with ATAs but not without, or vice versa. This is to help illuminate whether ATA contributions to coexistence and biodiversity maintenance are likely to be negligible or meaningfully large. G3) We will provide an empirical example of species coexistence which highlights the role ATAs can play and the potential importance of ATAs relative to other mechanisms of coexistence. The example is a diatom system in a chemostat. In the Discussion, we consider whether climate change may alter ATAs of environmental variables and thereby influence competition and coexistence. Overall, our study presents a new mechanism of species coexistence and a means of understanding its theoretical and empirical importance.

2 Theory

We here pursue goal G1 from the Introduction: to augment MCT to show formally how ATAs play a role in coexistence.

2.1 Theoretical setup

We develop our new theory for a general two-species model, later applying it to specific scenarios. Our mathematical notation parallels that of Ellner *et al.* (2016, 2019). It is assumed that the growth rate

123 $r_i(t) = \ln(N_i(t+1)/N_i(t))$ of species i can be written as an increasing function of an environment-
 124 dependent factor $E_i(t)$ and as a decreasing function of a quantity representing competitive pressure on
 125 species i , $C_i(t)$, i.e., $r_i(E_i, C_i)$. We also assume, for simplicity, that the $E_i(t)$ are iid through time, and
 126 likewise for the $C_i(t)$. Though the iid assumption is not necessary, it simplifies the presentation of new
 127 ideas.

128 2.2 The storage effect

129 MCT and its recent computational extensions (Ellner *et al.*, 2016, 2019) quantify the contributions of
 130 multiple mechanisms to coexistence. But we show below that, for purely temporal variation, only one
 131 mechanism relates to tail associations: storage effects. So we begin by defining storage effects. The
 132 storage effect for species i is the contribution of covariation between E and C to a difference between rare
 133 and common species mean growth rates, when i is rare. Specifically, storage effects for species i are

$$\Delta_i^{(EC)} = (\bar{r}_{i|i} - q_{ij}\bar{r}_{j|i}) - (\bar{r}_{i|i}^\# - q_{ij}\bar{r}_{j|i}^\#), \quad (2)$$

134 where: $\bar{r}_{i|i}$ refers to the mean “growth when rare” (GWR) of species i , that is, the mean growth rate
 135 of species i when it is at negligible abundance and species j (the other species) is at stochastic steady
 136 state; $\bar{r}_{j|i}$ refers to the mean steady-state growth rate of species j when species i is absent or at negligible
 137 abundance (this is 0, *a priori*); and $\bar{r}_{i|i}^\#$ and $\bar{r}_{j|i}^\#$ are analogous quantities, but for an alternative modelling
 138 scenario, identical except that influences of environment and competition on either species have been
 139 rendered independent. A subscript $i|i$ always indicates a quantity computed for species i when that species
 140 is at negligible abundance, and a subscript $j|i$ indicates a quantity computed for j when i is absent. The
 141 *scaling factor* q_{ij} measures the relative sensitivities to competition of the two species. See Chesson (1994),
 142 Ellner *et al.* (2016) and SI section S1 for the two alternative definitions of q_{ij} that we use, but one definition
 143 is $q_{ij} = 1$, and to understand the new ideas presented here it is sufficient to use that definition. Since it
 144 was assumed that $r_i = r_i(E_i, C_i)$, we can write $\bar{r}_{i|i} = \mathbb{E}[r_i(E_i, C_{i|i})]$, where $\mathbb{E}(\cdot)$ denotes expected value
 145 just as does an overbar, but we use \mathbb{E} for longer expressions. Also, $\bar{r}_{j|i} = \mathbb{E}[r_j(E_j, C_{j|i})]$. An expression
 146 for $\bar{r}_{i|i}^\#$ is obtained from $\bar{r}_{i|i}$ by replacing the bivariate random variable $(E_i, C_{i|i})$ by a random variable
 147 with the same marginal distributions, but independent components, $(E_i^\#, C_{i|i}^\#)$, so $\bar{r}_{i|i}^\# = \mathbb{E}[r_i(E_i^\#, C_{i|i}^\#)]$.
 148 Likewise, $\bar{r}_{j|i}^\# = \mathbb{E}[r_j(E_j^\#, C_{j|i}^\#)]$.

149 2.3 Decomposing the storage effect

150 We now specify how to decompose storage effects into contributions due to ATAs and due to EC correlation
 151 *per se*. Storage effects for species i were computed by comparing differences between rare and common
 152 species mean growth rates for the original model and for a modified model for which the components
 153 of $(E_i, C_{i\setminus i})$ and those of $(E_j, C_{j\setminus i})$ were rendered independent of each other [see (2)]. Because these
 154 components were rendered completely independent in the modified model, storage effects quantify the
 155 contribution of the whole EC relationship, in all its aspects, to the rare/common species growth rate
 156 difference. But we can instead consider distributions $(E_i^{\parallel}, C_{i\setminus i}^{\parallel})$ and $(E_j^{\parallel}, C_{j\setminus i}^{\parallel})$ with the same marginal
 157 distributions, respectively, as $(E_i, C_{i\setminus i})$ and $(E_j, C_{j\setminus i})$, and with some but not all aspects of the relationship
 158 between the components altered relative to the original distributions. Specifically, asymmetries of tail
 159 association are removed – see SI section S2 for how this is done. We then define $\bar{r}_{i\setminus i}^{\parallel}$ and $\bar{r}_{j\setminus i}^{\parallel}$ based on a
 160 modified model using $(E_i^{\parallel}, C_{i\setminus i}^{\parallel})$ and $(E_j^{\parallel}, C_{j\setminus i}^{\parallel})$, and we consider the decomposition

$$\Delta_i^{(EC)} = [(\bar{r}_{i\setminus i} - q_{ij}\bar{r}_{j\setminus i}) - (\bar{r}_{i\setminus i}^{\parallel} - q_{ij}\bar{r}_{j\setminus i}^{\parallel})] + [(\bar{r}_{i\setminus i}^{\parallel} - q_{ij}\bar{r}_{j\setminus i}^{\parallel}) - (\bar{r}_{i\setminus i}^{\#} - q_{ij}\bar{r}_{j\setminus i}^{\#})] \quad (3)$$

$$= \Delta_i^{[EC]} + \Delta_i^{[E\parallel C]}. \quad (4)$$

161 The term $\Delta_i^{[EC]}$ is the component of storage effects due to ATAs between E_i and $C_{i\setminus i}$, and between E_j
 162 and $C_{j\setminus i}$. We will refer to this term as the *ATA effect on coexistence*. The term $\Delta_i^{[E\parallel C]}$ is the component
 163 of storage effects due to EC correlation *per se*, remaining after having removed the effects of ATAs. The
 164 notation \parallel was chosen because this new symbol is part of the symbol $\#$ (i.e., two of its four lines),
 165 corresponding to the removal of part of the relationship between E and C components (namely, ATAs).
 166 The new symbol should correspondingly be pronounced “partial sharp”. The brackets in $\Delta_i^{[E\parallel C]}$ and $\Delta_i^{[EC]}$
 167 are intended to indicate that (4) is a decomposition within a decomposition, i.e., (4) is a decomposition of
 168 storage effects, which are themselves a term in the MCT decomposition (Ellner *et al.*, 2019) – see below
 169 for additional details.

170 2.4 Our decomposition as an extention of modern coexistence theory

171 The other mechanisms in MCT that apply in our modelling context of purely temporal variation make
 172 no reference to covariation between quantities, whereas ATAs are strictly about covariation. Therefore,
 173 storage effects are the only mechanism of coexistence for which ATAs are relevant. Mathematical details
 174 supporting this claim are in SI section S3. Ellner *et al.* (2016) and Ellner *et al.* (2019) provide a decompo-
 175 sition of the coexistence metric $\bar{r}_{i\setminus i} - q_{ij}\bar{r}_{j\setminus i}$, which equals GWR of species i . The decomposition, which

we use below, is similar to and motivated by the original decomposition of Chesson (1994),

$$\bar{r}_{i \setminus i} - q_{ij} \bar{r}_{j \setminus i} = \Delta_i^0 + \Delta_i^E + \Delta_i^C + \Delta_i^{(E \# C)} + \Delta_i^{(EC)}, \quad (5)$$

where: Δ_i^0 is a baseline; Δ_i^E is a contribution to coexistence of environmental variation; Δ_i^C is a contribution to coexistence of variation in competition; $\Delta_i^{(E \# C)}$ is a contribution to coexistence of having simultaneous variation in both environment and competition, but not including the effects of covariation in these quantities; and $\Delta_i^{(EC)}$ is a contribution to coexistence of *EC* covariation itself – storage effects. Combining our decomposition (4) with the decomposition (5) of Ellner *et al.* (2019) gives

$$\bar{r}_{i \setminus i} - q_{ij} \bar{r}_{j \setminus i} = \Delta_i^0 + \Delta_i^E + \Delta_i^C + \Delta_i^{(E \# C)} + \Delta_i^{[E \parallel C]} + \Delta_i^{[EC]}, \quad (6)$$

which is the extension of MCT that was goal G1 of the Introduction.

2.5 ATA rescue and exclusion

To evaluate the importance of ATAs for a given scenario, one can quantify the magnitude of the new ATA effect term, $\Delta_i^{[EC]}$, relative to the magnitudes of the other terms for the scenario. One typically (but see below) must examine this quantity for each species, i , to obtain complete information about coexistence, since coexistence requires both species populations to be able to grow when rare. We also defined scenarios of “ATA rescue” and “ATA exclusion”. *ATA rescue* was considered to have occurred for a given scenario if coexistence was possible when ATAs were taken into account, i.e., $\text{GWR} > 0$ for both species, but impossible otherwise, i.e., the sum of the non-ATA terms in (6) was negative for at least one species. *ATA exclusion* was considered to have occurred if the species did not coexist when ATAs were taken into account, i.e., $\text{GWR} < 0$ for at least one species, but would have coexisted were it not for ATAs, i.e., the sum of the non-ATA terms in (6) was positive for both species.

3 Methods

3.1 Versions of the lottery model

To achieve goal G2 of the Introduction, we applied the framework of Theory to the lottery model, comparing the magnitude of the ATA effect on coexistence, $\Delta_i^{[EC]}$, to the magnitudes of the other terms of the decomposition (6) for various model parameterizations. We used two versions of the lottery model

which we now specify. The versions both used the same dynamical equations (Introduction) and assumed temporally independent and identically distributed (iid) fecundities, but the versions differed in the distributions of (B_1, B_2) used. Both distributions were based on transformations of the distributions (b_1, b_2) pictured in Fig. 1a-c; the details of how the left- (Fig. 1a), right- (Fig. 1c), and symmetrically (Fig. 1b) tail associated alternatives for (b_1, b_2) were generated are in SI section S4.

The *log-normal fecundities lottery model* used $B_i = \exp(\mu_i + \sigma b_i)$, and therefore had parameters σ , μ_1 and μ_2 in addition to the death rate parameter δ (Introduction) that both versions of the lottery model used. The parameter σ is the standard deviation of the log-fecundities and μ_i is the mean log fecundity for species i .

The *beta fecundities lottery model* used $B_i = \eta_i F_\beta^{-1} \circ \varphi(b_i)$, where φ is the CDF of the standard normal distribution and F_β is the CDF of a beta distribution with shape and scale parameters 0.5 (probability density function proportional to $x^{-0.5}(1-x)^{-0.5}$ on the unit interval). So the beta fecundities model had parameters η_1 , η_2 and δ , and produced fecundities with U -shaped distributions between 0 and η_1 , for B_1 , and η_2 , for B_2 . The mean fecundity for species i was $\eta_i/2$, and larger η_i also corresponded to more variable fecundities for species i . The parameter η_i represents the upper bound on what fecundities could occur for species i .

For both versions of the lottery model, fecundities were taken to directly reflect the environment, i.e., the E_i of Theory was set equal to B_i . Competition, $C_i(t)$, in the lottery model occurs at the stage of juveniles occupying open sites. For both model versions, C_i was therefore taken to be the number of new offspring divided by the number of open sites, $C_i(t) = (B_1(t)N_1(t) + B_2(t)N_2(t))/(\delta N)$, which does not depend on i . These choices for $E_i(t)$ and $C_i(t)$ fulfill the assumption of Theory that the growth rate, $r_i(t)$ is an increasing function of $E_i(t)$ and a decreasing function of $C_i(t)$ (see SI section S5 for details).

3.2 How results were plotted for goal G2

To explore, using the log-normal fecundities lottery model, the relative magnitudes of the contributions to coexistence that come from ATAs versus other mechanisms, we plotted the terms of the decomposition (6) for that model against the model parameters μ_1 , μ_2 , σ and δ . We labeled regions of the plot which corresponded to ATA rescue or exclusion, i.e., regions for which GWR and $\text{GWR-}\Delta_i^{[EC]}$ had opposite signs. Some mathematical shortcuts, summarized here, simplified plotting. First, we assumed, without loss of generality, that $\mu_1 \leq \mu_2$. To understand coexistence, it was then sufficient to decompose GWR of the weaker competitor, species 1. Second, we showed that, for the log-normal fecundities lottery model, none of the components of (6) depends independently on μ_1 and μ_2 ; instead they depend only on $\mu_1 - \mu_2$

(SI section S5). So we plotted against $\mu_1 - \mu_2$. Third, we showed that the values of all components in (6) were the same for both our left- and right-tail associated noises (SI section S5). So we only generated plots for left-tail associated noise.

For each combination of $\delta = 0.2, 0.4, 0.6$ and $\mu_1 - \mu_2 = 0, -0.5, -2, -4$, we plotted the components of (6) against σ for σ ranging from 0 to 7. Chesson & Warner (1981) showed that coexistence is impossible for $\delta = 1$, and it is known that the storage effect (and therefore its ATA component) is weak for larger δ , so we only considered values of δ up to 0.6. Some of the μ differences and σ values we considered were very unrealistic (see Results), so we considered after plotting whether conclusions about the importance of ATAs depended on realistic values of parameters. The simulation methods of Ellner *et al.* (2019) were used to compute the components of (6). Computationally efficient means of performing those simulations are in SI section S6.

To explore, using the beta fecundities lottery model, the relative magnitudes of the contributions to coexistence that come from ATAs versus other mechanisms, we plotted the terms of the decomposition (6) for that model against the model parameters η_1 , η_2 , and δ , again labelling regions corresponding to ATA rescue or exclusion. Some mathematical shortcuts, summarized here, simplified plotting. First, we assumed, without loss of generality, that $\eta_1 \leq \eta_2$. To understand coexistence, it was then sufficient to decompose GWR of the weaker competitor, species 1. Second, we showed that, for the beta fecundities lottery model, none of the components of (6) depends independently on η_1 and η_2 ; instead they depend only on η_2/η_1 (SI section S5). So we plotted against η_2/η_1 .

For each combination of $\delta = 0.2, 0.4, 0.6$ and for left- and right-tail associated noise, we plotted the components of (6) against the upper bound ratio η_2/η_1 , using the fairly realistic (see Results) range $1 \leq \eta_2/\eta_1 \leq 5$. The simulation methods of Ellner *et al.* (2019) were again used. Computationally efficient means of performing these simulations are in SI section S6.

3.3 Diatom chemostat system

To achieve goal G3 from the Introduction, i.e., to provide an empirical example of species coexistence which highlights the role ATAs can play, we used a laboratory chemostat system of freshwater diatoms explored by Descamps-Julien & Gonzalez (2005). Those authors used measurements of growth rates of *Fragilaria crotonensis* and *Cyclotella pseudostelligera* over a range of temperatures to parametrize a

258 resource competition model. The model is

$$\frac{dS}{dt} = D(S_0 - S) - Q_1 x_1 \frac{V_1 S}{K_1 + S} - Q_2 x_2 \frac{V_2 S}{K_2 + S} \quad (7)$$

$$\frac{dx_j}{dt} = x_j \frac{V_j S}{K_j + S} - D x_j, \quad (8)$$

259 for $j = 1, 2$, where S is an extracellular silicate concentration in the chemostat, x_1 is the population
 260 density of *F. crotonensis* and x_2 is that of *C. pseudostelligera*, D is the chemostat outflow rate, S_0 is
 261 concentration of silicates in the chemostat inflow, the Q_j are amounts of silicate per cell, the V_j are
 262 maximum population growth rates, and the K_j are half-saturation constants for the dependence of growth
 263 rates on nutrient concentration. The temperature-dependent parameters Q_j , V_j , and K_j were obtained
 264 by Descamps-Julien & Gonzalez (2005) through batch experiments and curve fitting or interpolation.
 265 Descamps-Julien & Gonzalez (2005) showed that permanent coexistence of the two species occurs when
 266 temperature fluctuates periodically, $\theta(t) = \theta_0 + a \sin(2\pi t/P)$, with parameters $\theta_0 = 18^\circ\text{C}$, $a = 6^\circ\text{C}$,
 267 $P = 60\text{d}$. Ellner *et al.* (2016, 2019) broke down coexistence into contributing mechanisms according to (5)
 268 for these same values of θ_0 , a and P . We further decompose coexistence according to (6), and we do so for
 269 ranges of values of θ_0 , a and P . In contrast to the lottery model case, for which simplifying assumptions
 270 made it sufficient to decompose only the GWR of species 1, for this example we considered $\bar{r}_{i \setminus i} - q_{ij} \bar{r}_{j \setminus i}$
 271 for both $i = 1, j = 2$ and for $i = 2, j = 1$. Further details of the model setup are in SI section S7 and
 272 specifics of how our decomposition extends to this empirical case are in SI section S8.

273 3.4 How results were plotted for goal G3

274 To display results for goal G3, we started by plotting the terms of (6) against one of the parameters θ_0 ,
 275 a and P at a time, while keeping the other two fixed at the values used by Descamps-Julien & Gonzalez
 276 (2005). We again labelled regions of parameter space corresponding to ATA rescue or exclusion.

277 We also generated two-dimensional plots, where two of the parameters θ_0 , a and P were varied and the
 278 third was kept fixed at the value used by Descamps-Julien & Gonzalez (2005). For the two-dimensional
 279 plots, the quantity $\Delta_i^{[EC]}/|\text{GWR}|$ was displayed using color, to convey the importance of the ATA con-
 280 tribution relative to the whole GWR. Larger magnitudes of this quantity indicate greater importance of
 281 ATAs. The case $\Delta_i^{[EC]} > \text{GWR} > 0$ (which produces $\Delta_i^{[EC]}/|\text{GWR}| > 1$) corresponds to ATA rescue, and
 282 the case $\Delta_i^{[EC]} < \text{GWR} < 0$ (which produces $\Delta_i^{[EC]}/|\text{GWR}| < -1$) corresponds to ATA exclusion. Thus
 283 the value of $\Delta_i^{[EC]}/|\text{GWR}|$ indicates the importance of ATAs and also whether ATA rescue or exclusion
 284 occurred.

285 All computations were done in R on a laptop running Ubuntu Linux. Complete computer codes for
286 the project are stored at (link to be added).

287 4 Results

288 4.1 Goal G2, lottery model results

289 To begin fulfilling goal G2 of the Introduction (to explore, using the lottery model, the relative magnitudes
290 of the contributions to coexistence that come from ATAs compared to other mechanisms; and to see if ATA
291 rescue or ATA exclusion can occur), Fig. 2 shows that, for the log-normal fecundities lottery model, the
292 ATA term of (6) sometimes, but not always, has magnitude comparable to the magnitudes of other terms
293 of the extended MCT decomposition. Magnitudes of $\Delta_i^{[EC]}$ tended to be larger, relative to the magnitudes
294 of the other terms of (6), for smaller-magnitude differences between μ_1 and μ_2 , i.e., for closer-to-equal
295 competitors. In the $\mu_1 = \mu_2$ case (panels a-c), for which the two species were equal competitors, storage
296 effects ($\Delta_i^{[EC]} + \Delta_i^{[E|C]}$) were the only means by which coexistence could occur, and ATA effects tended
297 to be negative, weakening total storage effects.

298 The ATA term was also often, or always (for the parameters we considered), comparable in magnitude
299 to the other terms of the decomposition (6) for the beta fecundities lottery model (Fig. 3). The term
300 contributed negatively to coexistence for environmental noise/fecundities showing left-tailed association,
301 and contributed positively for noise/fecundities showing right-tailed association.

302 Our results also show that ATAs can make the difference between coexistence and failure of two species
303 to coexist: both “ATA rescue” and “ATA exclusion” (see Theory) are possible. Starting with the log-normal
304 fecundities lottery model, for some of the panels on Fig. 2, the GWR line falls between the ATA line and
305 the x axis for some values of σ , e.g., see panel i. Such cases correspond to parameter combinations for
306 which the presence or absence of ATAs determine whether the species coexist or not. In the case of panel
307 i, for values of σ around 6, species 1 is excluded with ATAs but the two species can coexist without
308 ATAs. Fig. 3 highlights additional examples using the beta fecundities lottery model; examples were more
309 common than for the log-normal fecundities model.

310 For the log-normal fecundities lottery model, the ATA term from (6) tended only to be comparable in
311 magnitude to the other terms, and ATA exclusion or rescue tended only to occur, for unrealistic parameter
312 values; but ATA terms were large and ATA rescue and exclusion occurred for many realistic parameter
313 values for the beta fecundities lottery model. For instance, the ATA term in Fig. 2 had fairly small
314 magnitude, compared to the other terms of (6), for values of σ less than about 3. And ATA rescue and

315 exclusion only occurred for σ greater than about 3. The standard deviation of fecundity for species 1 when
 316 $\mu_1 = 0$ and $\sigma = 3$ was greater than 8000, so values of σ greater than 3 are probably unrealistic. Thus
 317 ATAs seem to be unimportant for coexistence for the log-normal fecundities lottery model with realistic
 318 parameter values. However, all the η_2/η_1 ratio values we plotted were fairly realistic, corresponding to
 319 upper-bound fecundities that were up to 5 times higher for species 2 than for species 1. And the ATA
 320 term plotted in Fig. 3 was comparable in magnitude to the other components of (6) across the whole
 321 range of parameters considered. And both ATA rescue and exclusion occurred for values of η_2/η_1 between
 322 1 and 2. Apparently the question of whether ATAs are important for realistic parameter values depends
 323 on specifics.

324 4.2 Goal G3, results for the diatom system

325 Starting to fulfill goal G3 of the Introduction (to provide an empirical example of species coexistence
 326 which highlights the role ATAs can play), Fig. 4a-c show that ATA contributions to coexistence often
 327 have magnitudes comparable to the magnitudes of other terms of the extended MCT decomposition, and
 328 that ATA rescue occurs for some combinations of parameters for this system.

329 Plotting against two parameters at a time, Fig. 4d-f reinforce the same conclusions. The plotted
 330 quantity $\Delta_i^{[EC]}/|\text{GWR}|$ was often large, indicating that ATAs were often a substantial contributor to
 331 whether the diatom species coexist. For instance, well over half the area of Fig. 4f showed values of
 332 $\Delta_i^{[EC]}/|\text{GWR}|$ bigger than 1/4, with large portions of Fig. 4d-e satisfying the same criterion. Substantial
 333 portions of panels d-f also show values of $\Delta_i^{[EC]}/|\text{GWR}|$ bigger than 1, corresponding to ATA rescue. ATA
 334 exclusion did not occur for this system for the parameter ranges we considered.

335 5 Discussion

336 We produced and applied a new extension of modern coexistence theory (MCT) that quantifies the impact
 337 of asymmetric tail associations (ATAs) on species coexistence. Building upon a recent, simulation-based
 338 approach to MCT (Ellner *et al.*, 2016, 2019), we decomposed storage effects into two new mechanisms,
 339 the contribution of ATAs to coexistence, and the contribution of *EC* correlation *per se*. Applications of
 340 our extended theory to the lottery model and to a laboratory diatom system demonstrated that ATA
 341 contributions to storage effects and to species coexistence can often be comparable in magnitude to the
 342 contributions of previously recognized mechanisms. Our results add coexistence and biodiversity main-
 343 tenance to the list of ecological theories and phenomena on which ATAs have been shown to have an

important impact (Ghosh *et al.*, 2020a,c,b, 2021). Though storage effects are typically described as the contribution of *EC covariance* to coexistence (Chesson *et al.*, 2012; Ellner *et al.*, 2016, 2019), our results suggest that storage effects should be redefined to constitute the contribution of *associations* between E and C , generally, including both ATA effects and correlation *per se*. The prior terminology, *covariance*, is typically construed as reflecting the linear relationship between variables, ignoring complexities of the association, such as ATAs, which we now know can be important. ATAs contributions to coexistence were less important than other mechanisms in some contexts (the log-normal fecundities lottery model), but were very important in other contexts (the beta fecundities lottery model), including our empirically based example (the diatom system). Though future work should seek to understand precisely when ATAs are or are not important for coexistence, our work demonstrates the overall importance of this new mechanism.

Contributions of ATAs to species coexistence open the possibility that “ATA specialists” may exist. For instance, if a strong competitor is present across a collection of habitat patches on a landscape and the GWR of a weaker competitor is only positive in a patch if there are ATAs between the temporal fluctuations of two environmental variables in that patch, then the weaker competitor can only persist in patches for which ATAs are present. The weaker competitor can therefore perhaps be regarded as an “ATA specialist” in the landscape. EC-associations can boil down to associations between two environmental variables, as was the case for the lottery model. For the lottery model, $B_i(t) = E_i(t)$ was assumed, and $C_{i \setminus i}$ simplified to $E_j(t)/\delta$ (see SI section S5.1). Thus, EC-associations parallel associations between the two environmental variables $E_i(t)$ and $E_j(t)$ for the lottery model, and ATA specialists may exist. Mechanisms of coexistence should correspond to means by which niche differentiation is possible. Thinking about our new mechanism of coexistence in terms of possible ATA specialists helps highlight this connection. Likewise, because we have described ATA exclusion as well as ATA rescue, it is possible to imagine a scenario in which a weaker competitor can only exist in habitat patches for which ATAs between environmental variables are absent, and is hence a specialist on scenarios with symmetric tail associations of variables (an “STA specialist”). Additional research will be needed to assess to what degree these possibilities are realized in nature.

An additional motivation for quantifying the importance of ATAs for species coexistence is that there is reason to believe climate change may alter ATAs of environmental variables which impact coexistence, as follows. It is well known that climate change can alter the intensity of extreme environmental events, including heat waves, floods, hurricanes and fires (Meehl & Tebaldi, 2004; Jentsch *et al.*, 2007; Ummenhofer & Meehl, 2017; Lyon *et al.*, 2019; Keelings & Moradkhani, 2020). If extreme events are not only becoming more intense, but are also increasing in duration (e.g., heat waves are not only hotter but also last longer, Meehl & Tebaldi, 2004; Lyon *et al.*, 2019; Keelings & Moradkhani, 2020), then the nature of the

376 covariation between phenologically separated environmental signals may be modified by these changes;
 377 in particular, ATAs between such variables may be altered. For instance, imagine a case in which early
 378 spring temperature influences the growth of a plant species, A, whereas late spring temperature influences
 379 plant species B. If these species are competitors, then EC covariation contributing to their coexistence,
 380 or failure to coexist, could boil down to covariation between early and late spring temperatures (e.g., if
 381 competitive dynamics are governed by the lottery model with E_i representing early spring temperature
 382 and E_j representing late spring temperature, see previous paragraph). Because longer lasting heat waves
 383 are more likely to contribute to both early and late spring temperature, a tendency for heat waves to
 384 become both more extreme and longer lasting increases the degree of right-tail association between early
 385 and late spring temperature. Likewise, a tendency for cold snaps to become both more intense (i.e.,
 386 colder temperatures) and longer lasting can increase left-tail association between early- and late-spring
 387 temperatures. As we showed in this study, changes in ATAs can then result in different competitive
 388 outcomes between species. To our knowledge, the potential importance of climatic changes in ATAs for
 389 species coexistence has not been studied, though the importance for coexistence of changes in means and
 390 variability of environmental variables has been studied in many systems [e.g., White *et al.* (2001); Adler
 391 *et al.* (2006); Jentsch *et al.* (2007); Angert *et al.* (2009); di Paola *et al.* (2012); Descombes *et al.* (2020);
 392 Usinowicz & Levine (2021)]. Changes in variability and in extreme events are distinct from the changes in
 393 ATAs we consider here, because ATAs pertain to *relationships* between environmental and other variables
 394 in the extremes, which are distinct from and can be altered independently of changes in the extremes of
 395 the univariate marginal distributions themselves (Nelsen, 2006; Ghosh *et al.*, 2020a).

396 Our approach to exploring the influence of ATAs on coexistence relies on the computational extension
 397 of the MCT of Ellner *et al.* (2019), and our results help demonstrate strengths of that approach. Storage
 398 effects as computed using the original, analytic approach to MCT (Chesson, 1994, 2000) should equal our
 399 term $\Delta^{[E||C]}$, which we refer to as the contributions to coexistence of correlation *per se*. This is because
 400 the weak-noise/Taylor approximation approach used in the original MCT neglects the effects of ATAs
 401 when higher-order terms in Taylor expansions are dropped. The term $\Delta^{(E\#C)}$, which our theory inherits
 402 from Ellner *et al.* (2016), is also dropped. These observations do not diminish the major strengths of the
 403 original, analytic approach, which are well known and also elaborated by Ellner *et al.* (2019); one such
 404 strength is the generality that analytic approaches provide. It may be possible to expand the mathematics
 405 of the original MCT to consider ATAs. Additional discussion points are in SI sections S9-S10.

406 It seems reasonable to suppose that ATAs will play an increasingly important role in systems of greater
 407 complexity because such systems have more pairs of temporally variable quantities that may exhibit

asymmetries of association. Our prior work shows that ATAs are common in ecological and environmental variables (Ghosh *et al.*, 2020a). We have here used simple mathematical and laboratory models to provide an initial exploration of the potential importance of ATAs for coexistence. Future work should attempt to generalize lessons learned here to field systems with multiple species, stage structure, spatial extent, non-competitive interactions such as predation and facilitation that can also mediate coexistence, and other complexities.

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Table 1: Summary of frequently used notation and abbreviations.

Notation	Meaning
General	
ATA	Asymmetric tail associations
MCT	Modern coexistence theory
GWR	Growth rate when rare
E, C	Environment, competition
\mathbb{E}	Expected value
ATA rescue	Coexistence occurs, but not after ATA effects are removed
ATA exclusion	Coexistence does not occur, but does after ATA effects are removed
Lottery model	
$N_i(t)$	Population density of species i , time t
N	$N_1(t) + N_2(t)$
$B_i(t)$	Fecundity of species i , time t
δ	Mortality rate
σ	Standard deviation of log fecundities for the log-normal fecundities model
μ_i	Mean log fecundity, species i , log-normal fecundities model
η_i	Upper bound fecundity, species i , log-normal fecundities model
Theory	
$r_i(t)$	Species i growth rate, $\ln(N_i(t+1)/N_i(t))$
$E_i(t)$	Environment experienced by the i^{th} species
$C_i(t)$	Competition experienced by the i^{th} species
$\bar{r}_{i \setminus i}$	Mean GWR of species i
$\bar{r}_{j \setminus i}$	Mean growth of j when i is absent
$i \setminus i$	As subscript, refers to computing a quantity for i when i is rare
$j \setminus i$	As subscript, refers to computing a quantity for j when i is absent
$\#$	As superscript, refers to computing a quantity after rendering E and C independent
\parallel	As superscript, refers to computing a quantity after removing ATAs between E and C
q_{ij}	Scaling factor
$\Delta_i^{(EC)}$	Storage effects, species i
$\Delta_i^{[EC]}$	ATA effect to coexistence, species i
$\Delta_i^{[E C]}$	Component of storage effects due to EC correlation <i>per se</i> , species i
Diatom chemostat system	
S	Extracellular silicate concentration
x_1	Population density of <i>F. crotonensis</i>
x_2	Population density of <i>C. pseudostelligera</i>
Θ	Temperature
Θ_0	Average temperature
a	Amplitude of temperature fluctuations
P	Period of temperature fluctuations

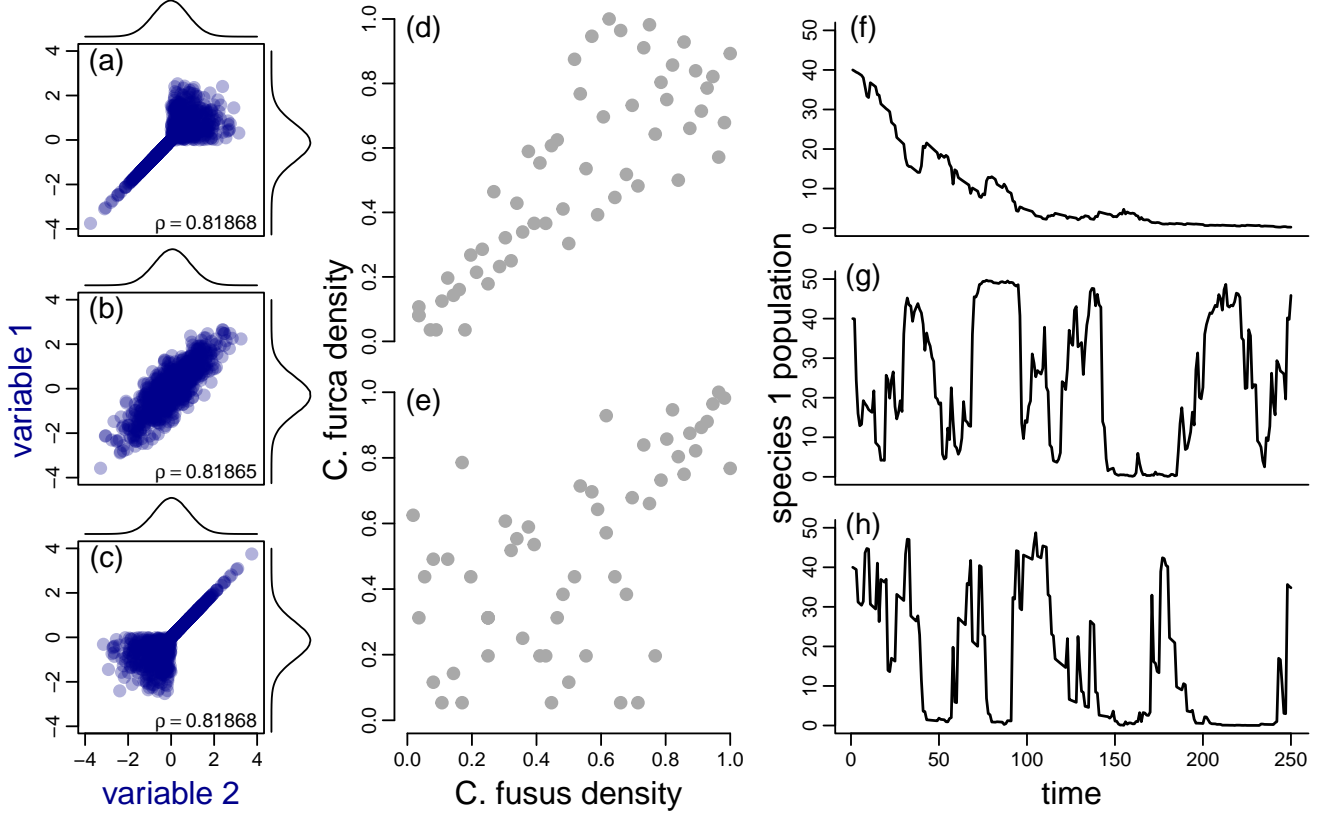


Figure 1: Examples motivating our study of the effects of asymmetric tail associations (ATAs) on competition and coexistence. (a-c) Bivariate random variables with standard normal marginals showing alternative patterns of association in the left and right parts of the distributions. The two variables in (a) are more strongly related to each other in the left parts of the distributions, termed “left-tail association;” those in (b) are symmetrically associated; and those in (c) are more strongly related to each other in the right parts, termed “right-tail association”. All three cases have the same Pearson correlation, ρ , up to sampling variation, so Pearson correlation does not identify these very different patterns of association. For (a, c), we used asymmetrically tail associated cases which are perfectly correlated in the lower or upper halves of the distributions, though it is also possible to generate asymmetrically tail associated noise with imperfect correlations in both halves of the distributions [Nelsen, 2006; Ghosh *et al.*, 2020a; see also (d,e)]. The variables (B_1, B_2) described in the Introduction and Methods were obtained by generating noise as pictured and then transforming the marginals as specified in Methods. (d,e) Two examples of ATAs found in nature. Axes are population densities of two plankton species, *Ceratium fusus* and *Ceratium furca*, sampled in successive years in two of the 15 locations in the North Sea considered by (Ghosh *et al.*, 2020b). ATAs differed by location, with (d) showing left-tail association and (e) showing right-tail association. (f-h) Lottery model population simulations using (B_1, B_2) obtained by transforming the respectively corresponding variables (a-c; see Introduction).

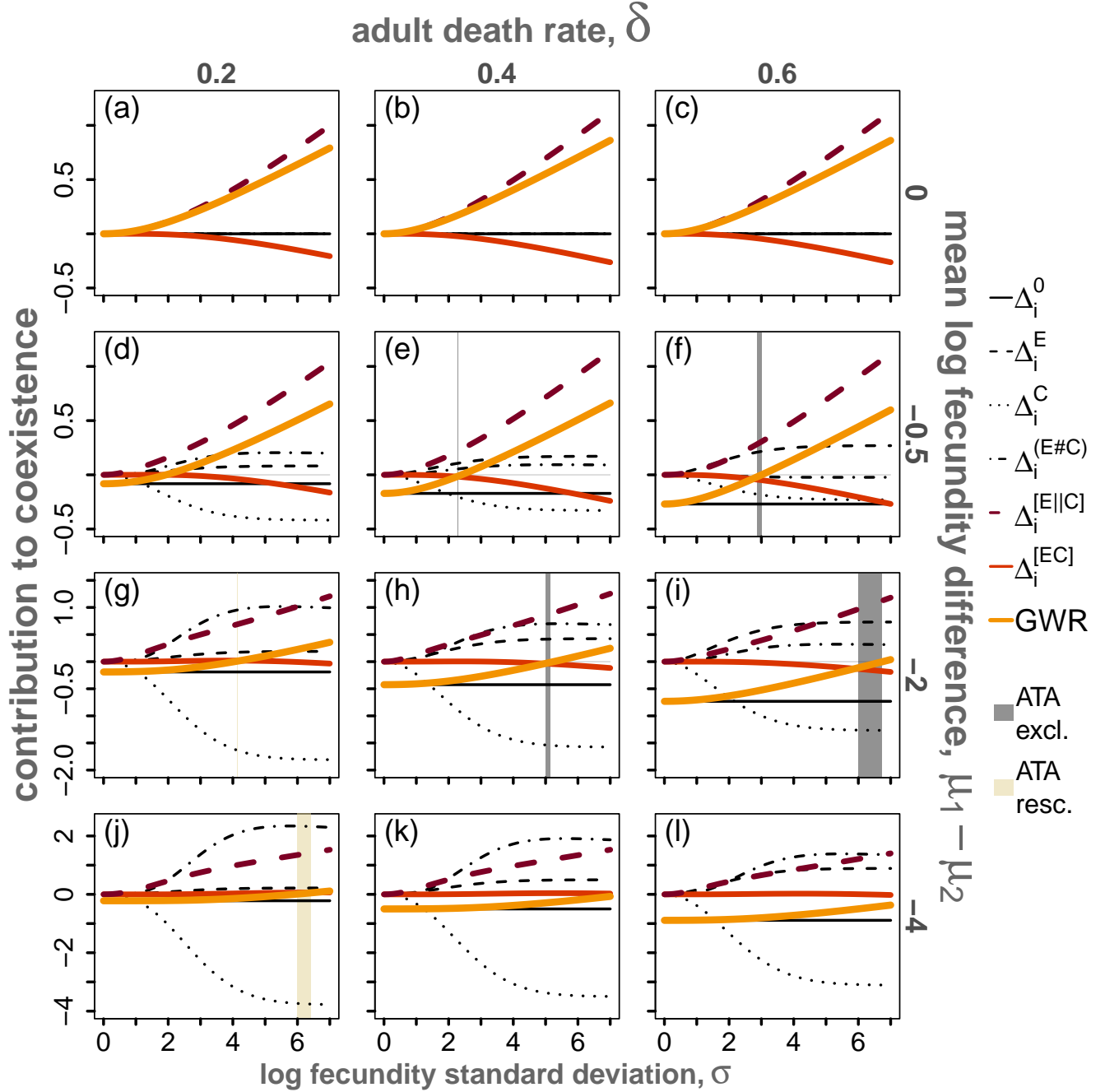


Figure 2: The contribution of ATAs to species coexistence was sometimes, but not always, meaningfully large compared to other components of the MCT decomposition for the log-normal fecundities lottery model. All panels show GWR and the decomposition of GWR provided by the extended MCT, equation (6). For each panel, δ and $\mu_1 - \mu_2$ are fixed at values specified in the margins, and GWR and components of the decomposition are plotted against σ . The contribution of ATAs ($\Delta_i^{[EC]}$) sometimes, but not always, has magnitude comparable to other components, indicating that ATAs can contribute meaningfully to species coexistence or failure to coexist. In some instances, the GWR line falls between the ATA line and the x axis, indicating that, for those parameter values, ATAs make the difference between species coexistence and exclusion of the weaker competitor. These instances, which are shaded, correspond to ATA rescue or exclusion (Theory). Standard errors of plotted quantities were never greater than 0.00641, so are not displayed. This plot uses $q_{ij} = 1$. An analogous plot (SI Fig. S2) uses $q_{ij} = \exp(\mu_i)/[(1 - \delta) \exp(\mu_j) + \delta \exp(\mu_i)]$; though results differed in detail, main conclusions were the same.

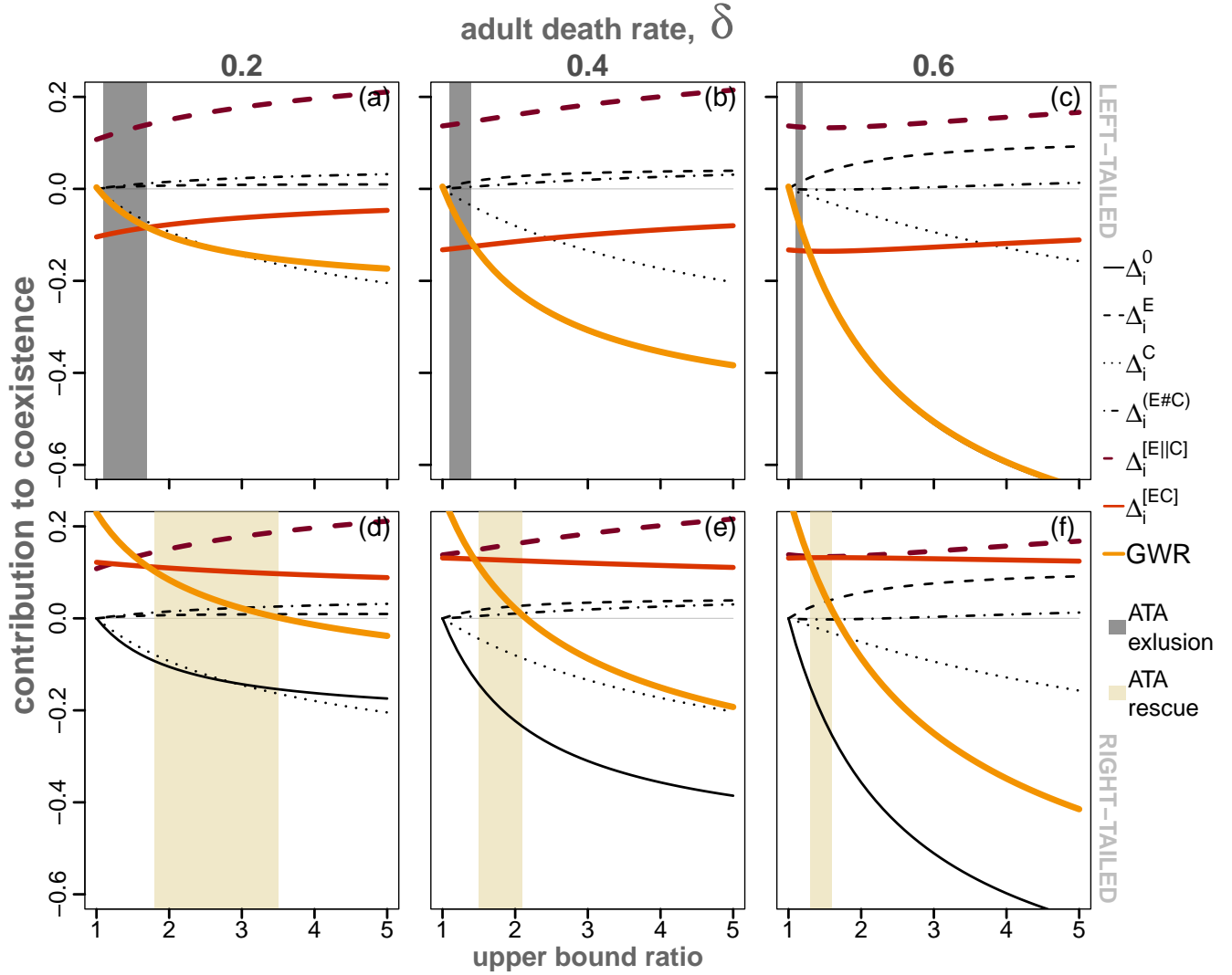


Figure 3: The contribution of ATAs to species coexistence was often meaningfully large compared to other components of the MCT decomposition for the beta fecundities lottery model. All panels show GWR and the decomposition of GWR provided by the extended MCT, equation (6). For each panel, δ is fixed at the value specified in the upper margin, and GWR and components of the decomposition are plotted against the upper bound ratio, η_2/η_1 . The contribution of ATAs ($\Delta_i^{[EC]}$) frequently has magnitude comparable to other components, indicating that ATAs can contribute meaningfully to species coexistence or failure to coexist. In some instances, the GWR line falls between the ATA line and the x axis, indicating that, for those parameter values, ATAs make the difference between species coexistence and exclusion of the weaker competitor. These instances, which are shaded, correspond to ATA rescue or exclusion (Theory). Standard errors of plotted quantities were never greater than 0.00145, so are not displayed. This plot uses $q_{ij} = 1$. An analogous plot (SI Fig. S3) uses $q_{ij} = \eta_i/(\eta_j(1 - \delta) + \eta_i\delta)$; though results differed in detail, main conclusions were the same.

499 Figure 4. ATA effects and ATA rescue in the diatom system. The contribution of ATAs to the GWR
 500 of *F. crotonensis* in the diatom system of Descamps-Julien & Gonzalez (2005) was often meaningfully
 501 large compared to other components of the MCT decomposition (a-c). Panels a-c show GWR and the
 502 decomposition of GWR provided by the extended MCT, equation (6). For each panel, two of the three
 503 parameters defining the temperature oscillation (the amplitude, a ; period, P ; and mean, θ_0 ; see Methods)
 504 were fixed at the values used by Descamps-Julien & Gonzalez (2005) ($a = 6^\circ\text{C}$, $P = 60\text{d}$, $\theta_0 = 18^\circ\text{C}$),
 505 and GWR and components of the MCT decomposition were plotted against the third parameter. The
 506 original values of the varying parameters are indicated by vertical dotted lines. ATA contributions ($\Delta_i^{[EC]}$)
 507 had magnitude comparable to other components, indicating that ATAs can contribute meaningfully to
 508 coexistence in this system. In some instances, the GWR line falls between the ATA line and the horizontal
 509 axis, indicating that, for those parameter values, ATA rescue occurs. Standard errors of plotted quantities
 510 were always less than $4\text{e-}05$, so are not shown. Panels d-f show bivariate plots (Methods) for which the
 511 third parameter was fixed at the values used by Descamps-Julien & Gonzalez (2005). ATAs are again
 512 often an important factor helping determine coexistence or exclusion, and ATA rescue happened for an
 513 appreciable fraction of the explored parameter space. For the parameters we considered, GWR of the
 514 other diatom species in the system, *C. pseudostelligera*, was always positive both including and excluding
 515 the effects of ATAs, so GWR for *F. crotonensis*, decomposed here, is a sufficient coexistence metric.