

Asymmetric relationships and their effects on coexistence

Pimsupa Albert¹ and Daniel Reuman¹

¹University of Kansas

May 30, 2023

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.

Asymmetric relationships and their effects on coexistence

Pimsupa Jasmin Albert^{a,b} and Daniel C. Reuman^{a,c,*}

^aDepartment of Ecology and Evolutionary Biology and Center for Ecological Research,
University of Kansas

^bEnvironmental Studies Program and Department of Biology, University of Oregon

^cLaboratory of Populations, Rockefeller University

*Corresponding author, reuman@ku.edu

Running head: Asymmetric relationships and coexistence

Key words: asymmetric tail association, biodiversity, coexistence, competition, copula, modern coexistence theory, niche differentiation, storage effects

Type of article: Letter

Words in Abstract: 150; **Words in main text:** 5013; **Words in text boxes:** 0

Number of references: 37; **Number of figures:** 4; **Number of tables:** 1; **Number of text boxes:** 0

Corresponding author: Daniel C. Reuman, Department of Ecology and Evolutionary Biology, University of Kansas, 2101 Constant Ave, Lawrence, KS 66047; Phone: 626-560-7084

Author emails: pimsupaa@uoregon.edu, reuman@ku.edu

Statement of Authorship: The authors jointly carried out all parts of the study.

Data accessibility statement: All codes associated with this study will be released in a Zenodo repository prior to publication.

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.

33 1 Introduction

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

54 Competition, coexistence, and the maintenance of biodiversity are research topics at the core of modern
55 ecology (MacArthur, 1958; Hutchinson, 1961; Schmid & Ellner, 1984). The competitive exclusion princi-
56 ple states that two species competing for the same limiting resource cannot coexist at constant densities
57 - one will instead outcompete the other and drive it extinct (Hardin, 1960). Modern coexistence theory
58 [MCT; Chesson (1994, 2000); Barabas *et al.* (2018)] is a framework for understanding how species never-
59 theless coexist, and biodiversity is maintained, in real ecosystems, through the niche partitioning effects
60 of environmental variation. MCT breaks down coexistence into the contributions of various mechanisms,
61 with names such as “relative nonlinearity in competition” and “storage effects” (Chesson, 1994) which will
62 be familiar to many readers. MCT has been applied to several systems, including annual (Angert *et al.*,
63 2009; Hallett *et al.*, 2019) and perennial plants (Adler *et al.*, 2006, 2010), tropical trees (Usinowicz *et al.*,

64 2012), plankton (Cáceres, 1997; Descamps-Julien & Gonzalez, 2005; Narawani *et al.*, 2013), and corals
65 (Álvarez-Noriega *et al.*, 2020). Although MCT is somewhat mathematically complex, recent extensions
66 make it more accessible (Ellner *et al.*, 2016, 2019).

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

84 To further demonstrate the plausibility of ATAs altering coexistence between species, we carried out
85 simple simulations using a two-species model, the well-known lottery model. The simulations described in
86 this paragraph are sufficient to demonstrate that ATAs influence coexistence in some manner; the precise
87 nature of that influence is the subject of the rest of the paper. The lottery model, which was originally
88 introduced as a model of coral reef fish competing for a set of N breeding territories, is as follows. Letting
89 $N_i(t)$ denote the adult population density of species $i = 1, 2$ at time t , and defining $N = N_1(t) + N_2(t)$,
90 model equations are

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

91 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
92 postulates that adults die at rate δ at each time step, and are replaced by juveniles in proportion to the
93 reproductive outputs of the two species that year. Note that N is constant through time. Notation for the

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

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

117 **2 Theory**

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

120 **2.1 Theoretical setup**

121 We develop our new theory for a general two-species model, later applying it to specific scenarios. Our
122 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

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

134 where: $\bar{r}_{i\setminus i}$ 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; $\bar{r}_{j\setminus i}$ 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 $\bar{r}_{i\setminus i}^\#$ and $\bar{r}_{j\setminus i}^\#$ 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 $i\setminus i$ always indicates a quantity computed for species i when that species
 140 is at negligible abundance, and a subscript $j\setminus i$ 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 $\bar{r}_{i\setminus i} = \mathbb{E}[r_i(E_i, C_{i\setminus i})]$, where $\mathbb{E}(\cdot)$ denotes expected value
 145 just as does an overbar, but we use \mathbb{E} for longer expressions. Also, $\bar{r}_{j\setminus i} = \mathbb{E}[r_j(E_j, C_{j\setminus i})]$. An expression
 146 for $\bar{r}_{i\setminus i}^\#$ is obtained from $\bar{r}_{i\setminus i}$ by replacing the bivariate random variable $(E_i, C_{i\setminus i})$ by a random variable
 147 with the same marginal distributions, but independent components, $(E_i^\#, C_{i\setminus i}^\#)$, so $\bar{r}_{i\setminus i}^\# = \mathbb{E}[r_i(E_i^\#, C_{i\setminus i}^\#)]$.
 148 Likewise, $\bar{r}_{j\setminus i}^\# = \mathbb{E}[r_j(E_j^\#, C_{j\setminus i}^\#)]$.

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

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

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

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

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

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

183 2.5 ATA rescue and exclusion

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

194 3 Methods

195 3.1 Versions of the lottery model

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

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

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

208 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
 209 distribution and F_β is the CDF of a beta distribution with shape and scale parameters 0.5 (probability
 210 density function proportional to $x^{-0.5}(1-x)^{-0.5}$ on the unit interval). So the beta fecundities model had
 211 parameters η_1 , η_2 and δ , and produced fecundities with *U*-shaped distributions between 0 and η_1 , for B_1 ,
 212 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
 213 fecundities for species i . The parameter η_i represents the upper bound on what fecundities could occur
 214 for species i .

215 For both versions of the lottery model, fecundities were taken to directly reflect the environment, i.e.,
 216 the E_i of Theory was set equal to B_i . Competition, $C_i(t)$, in the lottery model occurs at the stage of
 217 juveniles occupying open sites. For both model versions, C_i was therefore taken to be the number of new
 218 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
 219 depend on i . These choices for $E_i(t)$ and $C_i(t)$ fulfill the assumption of Theory that the growth rate, $r_i(t)$
 220 is an increasing function of $E_i(t)$ and a decreasing function of $C_i(t)$ (see SI section S5 for details).

221 3.2 How results were plotted for goal G2

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

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

233 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
234 (6) against σ for σ ranging from 0 to 7. Chesson & Warner (1981) showed that coexistence is impossible
235 for $\delta = 1$, and it is known that the storage effect (and therefore its ATA component) is weak for larger δ ,
236 so we only considered values of δ up to 0.6. Some of the μ differences and σ values we considered were
237 very unrealistic (see Results), so we considered after plotting whether conclusions about the importance
238 of ATAs depended on realistic values of parameters. The simulation methods of Ellner *et al.* (2019) were
239 used to compute the components of (6). Computationally efficient means of performing those simulations
240 are in SI section S6.

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

249 For each combination of $\delta = 0.2, 0.4, 0.6$ and for left- and right-tail associated noise, we plotted the
250 components of (6) against the upper bound ratio η_2/η_1 , using the fairly realistic (see Results) range
251 $1 \leq \eta_2/\eta_1 \leq 5$. The simulation methods of Ellner *et al.* (2019) were again used. Computationally efficient
252 means of performing these simulations are in SI section S6.

253 3.3 Diatom chemostat system

254 To achieve goal G3 from the Introduction, i.e., to provide an empirical example of species coexistence
255 which highlights the role ATAs can play, we used a laboratory chemostat system of freshwater diatoms
256 explored by Descamps-Julien & Gonzalez (2005). Those authors used measurements of growth rates
257 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

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

354 Contributions of ATAs to species coexistence open the possibility that “ATA specialists” may exist.
355 For instance, if a strong competitor is present across a collection of habitat patches on a landscape and the
356 GWR of a weaker competitor is only positive in a patch if there are ATAs between the temporal fluctuations
357 of two environmental variables in that patch, then the weaker competitor can only persist in patches for
358 which ATAs are present. The weaker competitor can therefore perhaps be regarded as an “ATA specialist”
359 in the landscape. EC-associations can boil down to associations between two environmental variables, as
360 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
361 $E_j(t)/\delta$ (see SI section S5.1). Thus, EC-associations parallel associations between the two environmental
362 variables $E_i(t)$ and $E_j(t)$ for the lottery model, and ATA specialists may exist. Mechanisms of coexistence
363 should correspond to means by which niche differentiation is possible. Thinking about our new mechanism
364 of coexistence in terms of possible ATA specialists helps highlight this connection. Likewise, because we
365 have described ATA exclusion as well as ATA rescue, it is possible to imagine a scenario in which a weaker
366 competitor can only exist in habitat patches for which ATAs between environmental variables are absent,
367 and is hence a specialist on scenarios with symmetric tail associations of variables (an “STA specialist”).
368 Additional research will be needed to assess to what degree these possibilities are realized in nature.

369 An additional motivation for quantifying the importance of ATAs for species coexistence is that there
370 is reason to believe climate change may alter ATAs of environmental variables which impact coexistence,
371 as follows. It is well known that climate change can alter the intensity of extreme environmental events,
372 including heat waves, floods, hurricanes and fires (Meehl & Tebaldi, 2004; Jentsch *et al.*, 2007; Ummenhofer
373 & Meehl, 2017; Lyon *et al.*, 2019; Keelings & Moradkhani, 2020). If extreme events are not only becoming
374 more intense, but are also increasing in duration (e.g., heat waves are not only hotter but also last
375 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

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

414 **6 Acknowledgments**

415 The authors thank Shyamolina Ghosh for suggesting the research problem, and Lawrence Sheppard, Max
416 Castorani, Jon Walter, Jude Kastens, Vadim Karatayev, Emily Arsenault, Jordan Rodriguez, Lauren
417 Hallett, and Robin Snyder for helpful discussions. The authors especially thank Steve Ellner for key advice
418 at several watershed moments in the development of the project. The authors were partly supported by
419 US National Science Foundation grants 1714195 and 2023474, the James S McDonnell Foundation, the
420 California Department of Fish and Wildlife Delta Science Program, and the Alexander von Humboldt
421 Foundation.

422 **References**

- 423 Adler, P., Ellner, S. & Levine, J. (2010). Coexistence of perennial plants: an embarrassment of niches.
424 *Ecology Letters*, 13, 1019–1029.
- 425 Adler, P., HilleRisLambers, J., Kyriakidis, P., Guan, Q. & Levine, J. (2006). Climate variability has a
426 stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences*,
427 103, 12793–12798.
- 428 Álvarez-Noriega, M., Madin, J., Baird, A., Dornelas, M. & Connolly, S. (2020). Disturbance-induced
429 changes in size-structure promote coral biodiversity. *bioRxiv*.
- 430 Anderson, M., de Valpine, P., Pennett, A. & Miller, A. (2019). A pathway for multivariate analysis of
431 ecological communities using copulas. *Ecology and Evolution*, 9, 3276–3294.
- 432 Angert, A., Huxman, T., Chesson, P. & Venable, D. (2009). Functional tradeoffs determine species
433 coexistence via the storage effect. *Proceedings of the National Academy of Sciences*, 106, 11641–11645.

- 434 Barabas, G., D'Andrea, R. & Stump, S. (2018). Chesson's coexistence theory. *Ecological Monographs*, 88,
435 277–303.
- 436 Cáceres, C. (1997). Temporal variation, dormancy, and coexistence: a field test of the storage effect.
437 *Proceeding of the National Academy of Sciences*, 94, 9171–9175.
- 438 Chesson, P. (1994). Multispecies competition in variable environments. *Theoretical Population Biology*,
439 45, 227–276.
- 440 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and*
441 *Systematics*, 31, 343–366.
- 442 Chesson, P., Huntly, N., Roxburg, S., Pantastico-Caldas, M. & Facelli, J. (2012). The storage effect:
443 definition and tests in two plant communities. In: *Temporal dynamics and ecological process*. Cambridge
444 University Press, pp. 11–40.
- 445 Chesson, P. & Warner, R. (1981). Environmental variability promotes coexistence in lottery competitive
446 systems. *The American Naturalist*, 117, 923–943.
- 447 de Valpine, P., Scranton, K., Knape, J., Ram, K. & Mills, N. (2014). The importance of individual
448 development variation in stage-structured population models. *Ecology Letters*, 17, 1026–1038.
- 449 Descamps-Julien, B. & Gonzalez, A. (2005). Stable coexistence in a fluctuating environment: An experi-
450 mental demonstration. *Ecology*, 86, 2815–2824.
- 451 Descombes, P., Pitteloud, C., Glauser, G., Defosse, E., Keergunteil, A., Allard, P., Rasmann, S. &
452 Pellissier, L. (2020). Novel trophic interactions under climate change promote alpine plant coexistence.
453 *Science*, 370, 1469–1473.
- 454 di Paola, A., Valentini, R. & Paparella, F. (2012). Climate change threatens coexistence within commu-
455 nities of mediterranean forested wetlands. *PLOS ONE*, 7, e44727.
- 456 Ellner, S., Snyder, R. & Adler, P. (2016). How to quantify the temporal storage effect using simulations
457 instead of math. *Ecology Letters*, 19, 1333–1342.
- 458 Ellner, S., Snyder, R., Adler, P. & Hooker, G. (2019). An expanded modern coexistence theory for empirical
459 applications. *Ecology Letters*, 22, 3–18.
- 460 Ghosh, S., Cottingham, K. & Reuman, D. (2021). Species relationships in the extremes and their influence
461 on community stability. *Philosophical Transactions of the Royal Society B*, 376, 20200343.

- 462 Ghosh, S., Sheppard, L., Holder, M., Loecke, T., Reid, P., Bever, J. & DC, R. (2020a). Copulas and their
463 potential for ecology. *Advances in Ecological Research*, 62, 409–468.
- 464 Ghosh, S., Sheppard, L., Reid, P. & Reuman, D. (2020b). A new approach to interspecific synchrony in
465 population ecology using tail association. *Ecology and Evolution*, 10, 12764–12776.
- 466 Ghosh, S., Sheppard, L. & Reuman, D. (2020c). Tail associations in ecological variables and their impact
467 on extinction risk. *Ecosphere*, 11.5, e03132.
- 468 Hallett, L., Shoemaker, L., White, C. & Suding, K. (2019). Rainfall variability maintains grass-forb species
469 coexistence. *Ecology Letters*, 22, 1658–1667.
- 470 Hardin, G. (1960). The competitive exclusion principle. *Science*, 131, 1292–1297.
- 471 Hutchinson, G. (1961). The paradox of the plankton. *The American Naturalist*, 95, 197–145.
- 472 Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007). A new generation of climate-change experiments:
473 events, not trends. *Frontiers in Ecology and the Environment*, 5, 365–374.
- 474 Keelings, D. & Moradkhani, H. (2020). Spatiotemporal evolution of heat wave severity and coverage across
475 the United States. *Geophysical Research Letters*, 47, e2020GL087097.
- 476 Lyon, B., Barnston, A., Coffel, E. & Horton, R. (2019). Projected increase in the spatial extent of
477 contiguous US summer heat waves and associated attributes. *Environmental Research Letters*, 14,
478 114029.
- 479 MacArthur, R. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*,
480 39, 599–619.
- 481 Meehl, G. & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st
482 century. *Science*, 305, 994–997.
- 483 Narawani, A., Alexandrou, M., Oakley, T., Carroll, I. & Cardinale, B. (2013). Experimental evidence that
484 evolutionary relatedness does not effect the ecological mechanisms of coexistence in freshwater algae.
485 *Ecology Letters*, 16, 1373–1381.
- 486 Nelsen, N. (2006). *An Introduction to Copulas, 2nd Edn.* Springer, New York.

- 487 Popovic, G., Warton, D., Thomson, F., Hui, F. & Moles, A. (2019). Untangling direct species association
488 from indirect mediator species effects with graphical models. *Methods in Ecology and Evolution*, 10,
489 1571–1583.
- 490 Schmida, A. & Ellner, S. (1984). Coexistence of plant species with similar niches. *Vegetatio*, 58, 29–55.
- 491 Ummenhofer, C. & Meehl, G. (2017). Extreme weather and climate events with ecological relevance: a
492 review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160135.
- 493 Usinowicz, J. & Levine, J. (2021). Climate-driven range shifts reduce persistence of competitors in a
494 perennial plant family. *Global Change Biology*, 27, 1890–1903.
- 495 Usinowicz, J., Wright, S. & Ives, A. (2012). Coexistence in tropical forests through asynchronous variation
496 in annual seed production. *Ecology*, 93, 9.
- 497 White, T., Campell, B., Kemp, P. & Hunt, C. (2001). Impacts of extreme climatic events on competition
498 during grassland invasions. *Global Change Biology*, 7, 1–13.

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
$\bar{r}_{i i}$	Mean GWR of species i
$\bar{r}_{j i}$	Mean growth of j when i is absent
$i i$	As subscript, refers to computing a quantity for i when i is rare
$j i$	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

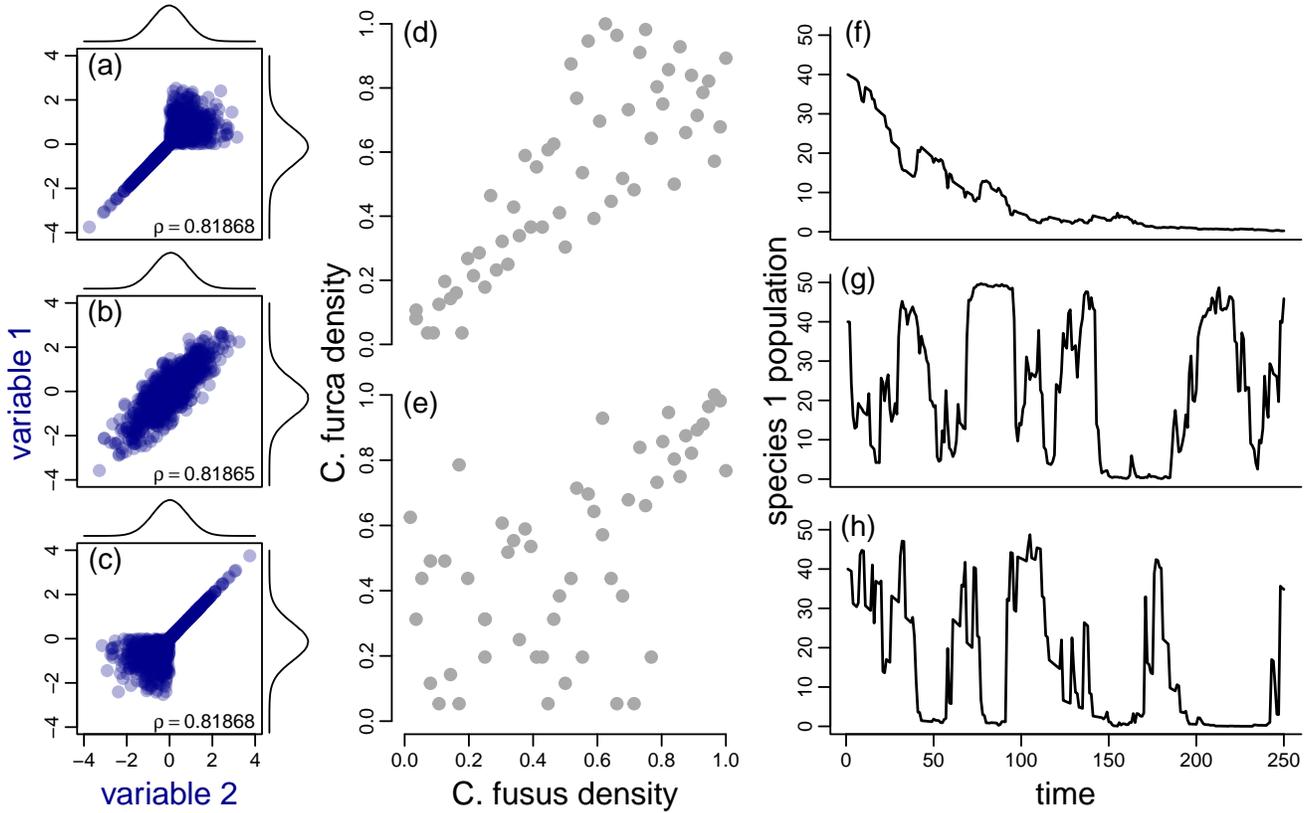


Figure 1: Examples motivating our study of the effects of asymmetric tail associations (ATAs) on competition and coexistence. (a-c) Bivariate random variables with standard normal marginals showing alternative patterns of association in the left and right parts of the distributions. The two variables 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).

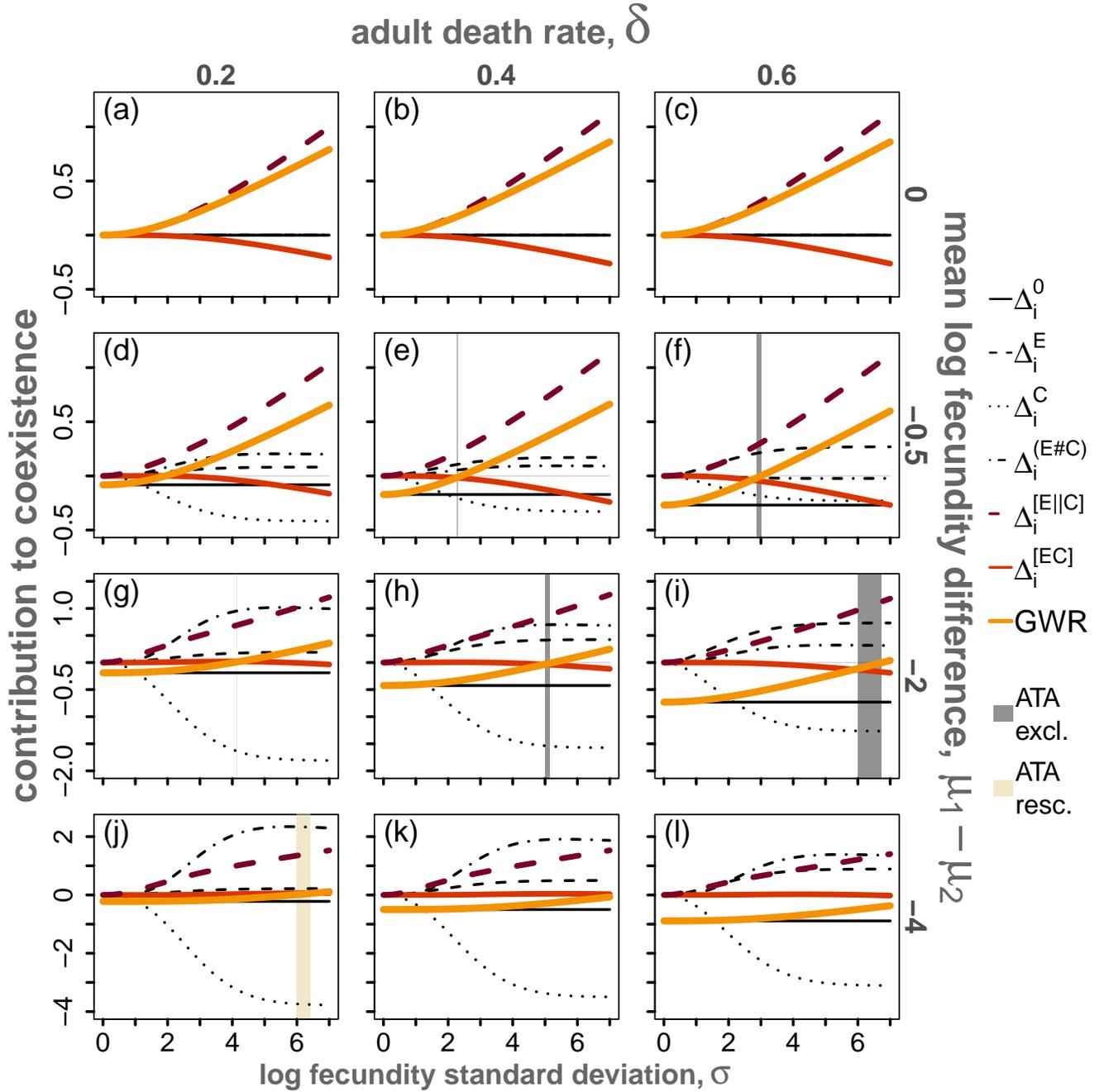


Figure 2: The contribution of ATAs to species coexistence was sometimes, but not always, meaningfully large compared to other components of the MCT decomposition for the log-normal fecundities lottery model. All panels show GWR and the decomposition of GWR provided by the extended MCT, equation (6). 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.

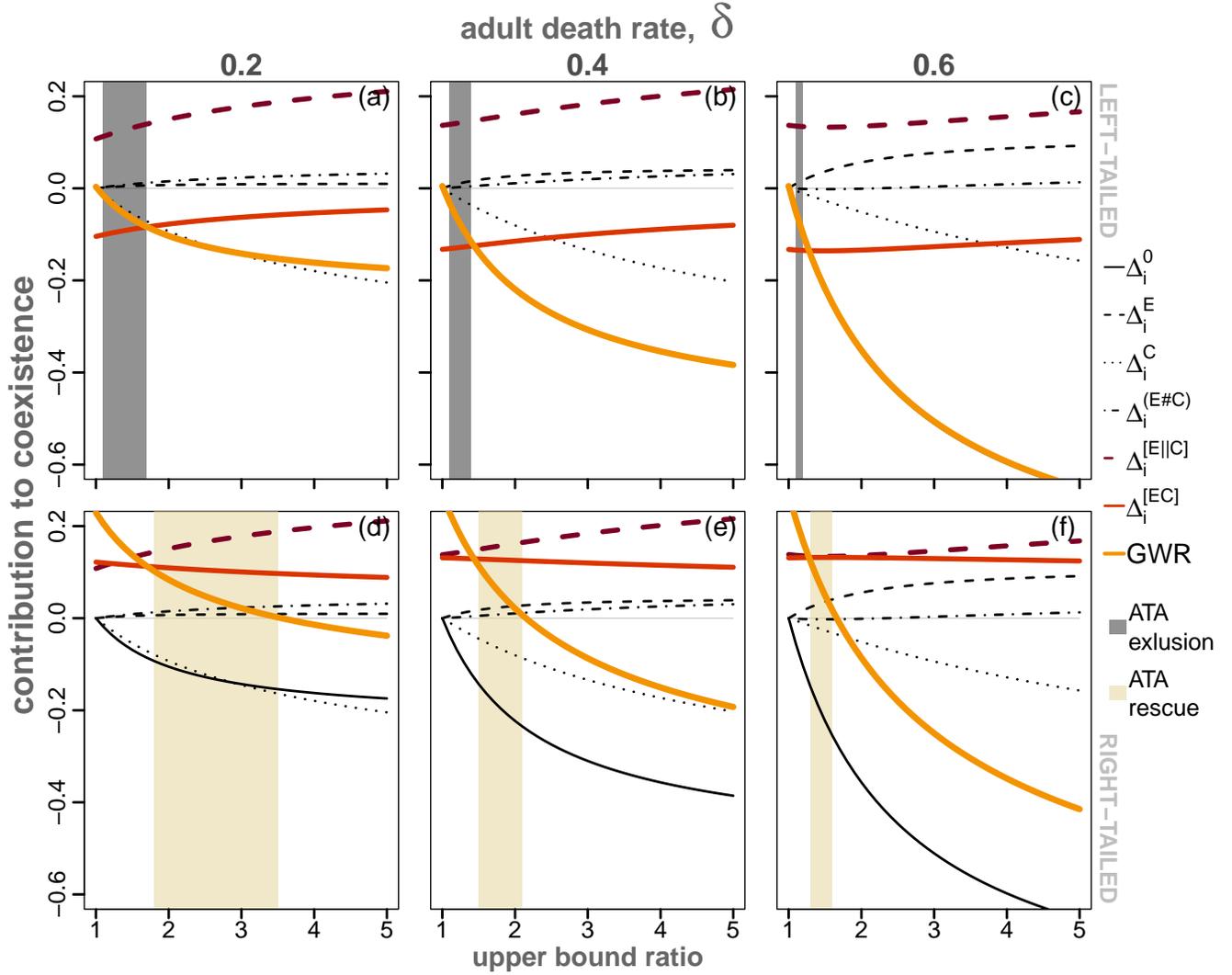


Figure 3: The contribution of ATAs to species coexistence was often meaningfully large compared to other components of the MCT decomposition for the beta fecundities lottery model. All panels show GWR and the decomposition of GWR provided by the extended MCT, equation (6). For each panel, δ is fixed 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.