

# Asymmetric relationships and their effects on coexistence

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## Funding information

Alexander von Humboldt-Stiftung; California Department of Fish and Wildlife; Directorate for Biological Sciences, Grant/Award Number: 1714195 and 2023474; James S McDonnell Foundation

Editor: Montserrat Vila

## 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 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 may be an important new mechanism of coexistence.

## KEY WORDS

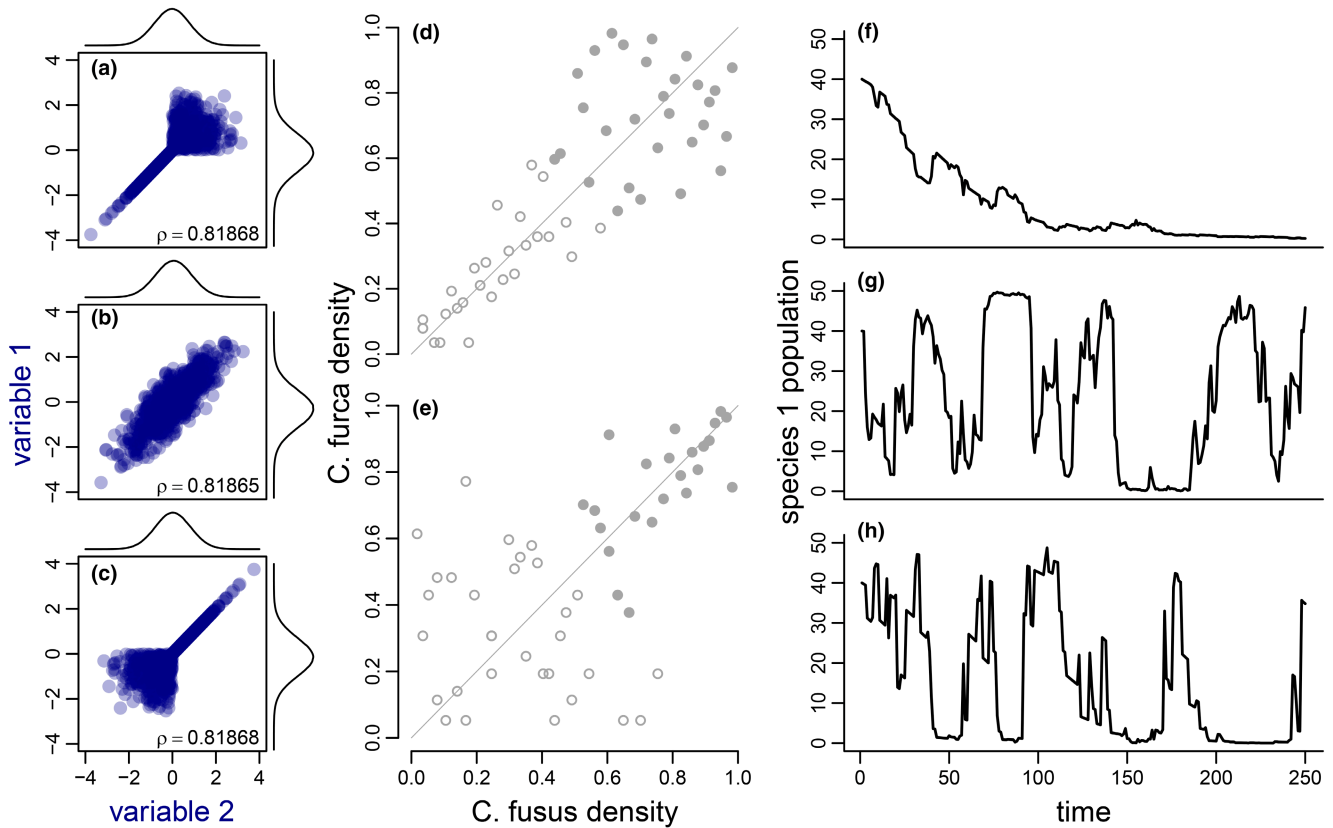
asymmetric tail association, biodiversity, coexistence, competition, copula, modern coexistence theory, niche differentiation, storage effects

## INTRODUCTION

At the core of ecology is the study of relationships between organisms and their environments. Ecologists ask, for instance, how the local environment relates to the population growth rate. To study relationships, ecologists commonly use metrics such as correlation. However standard measures of the strength and direction of association between variables do not tell the whole story (Ghosh, Sheppard, Holder, et al., 2020). To illustrate, the three pairs of variables in [Figure 1a–c](#) have the same Pearson correlation despite striking differences in association structure: [Figure 1b](#) shows a symmetric type of association, while [Figure 1a,c](#) exhibit what has been called ‘asymmetric tail association’ (ATA; Ghosh, Sheppard, Holder, et al., 2020). Metrics of association other than correlations are also used (e.g. various forms of regression), but other common methods also reveal only a small portion of the information in the relationship (Nelsen, 2006). ATAs and related ideas had previously been seldom considered in ecology, but recently, insights were gained by studying how features of associations beyond standard measures impact ecological phenomena (Anderson et al., 2019; de Valpine et al., 2014;

Ghosh et al., 2021; Ghosh, Sheppard, Holder, et al., 2020; Ghosh, Sheppard, Reid, & Reuman, 2020; Ghosh, Sheppard, & Reuman, 2020; Popovic et al., 2019). Ghosh, Sheppard, and Reuman (2020) argued that extinction risks can become elevated when metapopulations are subject to ATAs, for example, if environmental ‘catastrophes’ are more spatially synchronous across component populations than are years of good environment, limiting rescue effects. And Ghosh et al. (2021) showed that ATAs alter the stability of ecosystem functioning. [Figure 1d,e](#) show contrasting examples of ATAs using plankton population density time series; these examples are intended only to empirically illustrate what ATAs look like, as they use data of a different type from the focus of this paper. Many other examples of ATAs in nature have also been explored (Ghosh et al., 2021; Ghosh, Sheppard, Holder, et al., 2020; Ghosh, Sheppard, Reid, & Reuman, 2020). To our knowledge, the implications of ATAs for competition have not been investigated. Doing so is our goal here.

Competition and coexistence are topics at the core of modern ecology (Hutchinson, 1961; MacArthur, 1958; Schmid & Ellner, 1984). The competitive exclusion principle states that two species competing for the



**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,  $\rho$ , 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 [Nelsen, 2006; Ghosh, Sheppard, Holder, et al., 2020; see also (d,e)]. (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, Sheppard, Reid, and Reuman (2020) and Sheppard et al. (2019). ATAs were statistically significant and differed by location, with associations being primarily in the left tails in panel d, and primarily in the right tails in panel e (Section S1). One can see these asymmetries by noting that the open points in panel (d), which are in the left halves of the distributions, are more tightly clustered around the line  $y = x$  than are the closed points, which are in the right halves of the distributions; and vice versa for panel (e). (f–h) Lottery model population simulations obtained by transforming the respectively corresponding variables (a–c; see Introduction).

same limiting resource cannot coexist at constant densities—one will drive the other extinct (Hardin, 1960). Modern coexistence theory (MCT; Chesson, 1994, 2000; Barabas et al., 2018) is a framework for understanding how species nevertheless coexist in real ecosystems, through the niche partitioning effects of environmental variation. 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; Letten et al., 2018), and corals (Álvarez-Noriega et al., 2020). Although MCT is mathematically complex, recent extensions make it more accessible (Ellner et al., 2016, 2019). MCT breaks down coexistence into the contributions of various mechanisms, with names such as ‘storage effects’ (Chesson, 1994). Storage

effects, which are reviewed conceptually below and defined formally in Theory, refer to a type of niche partitioning which allows species to effectively ‘store’ population growth benefits from favourable periods in order to persist through unfavourable periods.

We indicate why it is plausible that ATAs may influence one mechanism of coexistence in particular, storage effects, starting by conceptually reviewing what storage effects are (Barabas et al., 2018; Chesson, 1994; Chesson et al., 2012; Ellner et al., 2016). 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 covariation between the fluctuating quality of the environment for a species ( $E$ ) and the competition ( $C$ ) experienced by that species (called  $EC$  covariance); and on the assumption that no two species respond identically

to environmental variation. 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 a benefit to the rare species. Storage effects can be quantified by measuring how much  $EC$  covariance contributes to differences between growth rates of currently rare versus currently common species (Chesson, 1994; Ellner et al., 2016). ATAs may, in principle, influence storage effects simply because storage effects hinge on  $EC$  covariation, and ATAs can be an aspect of  $EC$  covariation. One scenario in which it is reasonable to imagine that ATAs may be present in  $EC$  covariation pertains to water limitation. Suppose two plants compete primarily for water, when water is scarce, but their niches become differentiated when water is abundant. Then the quality of the environment,  $E$ , as experienced by whichever plant is currently rare, may only correspond closely to the competition,  $C$ , imposed on it by the currently abundant plant when water is scarce and  $E$  is low.

To further demonstrate the plausibility of ATAs altering coexistence, we carried out simulations using a two-species model, the lottery model. The simulations described in this paragraph demonstrate that ATAs influence coexistence in some manner; the nature of that influence is the subject of the rest of the paper. The lottery model, which was introduced as a model of coral reef fish competing for a set of  $N$  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,  $\delta$  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  $\delta$  at each time step, and are replaced by juveniles in proportion to the reproductive outputs of the species that year. Note that  $N = N_1(t) + N_2(t)$  is constant. We assume that the random variables ( $B_1(t), B_2(t)$ ) are independent and identically distributed (iid) through time. In three distinct simulations (Figure 1f–h),  $B_1$  and  $B_2$  were, respectively, left- (Figure 1a), right- (Figure 1c) and symmetrically (Figure 1b) tail associated, while the same marginal distributions were used in all simulations (see Methods for details). Thus, the setup was identical in the three simulations except for different ATAs. ATAs substantially influenced aspects of coexistence in these simulations (Figure 1f–h). Notation for the paper is summarized in Table 1. Typesetting of mathematics by ecological journals is sub-optimal, so, for mathematical readers,

**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 $t$
$\delta$	Mortality rate
$\sigma$	Standard deviation of log fecundities for the log-normal fecundities model
$\mu_i$	Mean log fecundity, species $i$ , log-normal fecundities model
$\eta_i$	Upper bound fecundity, species $i$ , beta 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 $i^{\text{th}}$ species
$C_i(t)$	Competition experienced by the $i^{\text{th}}$ species
$\bar{r}_{Ni}$	Mean GWR of species $i$
$\bar{r}_{j i}$	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
	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 per se, 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>
$\Theta$	Temperature
$\Theta_0$	Average temperature
$a$	Amplitude of temperature fluctuations
$P$	Period of temperature fluctuations

we appended a latex version of this main text to the end of the Supporting Information.

We next give some intuition about how ATA effects on coexistence work, with details in the Discussion. It is known that storage effects can occur if a buffering mechanism reduces population losses in bad years so that gains in good years can more than make up for them. Bad years happen when the negative effects of  $C$  outweigh any positive effects of  $E$ ; but this occurs both (1) when  $E$  is moderately favourable but  $C$  is very strong, and (2) when  $E$  is unfavourable and  $C$  is not too weak. Conversely, good years happen when positive effects of  $E$  outweigh negative effects of  $C$ ; but this occurs (1) when  $E$  is favourable and  $C$  is not too strong, and (2) when  $E$  is moderately unfavourable but  $C$  is very weak. It turns out that the potential for storage events to occur when  $E$  and  $C$  are both higher than average (the cases 1, above); versus the potential when  $E$  and  $C$  are both lower than average (cases 2) are not necessarily equal—storage potential may differ across the spectrum from 1 to 2. ATA effects quantify the extent to which asymmetries of association between  $E$  and  $C$  are aligned with differences in the potential for storage across the spectrum from 1 to 2. If  $E$  and  $C$  are largely unassociated in the parts of their distribution where storage potential is high, ATA effects will be high. ATA effects quantify how temporal niche partitioning varies across the  $EC$  spectrum spanned by the cases 1–2 above.

We previously demonstrated that ATAs are common in nature and can influence ecological phenomena (Ghosh et al., 2021; Ghosh, Sheppard, Holder, et al., 2020; Ghosh, Sheppard, Reid, & Reuman, 2020; Ghosh, Sheppard, & Reuman, 2020); and our arguments above indicate that ATAs may influence coexistence. Thus, we here seek to quantify the consequences of ATAs for competition and coexistence, via the following specific goals. G1) We 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. G2) We explore, using the lottery model, the relative magnitudes of the contributions to coexistence that come from ATAs compared to other, previously known mechanisms of coexistence; and we determine whether species may sometimes coexist with ATAs but not without, or vice versa. This is to help illuminate whether ATA contributions to coexistence are negligible or meaningfully large. G3) We provide an empirical example of species coexistence which highlights the role ATAs can play and their potential importance. The example is a laboratory diatom system. In the Discussion, we consider whether climate change may alter ATAs of environmental variables and thereby influence competition. Overall, our study presents a new mechanism of species coexistence and a means of understanding its importance.

## THEORY

We here pursue goal G1: to augment MCT to show the role of ATAs for coexistence.

### Setup

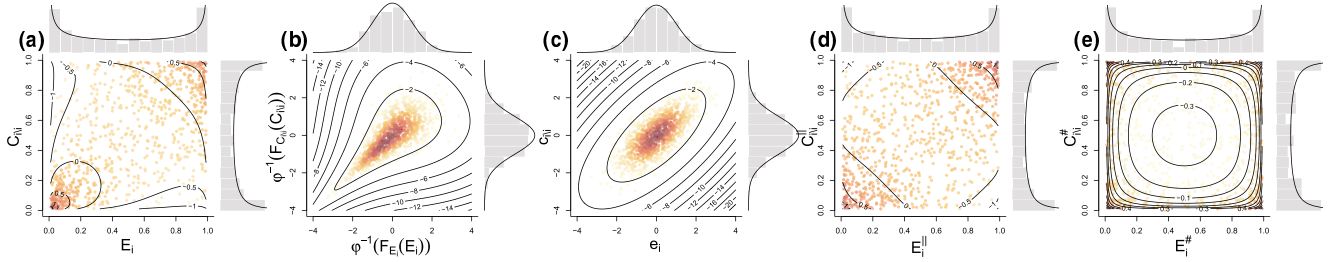
We first develop our theory for a general two-species model. Our notation parallels Ellner et al. (2016, 2019). It is assumed that the growth rate  $r_i(t) = \ln(N_i(t+1)/N_i(t))$  of species  $i$  can be written as an increasing function of an environmental factor  $E_i(t)$  and as a decreasing function of competitive pressure on species  $i$ ,  $C_i(t)$ , that is,  $r_i(E_i, C_i)$ . We also assume, for simplicity, that the  $E_i(t)$  are iid through time, and likewise for the  $C_i(t)$ . Though this assumption is probably unnecessary, it simplifies the presentation of new ideas.

### The storage effect

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

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

where  $\bar{r}_{i\setminus i}$  is the mean ‘growth when rare’ (GWR) of species  $i$ , that is, the mean growth rate of species  $i$  when it is at negligible abundance and species  $j$  (the other species) is at stochastic steady state;  $\bar{r}_{j\setminus i}$  is the mean steady-state growth rate of species  $j$  when species  $i$  is absent or at negligible abundance (equals 0, a priori); and  $\bar{r}_{i\setminus i}^{\#}$  and  $\bar{r}_{j\setminus i}^{\#}$  are analogous quantities, but for an alternative modelling scenario, identical except that influences of environment and competition have been rendered independent. A subscript  $i\setminus i$  indicates a quantity computed for species  $i$  when that species is at negligible abundance, and  $j\setminus i$  indicates a quantity computed for  $j$  when  $i$  is absent. The *scaling factor*  $q_{ij}$  measures the relative sensitivities to competition of the two species. See Chesson (1994), Ellner et al. (2016) and Section S2 for the two alternative definitions of  $q_{ij}$  we use; but one definition is  $q_{ij} = 1$ , and to understand the ideas presented here it is sufficient to use that definition. Since it 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 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 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 with the same marginal



**FIGURE 2** Illustration of how asymmetric tail associations are removed while retaining marginal distributions and correlation between variables (see Theory). (a) An example original bivariate distribution ( $E_i, C_{i\setminus i}$ ), with ATAs present. (b) Marginals are now normalized. The variables  $E_i$  and  $C_{i\setminus i}$  are individually transformed to have standard normal marginals through a composition of the inverse of the standard normal cumulative distribution function (CDF),  $\varphi^{-1}$ , and each variable's CDF,  $F_{E_i}$  and  $F_{C_{i\setminus i}}$ , respectively. (c) A newly generated bivariate normal distribution,  $(e_i, c_{i\setminus i})$ , with correlation  $\tilde{\rho} = \rho$  selected to match that of the original distribution (see Theory). (d) Two new variables,  $E_i^{\parallel}$  and  $C_{i\setminus i}^{\parallel}$ , which have the same marginals and correlation as the original  $E_i$  and  $C_{i\setminus i}$  variables of (a) but which have symmetric association structure. These are the distributions used to compute ATA effects,  $\Delta_i^{[EC]}$  (Theory). These variables are obtained by transforming the marginals from (c),  $e_i$  and  $c_{i\setminus i}$ , using the inverses of the functions used in (b). Panel (e) shows the distribution  $(E_i^{\#}, C_{i\setminus i}^{\#})$ , defined in Theory following Ellner et al. (2016), for comparison. These are the distributions used to compute storage effects,  $\Delta_i^{(EC)}$  (Theory). For illustration purposes we started with beta distributed  $E_i$  and  $C_{i\setminus i}$ . Contour lines are  $\log_{10}$  of probability density on all panels. See Table 1 for used annotations and abbreviations.

distributions, but independent components,  $(E_i^{\#}, C_{i\setminus i}^{\#})$ , so  $\bar{r}_{i\setminus i}^{\#} = \mathbb{E}[r_i(E_i^{\#}, C_{i\setminus i}^{\#})]$ . Likewise,  $\bar{r}_{j\setminus i}^{\#} = \mathbb{E}[r_j(E_j^{\#}, C_{j\setminus i}^{\#})]$ .

## Decomposing the storage effect

We now specify how to decompose storage effects into contributions due to ATAs and to  $EC$  correlation *per se*. Storage effects for species  $i$  were computed by comparing differences between rare and common species mean growth rates for the original model and for a modified model for which  $E$  and  $C$  were rendered independent [see (2)]. Because components were completely independent in the modified model, storage effects quantify the contribution of the whole  $EC$  relationship to the rare/common species growth rate 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 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  $EC$  relationship altered. Specifically, ATAs are removed—see below for how. We then define  $\bar{r}_{i\setminus i}^{\parallel}$  and  $\bar{r}_{j\setminus i}^{\parallel}$  based on a 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

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

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

The term  $\Delta_i^{[EC]}$  is the *ATA effect on coexistence*. The term  $\Delta_i^{[E\parallel C]}$  is the component of storage effects due to  $EC$  correlation *per se*, remaining after having removed the effects of ATAs. Note that brackets,  $[\cdot]$ , and parentheses,  $(\cdot)$ , are used distinctly throughout the paper—they are not interchangeable. The notation  $\parallel$  was chosen because this

new symbol is part of the symbol # (two of its four lines), corresponding to the removal of part of the relationship between  $E$  and  $C$  components (ATAs). The symbol should be pronounced ‘partial sharp’. See Section S3 for technical comments on the notation. The brackets in  $\Delta_i^{[EC]}$  and  $\Delta_i^{[E\parallel C]}$  are intended to indicate that (4) is a decomposition within a decomposition, that is, (4) is a decomposition of storage effects, which are a term in the MCT decomposition (Ellner et al., 2019)—see below for details.

How are asymmetries of tail association removed while leaving  $E$  and  $C$  marginal distributions and overall correlation unchanged? Figure 2 provides an illustration of the steps we describe here. We assume, for simplicity, that the cumulative distribution functions (CDFs) of  $E_i$  and  $C_{i\setminus i}$ , which we denote  $F_{E_i}$  and  $F_{C_{i\setminus i}}$ , are strictly monotonic and continuous. Letting  $\varphi$  be the CDF of a standard normal distribution, we consider the random variables  $\varphi^{-1} \circ F_{E_i}(E_i)$  and  $\varphi^{-1} \circ F_{C_{i\setminus i}}(C_{i\setminus i})$ , which are standard normally distributed, although they are not necessarily jointly bivariate normal (Figure 2a,b). Let  $\rho_i$  be their covariance. We then define a bivariate normal random variable  $(e_i, c_{i\setminus i})$  such that  $\mathbb{E}(e_i) = \mathbb{E}(c_{i\setminus i}) = 0$  and  $\text{var}(e_i) = \text{var}(c_{i\setminus i}) = 1$ , and we denote  $\text{cov}(e_i, c_{i\setminus i})$  by  $\tilde{\rho}_i$  (Figure 2c). We define  $E_i^{\parallel} = F_{E_i}^{-1} \circ \varphi(e_i)$  and  $C_{i\setminus i}^{\parallel} = F_{C_{i\setminus i}}^{-1} \circ \varphi(c_{i\setminus i})$  (Figure 2d). The value of  $\tilde{\rho}_i$  is determined in one of four ways: either by setting  $\tilde{\rho}_i = \rho_i$ ; or so that the Pearson, Spearman or Kendall correlation of  $E_i^{\parallel}$  and  $C_{i\setminus i}^{\parallel}$  matches that of  $E_i$  and  $C_{i\setminus i}$ . The choice of bivariate normal  $(e_i, c_{i\setminus i})$  ensures that  $E_i^{\parallel}$  and  $C_{i\setminus i}^{\parallel}$  are symmetrically tail associated. For those familiar with copula statistics (see, e.g. Genest & Favre, 2007 and Ghosh, Sheppard, Holder, et al., 2020), we replaced the copula of  $(E_i, C_{i\setminus i})$  with a normal copula to form  $(E_i^{\parallel}, C_{i\setminus i}^{\parallel})$ . The choice of  $\tilde{\rho}_i$  ensures that  $E_i^{\parallel}$  and  $C_{i\setminus i}^{\parallel}$  are correlated to the same extent as  $E_i$  and  $C_{i\setminus i}$ , according to whichever definition of correlation is preferable. Thus  $E_i^{\parallel}$  and  $C_{i\setminus i}^{\parallel}$  have had their tail association rendered symmetric while retaining

their correlation *per se*. The random variable  $(E_j^{\parallel}, C_{j\setminus i}^{\parallel})$  is created similarly. For comparison, Figure 2 also shows, for the example explored by that figure, the distribution  $(E_i^{\#}, C_{i\setminus j}^{\#})$  defined above (following Ellner et al. (2016)).

The question of uniqueness of  $(E_i^{\parallel}, C_{i\setminus j}^{\parallel})$  is addressed fully in Section S4. Briefly, a choice is made as to what type of correlation (e.g. Pearson, Spearman, etc.) is to be preserved. Additionally, another choice involves the use of a bivariate normal distribution  $(e_i, c_{i\setminus j})$ ; any other symmetrically associated bivariate distribution with standard normal marginals could be used instead. But the normal distribution is a natural choice, and other choices may be somewhat esoteric (Section S4). Future work could explore the consequences of this choice.

## Our decomposition as an extension of modern coexistence theory

The other mechanisms in MCT make no reference to covariation between quantities, whereas ATAs are about covariation. Therefore, storage effects are the only mechanism of coexistence for which ATAs are relevant. The Ellner et al. (2019) version of MCT comprises a decomposition of the coexistence metric  $\bar{r}_{i\setminus j} - q_{ij}\bar{r}_{j\setminus i}$ , which equals GWR of species  $i$ , as

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

where:  $\Delta_i^0$  is a baseline;  $\Delta_i^E$  is a contribution of environmental variation;  $\Delta_i^C$  is a contribution of variation in competition;  $\Delta_i^{(E\#C)}$  is a contribution 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 of *EC* covariation itself—storage effects. Combining our decomposition (4) with (5) of Ellner et al. (2019) gives

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

which is the extension of MCT that was goal G1. The derivation of (6) is in Section S5.

## ATA rescue and exclusion

To evaluate the importance of ATAs for a given scenario, we quantified the magnitude of the new ATA effect term,  $\Delta_i^{[EC]}$ , relative to the other terms (see Methods). But we also defined scenarios of ‘ATA rescue’ and ‘ATA exclusion’. *ATA rescue* is considered to have occurred if coexistence is possible when ATAs are taken into account, that is,  $\text{GWR} > 0$  for both species, but impossible otherwise, that is, the sum of the non-ATA terms in (6) is negative for at least one species. *ATA exclusion* occurs if the species do not coexist when ATAs are taken into account, that is,  $\text{GWR} < 0$  for at least one species, but

would coexist were it not for ATAs, that is, the sum of the non-ATA terms in (6) is positive for both species.

## METHODS

### Versions of the lottery model

For goal G2 of the Introduction, we applied our 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 (6) for various model parameterizations. We used two versions of the lottery model. The versions both used the same dynamical equations (Introduction), but differed in the distributions of  $(B_1, B_2)$  used. Both distributions were based on transformations of the distributions  $(b_1, b_2)$  of Figure 1a–c; the details of how the left- (Figure 1a), right- (Figure 1c), and symmetrically (Figure 1b) tail associated alternatives for  $(b_1, b_2)$  were generated are in Section S6.

The *log-normal fecundities lottery model* used  $B_i = \exp(\mu_i + \sigma b_i)$ , and therefore had parameters  $\sigma$ ,  $\mu_1$  and  $\mu_2$  in addition to the death rate parameter  $\delta$  (Introduction). The parameter  $\sigma$  is the standard deviation of the log-fecundities and  $\mu_i$  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  $\varphi$  is the CDF of the standard normal distribution and  $F_{\beta}$  is the CDF of a beta distribution with shape and scale parameters 0.5. So the beta fecundities model had parameters  $\eta_1$ ,  $\eta_2$  and  $\delta$ , and produced fecundities with *U*-shaped distributions between 0 and  $\eta_1$ , for  $B_1$ , and between 0 and  $\eta_2$ , for  $B_2$ . The mean fecundity for species  $i$  was  $\eta_i/2$ , and larger  $\eta_i$  also corresponded to more variable fecundities.

For both versions of the lottery model, fecundities directly reflected the environment, that is, 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:  $C_i$  was 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 fulfil the assumption of Theory that  $r_i(t)$  is an increasing function of  $E_i(t)$  and a decreasing function of  $C_i(t)$  (Section S7).

### How results were plotted for goal G2

To explore, using the log-normal fecundities lottery model, the relative magnitudes of the contributions to coexistence of ATAs versus other mechanisms, we plotted the terms of the decomposition (6) against model parameters  $\mu_1$ ,  $\mu_2$ ,  $\sigma$  and  $\delta$ . We labelled regions of the plot which corresponded to ATA rescue or exclusion, that is, 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 none of the components of (6) depends independently on  $\mu_1$  and  $\mu_2$ ; they depend only on  $\mu_1 - \mu_2$  (Section S7). 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 (Section S7). 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  $\sigma$  for  $\sigma$  from 0 to 7. Chesson and Warner (1981) showed that coexistence is impossible for  $\delta = 1$ , and it is known that the storage effect is weak for larger  $\delta$ , so we only considered  $\delta$  up to 0.6. Some of the  $\mu$  differences and  $\sigma$  values we considered were unrealistic (see Results), so we considered after plotting whether conclusions depended on realistic parameter values. Simulation methods of Ellner et al. (2019) were used to compute the components of (6). Computationally efficient means of performing simulations are in Section S8.

To explore, using the beta fecundities lottery model, the relative magnitudes of the contributions to coexistence of ATAs versus other mechanisms, we plotted the terms of the decomposition (6) against model parameters  $\eta_1, \eta_2$ , and  $\delta$ , again labelling regions of ATA rescue or exclusion. Mathematical shortcuts, summarized here, simplified plotting. First, we assumed, without loss of generality, that  $\eta_1 \leq \eta_2$ . It was then sufficient to decompose GWR of the weaker competitor, species 1. Second, we showed that none of the components of (6) depends independently on  $\eta_1$  and  $\eta_2$ ; instead they depend only on  $\eta_2/\eta_1$  (Section S7). So we plotted against  $\eta_2/\eta_1$ .

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  $\eta_2/\eta_1$ , using the fairly realistic (see Results) range  $1 \leq \eta_2/\eta_1 \leq 5$ . Simulation methods of Ellner et al. (2019) were again used, with computationally efficient means of simulating in Section S8.

## Diatom chemostat system

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

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

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

for  $j = 1, 2$ , where  $S$  is an extracellular silicate concentration in the chemostat,  $x_1$  is the population density of *F. crotonensis* and  $x_2$  is that of *C. pseudostelligera*,  $D$  is the chemostat outflow rate,  $S_0$  is concentration of silicates in the chemostat inflow, the  $Q_j$  are amounts of silicate per cell, the  $V_j$  are maximum population growth rates, and the  $K_j$  are half-saturation constants for the dependence of growth rates on nutrient concentration. The temperature-dependent parameters  $Q_j, V_j$ , and  $K_j$  were obtained by Descamps-Julien and Gonzalez (2005) through batch experiments and curve fitting or interpolation. Descamps-Julien and Gonzalez (2005) showed that permanent coexistence of the two species occurs when temperature fluctuates periodically,  $\theta(t) = \theta_0 + a \sin(2\pi t/P)$ , with parameters  $\theta_0 = 18^\circ\text{C}$ ,  $a = 6^\circ\text{C}$ ,  $P = 60\text{d}$ . Ellner et al. (2016, 2019) broke down coexistence into contributing mechanisms according to (5) for these same values of  $\theta_0, a$  and  $P$ . We further decompose coexistence according to (6), and we do so for ranges of values of  $\theta_0, a$  and  $P$ . In contrast to the lottery model case, for which simplifying assumptions made it sufficient to decompose only the GWR of species 1, for this example we considered  $\bar{r}_{i \setminus j} - q_{ij} \bar{r}_{j \setminus i}$  for both  $i = 1, j = 2$  and for  $i = 2, j = 1$ . Details of the model setup are in Section S9 and specifics of how our decomposition was computed are in Section S10.

## How results were plotted for goal G3

To display results for G3, we started by plotting the terms of (6) against one of the parameters  $\theta_0, a$  and  $P$  at a time, keeping the other two fixed at the values used by Descamps-Julien and Gonzalez (2005). We again labelled regions of parameter space corresponding to ATA rescue or exclusion.

We also generated two-dimensional plots, where two of the parameters  $\theta_0, a$  and  $P$  were varied and the third was kept fixed. For those plots, the quantity  $\Delta_i^{[EC]} / |\text{GWR}|$  was displayed using colour. Larger magnitudes of this quantity indicate greater importance of ATAs. The case  $\Delta_i^{[EC]} > \text{GWR} > 0$  (which produces  $\Delta_i^{[EC]} / |\text{GWR}| > 1$ ) corresponds to ATA rescue, and  $\Delta_i^{[EC]} < \text{GWR} < 0$  (which produces  $\Delta_i^{[EC]} / |\text{GWR}| < -1$ ) corresponds to ATA exclusion. Thus  $\Delta_i^{[EC]} / |\text{GWR}|$  indicates the importance of ATAs and also whether ATA rescue or exclusion occurred.

All computations were done in R on a laptop running Ubuntu Linux. The only data used were the phytoplankton time series of Figure 1, taken from <https://doi.org/10.5061/dryad.rq3jc84>. Complete computer codes and data are stored publicly as indicated in the Data Availability Statement.

## RESULTS

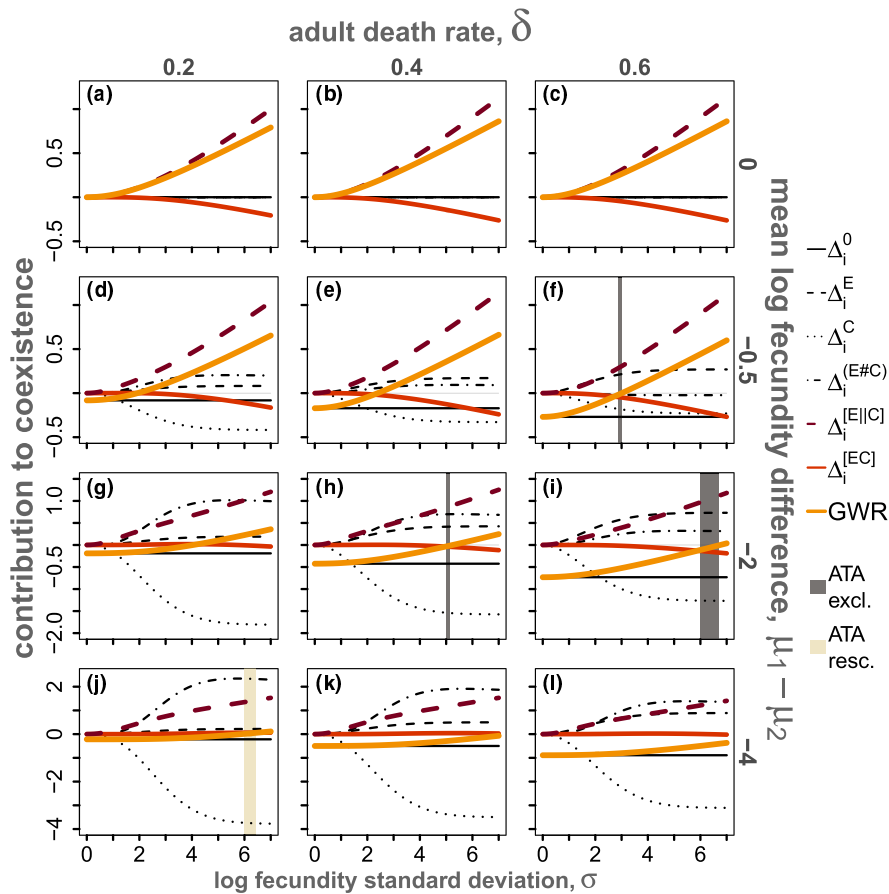
### Goal G2, lottery model results

To begin fulfilling goal G2 of the Introduction (to explore, using the lottery model, the relative magnitudes of the contributions of ATAs compared to other coexistence mechanisms; and to see if ATA rescue or exclusion occur), [Figure 3](#) shows that, for the log-normal fecundities lottery model, the ATA term of (6) sometimes, but not always, has magnitude comparable to the magnitudes of other terms. Magnitudes of  $\Delta_i^{[EC]}$  tended to be larger, relative to the magnitudes of the other terms of (6), for smaller-magnitude differences between  $\mu_1$  and  $\mu_2$ , that is, for closer-to-equal competitors. In the  $\mu_1 = \mu_2$  case (panels a-c), for which the two species were equal competitors, storage effects ( $\Delta_i^{[EC]} + \Delta_i^{[E|C]}$ ) were the only means by which

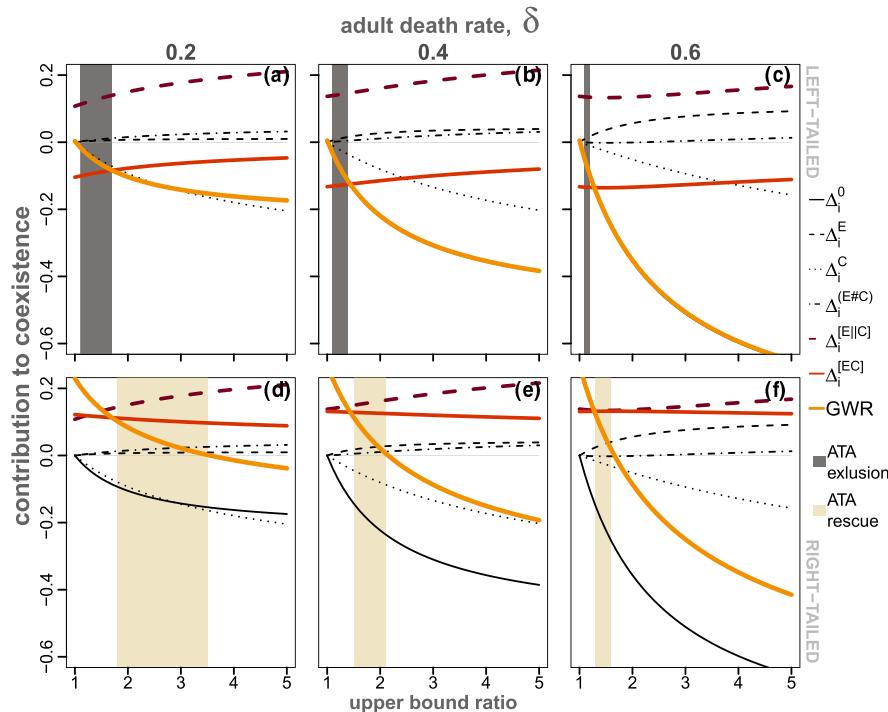
coexistence could occur, and ATA effects tended to be negative, weakening storage effects.

For the beta fecundities lottery model, the ATA term was often or always, for the parameters we considered, comparable in magnitude to the other terms of the decomposition (6) ([Figure 4](#)). The term contributed negatively to coexistence for environmental noise/fecundities showing left-tailed association, and positively for right-tailed association.

Our results also show that ATAs can make the difference between coexistence and competitive exclusion: both ‘ATA rescue’ and ‘ATA exclusion’ (see Theory) are possible. Starting with the log-normal fecundities lottery model, for some of the panels on [Figure 3](#), the GWR line falls between the ATA line and the x axis for some values of  $\sigma$ , for example, panel i. For such cases, the presence or absence of ATAs determine whether the species coexist or not. For panel i, for values of  $\sigma$  around 6, species 1



**FIGURE 3** 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,  $\delta$  and  $\mu_1 - \mu_2$  are fixed at values specified in the margins, and GWR and components of the decomposition are plotted against  $\sigma$ . 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  $>0.00641$ , so are not displayed. This plot uses  $q_{ij} = 1$ . An analogous plot ([Figure S1](#)) 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. See [Table 1](#) for used annotations and abbreviations.



**FIGURE 4** 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,  $\delta$  is fixed at the value specified in the upper margin, and GWR and components of the decomposition are plotted against the upper bound ratio,  $\eta_2/\eta_1$ . 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  $>0.00145$ , so are not displayed. This plot uses  $q_{ij} = 1$ . An analogous plot (Figure S2) uses  $q_{ij} = \eta_i / (\eta_j(1 - \delta) + \eta_i\delta)$ ; though results differed in detail, main conclusions were the same. See Table 1 for used annotations and abbreviations.

is excluded with ATAs but the two species coexist without ATAs. Figure 4 highlights additional examples using the beta fecundities lottery model, where examples were more common than for the log-normal fecundities model.

Contrasting the two models, ATAs were only important for the log-normal fecundities lottery model when that model was parameterized unrealistically; but ATAs were important for a wide range of realistic parameter values for the beta fecundities model. For instance, the ATA term in Figure 3 had large magnitude compared to the other terms of (6), and ATA rescue and exclusion occurred, only for  $\sigma$  greater than about 3. The standard deviation of fecundity for species 1 when  $\mu_1 = 0$  and  $\sigma = 3$  was greater than 8000, so values of  $\sigma$  greater than 3 are probably unrealistic. However, all the  $\eta_2/\eta_1$  ratio values we plotted for the beta fecundities model were fairly realistic, corresponding to upper-bound fecundities that were up to 5 times higher for species 2 than for species 1. The ATA term in Figure 4 was comparable in magnitude to other components of (6) across the whole range of parameters considered. And ATA rescue and exclusion occurred for values of  $\eta_2/\eta_1$  between 1 and 2. Apparently the question of whether ATAs are important for realistic parameter values depends on specifics.

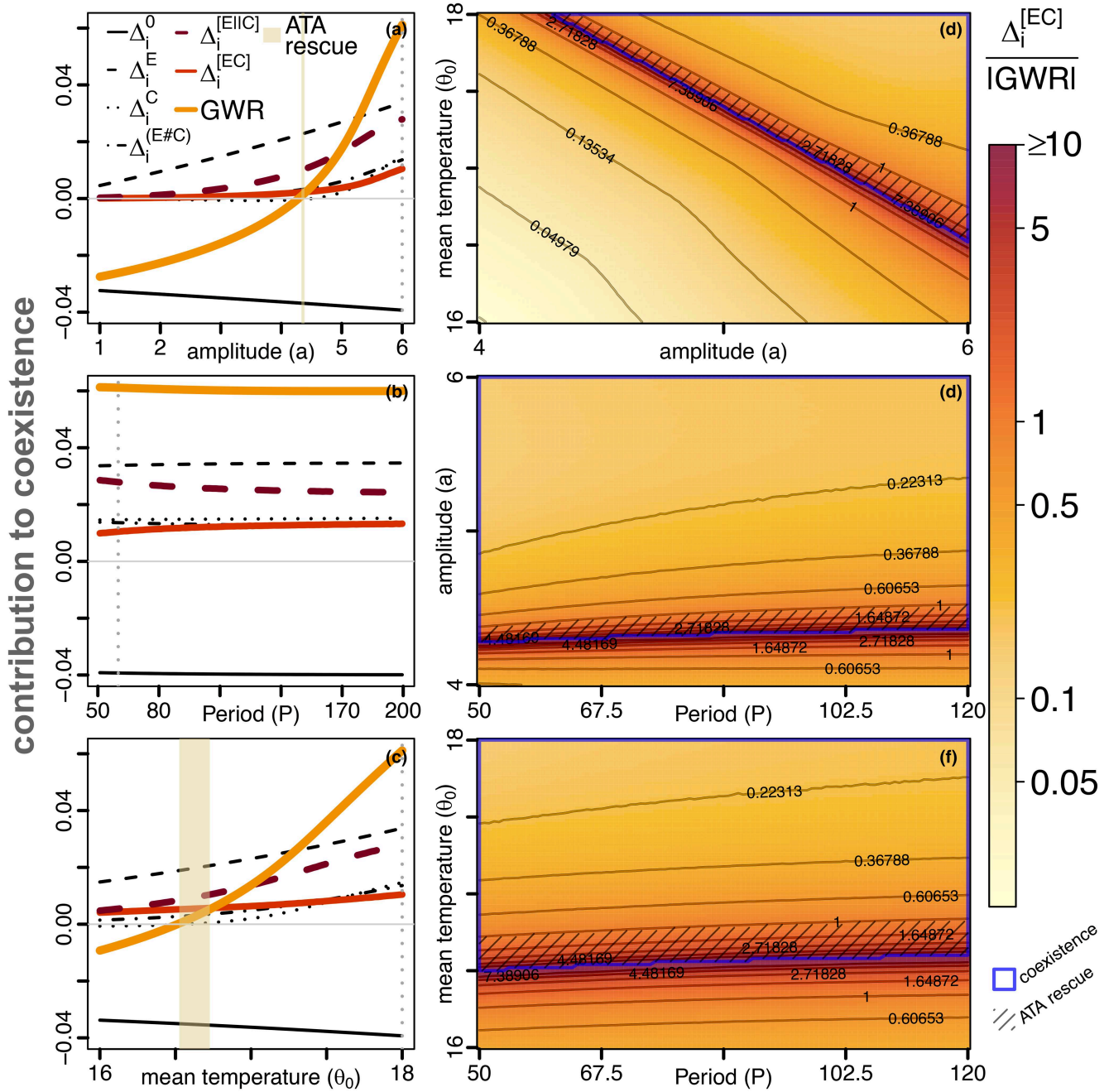
### Goal G3, results for the diatom system

Starting to fulfil goal G3 of the Introduction (to provide an empirical example of species coexistence which highlights the role ATAs can play), Figure 5a–c show that ATA contributions to coexistence often have magnitudes comparable to those of other terms of the extended MCT decomposition, and that ATA rescue occurs for some parameters for this system.

Plotting against two parameters at a time, Figure 5d–f reinforce the same conclusions. The quantity  $\Delta_i^{[EC]} / |GWR|$  was often large, indicating that ATAs were a substantial contributor to coexistence. For instance, well over half the area of Figure 5f shows values of  $\Delta_i^{[EC]} / |GWR|$  bigger than 1/4, with large portions of Figure 5d,e satisfying the same criterion. Substantial portions of panels d–f also show values of  $\Delta_i^{[EC]} / |GWR|$  bigger than 1, corresponding to ATA rescue. ATA exclusion did not occur for this system for the parameters we considered.

## DISCUSSION

We developed and applied a new extension of modern coexistence theory (MCT) that quantifies the impact of



**FIGURE 5** ATA effects and ATA rescue in the diatom system. The contribution of ATAs to the GWR of *F. crotonensis* in the diatom system of Descamps-Julien and Gonzalez (2005) was often meaningfully large compared to other components of the MCT decomposition (a–c). Panels a–c show GWR and the decomposition of GWR provided by the extended MCT, Equation (6). For each panel, two of the three parameters defining the temperature oscillation (the amplitude,  $a$ ; period,  $P$ ; and mean,  $\theta_0$ ; see Methods) were fixed at the values used by Descamps-Julien and Gonzalez (2005) ( $a = 6^\circ\text{C}$ ,  $P = 60\text{d}$ ,  $\theta_0 = 18^\circ\text{C}$ ), and GWR and components of the MCT decomposition were plotted against the third parameter. The original values of the varying parameters are indicated by vertical dotted lines. ATA contributions ( $\Delta_i^{[EC]}$ ) had magnitude comparable to other components, indicating that ATAs can contribute meaningfully to coexistence in this system. In some instances, the GWR line falls between the ATA line and the horizontal axis, indicating that, for those parameter values, ATA rescue occurs. Standard errors of plotted quantities were always  $<4e-05$ , so are not shown. Panels d–f show bivariate plots (Methods) for which the third parameter was fixed at the values used by Descamps-Julien and Gonzalez (2005). ATAs are again often an important factor helping determine coexistence or exclusion, and ATA rescue happened for an appreciable fraction of the explored parameter space. For the parameters we considered, GWR of the other diatom species in the system, *C. pseudostelligera*, was always positive both including and excluding the effects of ATAs, so GWR for *F. crotonensis*, decomposed here, is a sufficient coexistence metric. See Table 1 for used annotations and abbreviations.

asymmetric tail associations (ATAs) on species coexistence. Building upon a recent, simulation-based approach to MCT (Ellner et al., 2016, 2019), we decomposed

storage effects into two new mechanisms, the contribution of ATAs to coexistence, and the contribution of EC correlation *per se*. Applications of our extended theory

to the lottery model and to a laboratory diatom system demonstrated that ATA contributions to storage effects and to species coexistence can be comparable in magnitude to contributions of previously recognized mechanisms. Our results add coexistence to the list of ecological phenomena on which ATAs have been shown to have an important impact (Ghosh et al., 2021; Ghosh, Sheppard, Holder, et al., 2020; Ghosh, Sheppard, Reid, & Reuman, 2020; Ghosh, Sheppard, & Reuman, 2020). 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 as the contribution of *associations* between *E* and *C*, generally, including 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. ATA contributions to coexistence were less important than other mechanisms in some contexts, but were very important in other contexts, including our empirically based example (the diatom system). Our work therefore demonstrates the potential for ATAs to be an important mechanism of coexistence, generally. Future work should seek to understand precisely when ATAs are or are not important for coexistence.

We return to the task, begun in the Introduction, of building intuition for how ATA effects work. Just as for storage effects (Chesson, 1994, Box 2 of Stump & Vasseur, 2023), temporal niche differentiation is necessary for ATA effects (Section S11). If temporal niche differentiation occurs but is partial, as will be typical,  $E_i$  and  $C_{i\setminus i}$  for a species  $i$  will be positively but imperfectly associated, and the association may be asymmetric. Storage events occur for species  $i$  when the positive effects of  $E_i$  overwhelm the negative effects of  $C_{i\setminus i}$ , producing large values of  $r_i(E_i, C_{i\setminus i})$  which are not completely offset by population declines at other times. For instance, for the lottery model,  $r_i(E_i, C_{i\setminus i}) = \log(1 - \delta + E_i/C_{i\setminus i})$  can get large whenever  $C_{i\setminus i}$  is a small fraction of  $E_i$ , but can never get smaller than  $\log(1 - \delta)$ . The potential for storage events can differ when  $E_i$  and  $C_{i\setminus i}$  are both above their median values compared to when they are both below median. For instance, the ratio  $E_i/C_{i\setminus i}$ , and therefore the growth rate  $\log(1 - \delta + E_i/C_{i\setminus i})$ , can both get very big, corresponding to rapid growth, if  $C_{i\setminus i}$  is close to 0, even if  $E_i$  is fairly small. In contrast, if  $E_i$  and  $C_{i\setminus i}$  are both in the right portions of their distributions, so that  $C_{i\setminus i}$  is bounded away from 0, there may be much sharper limits on the ratio  $E_i/C_{i\setminus i}$  and the growth rate. ATA effects quantify the extent to which asymmetries of association between *E* and *C* are aligned with varying potential for storage across the *E*, *C* distribution. ATA effects help quantify different degrees of temporal niche differentiation occurring under different sets of environmental conditions, possibly via different

mechanisms. Further details and examples of this intuition are in Section S12 and Figures S4 and S5, where comparisons are also made between our two lottery models.

An additional motivation for quantifying the importance of ATAs for 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 (Jentsch et al., 2007; Keelings & Moradkhani, 2020; Lyon et al., 2019; Meehl & Tebaldi, 2004; Ummenhofer & Meehl, 2017). 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 covariation between phenologically separated environmental signals may be modified by these changes; in particular, ATAs between such variables may be altered. For instance, imagine a case in which early spring temperature influences the growth of a plant species, A, whereas late spring temperature influences species B. If these species are competitors, then *EC* covariation influencing their potential coexistence could boil down to covariation between early and late spring temperatures (e.g. if competitive dynamics are governed by the lottery model with  $E_i$  representing early spring temperature and  $E_j$  representing late spring temperature, see Section S13). Because longer lasting heat waves are more likely to contribute to both early and late spring temperature, a tendency for heat waves to become both more extreme and longer lasting increases the right-tail association between early and late spring temperature. As we showed in this study, changes in ATAs can then result in different competitive outcomes. To our knowledge, the potential importance of climatic changes in ATAs for species coexistence has not been studied, though the importance for coexistence of changes in means and variability of environmental variables has been studied in many systems (e.g. Adler et al., 2006; Angert et al., 2009; Descombes et al., 2020; di Paola et al., 2012; Jentsch et al., 2007; Usinowicz & Levine, 2021; White et al., 2001). Changes in variability and in extreme events are distinct from the changes in ATAs we consider here, because ATAs pertain to *relationships* between environmental and other variables in the extremes, which are distinct from and can be altered independently of changes in the extremes of the univariate marginal distributions themselves (Ghosh, Sheppard, Holder, et al., 2020; Nelsen, 2006). Additional discussion points are in Sections S13–S17.

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

Our prior work shows that ATAs are common in ecological and environmental variables (Ghosh, Sheppard, Holder, et al., 2020). We have here used 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, and other complexities.

## AUTHOR CONTRIBUTIONS

Both authors contributed about equally to all parts of the paper.

## ACKNOWLEDGEMENTS

The authors thank Shyamolina Ghosh for suggesting the research problem, and Lawrence Sheppard, Max Castorani, Jon Walter, Jude Kastens, Vadim Karatayev, Emily Arsenaault, Jordan Rodriguez, Lauren Hallett, Madelon Case, Chhaya Werner, Lina Aoyama, Steven Haring, Carmen Watkins, Robin Snyder, and three anonymous referees and the editor for helpful feedback. The authors especially thank Steve Ellner for key advice at several watershed moments in the development of the project.

## FUNDING INFORMATION

The authors were partly supported by US National Science Foundation grants 1714195 and 2023474, the James S McDonnell Foundation, the California Department of Fish and Wildlife Delta Science Program, and the Alexander von Humboldt Foundation.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14334>.

## DATA AVAILABILITY STATEMENT

All code and data for the project are available at <https://zenodo.org/record/8386993>, doi 10.5281/zenodo.8386993; and also at <https://github.com/jasminalbert/AsymmetricRelationshipsAndCoexistence>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Albert, P.J. & Reuman, D.C. (2023) Asymmetric relationships and their effects on coexistence. *Ecology Letters*, 00, 1–13. Available from: <https://doi.org/10.1111/ele.14334>