# Drivers of spatial synchrony in giant kelp populations

#### Daniel C. Reuman

#### 1 The Model

We used the lottery model, previously studied, for instance, by REFS. Model equations are

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

for species i=1,2. Here,  $N_i(t)$  is the population density of species i at time t, and  $N=N_1(t)+N_2(t)$  is fixed through time. The parameter,  $\delta$  is a mortality rate, and  $B_i(t)$  is the fecundiity of species i at time t. The model postulates that individuals die at rate  $\delta$  at each time step, and are replaced by juveniles in population to the reproductive output of the two species that year. We take, for each i,  $B_i(t)$  to be iid through time. We let  $B_i = \exp(b_i)$ , where  $(b_1, b_2)$  is some distribution such that  $b_i \sim N\left(\mu_i, \sigma^2\right)$  and such that  $\cot(b_1, b_2) = \rho$ , a fixed quantity we will specify later. However,  $(b_1, b_2)$  is not necessarily a bivariate normal distribution. We will consider various distributions of  $(b_1, b_2)$  with these properties, corresponding to our symmetric and asymmetric tail associations cases defined in the main text and elaborated below. We assume without loss of generality that  $\mu_1 \leq \mu_2$ , so that species 1 is the weaker competitor.

#### 2 Noise

We created three cases for  $(b_1,b_2)$ , the case of symmetric tail association and the cases of asymmetrical left- and right-tail association. To generate M points  $\left(b_1^{(i)},b_2^{(i)}\right)$ , i=1,...,M, for the left tail association case, we first generated M points  $(a_1^{(i)},a_2^{(i)})$ , i=1,...,M, from a bivariate normal distribution  $N\left(\vec{0},\Sigma\right)$ , where here  $\Sigma=\begin{pmatrix}1&0\\0&1\end{pmatrix}$ . Then, for each index i, we randomly, with 50% probability, either (A) let  $\tilde{b}_1^{(i)}=-|a_1^{(i)}|$  and  $\tilde{b}_2^{(i)}=-a|a_1^{(i)}|$ , or (B) let  $\tilde{b}_1^{(i)}=|a_1^{(i)}|$  and  $\tilde{b}_2^{(i)}=|a_2^{(i)}|$ . We then let  $b_1^{(i)}=\sigma \tilde{b}_1^{(i)}+\mu_1$  and  $b_2^{(i)}=\sigma \tilde{b}_2^{(i)}+\mu_2$ . Perfect association in the left tails of the resulting distribution  $(b_1,b_2)$  results from the fact that, in case (A) above, both  $\tilde{b}_1^{(i)}$  and  $\tilde{b}_2^{(i)}$  were assigned to the same value. For speed of computation, when samples  $(\tilde{b}_1^{(i)},\tilde{b}_2^{(i)})$ , i=1,...,M were needed for every distinct set of values of the parameters  $\mu_1,\mu_2$ , and  $\sigma^2$ , we used the same  $\left(\tilde{b}_1^{(i)},\tilde{b}_2^{(i)}\right)$ , i=1,...,M, simply transforming these values differently (using the different values of  $\mu_1,\mu_2,\sigma$ ) for each set of parameter values. Right-tail associated noise was generated in an analogous way.

Noise with symmetric tail association was generated by taking a very large sample (100000) of left-tail associated noise, as described above, and then calculating the Pearson correlation coefficient, rho. The value obtained was ... . The symmetric noise was then generated once from  $N\left(\vec{0},\Sigma\right)$  where  $\Sigma=\begin{pmatrix}1&\rho\\\rho&1\end{pmatrix}$ , denoting the points so generated by  $\begin{pmatrix}\tilde{b}_1^{(i)},\tilde{b}_2^{(i)}\end{pmatrix}$  for i=1,...,M. We then set  $b_1^{(i)}=\sigma\tilde{b}_1^{(i)}+\mu_1$  and  $b_2^{(i)}=\sigma\tilde{b}_2^{(i)}+\mu_2$ .

Thus, overall, our model was completely specified by specifying  $\delta$ ,  $\mu_1$ ,  $\mu_2$ ,  $\sigma$  and whether noise was generated from the left-tailed association, right-tailed association or symmetric tail association cases specified above.

## 3 Invasion growth rate of species 1, and storage effects

We consider the invasion growth rate of species 1,  $\bar{r}_1 = \mathrm{E}(\ln(\frac{N_1(t+1)}{N_1(t)}))$ , when  $N_1$  is close to 0 and  $N_2$  is close to N. Hence  $\mathrm{E}(\cdot)$  represents expected value. We have

$$\frac{N_1(t+1)}{N_1(t)} = (1-\delta) + \delta N \frac{B_1(t)}{B_1(t)N_1(t) + B_2(t)N_2(t)},\tag{2}$$

but setting  $N_1 = 0$  and  $N_2 = N$  here gives the result that

$$\bar{r}_1 = \mathrm{E}(\ln[(1-\delta) + \delta \exp(b_1 - b_2)]). \tag{3}$$

We considered the various cases for the joint distribution  $(b_1, b_2)$ , specified in the main text and in the previous section.

To study storage effect for the model, we also consider the contribution of EC covariance to the difference between the invader's and the resident's mean growth rates, to be denoted  $\Delta I$ . Following REF, we define

$$\bar{r}_1^{\#} = \mathrm{E}(\ln[(1-\delta) + \delta \exp(b_1^{\#} - b_2)]),$$
 (4)

where  $b_1^{\#}$  is distributed in the same way as  $b_1$ , but is independent of it and  $b_2$ . Then  $\bar{r}_1 - \bar{r}_1^{\#}$  is the contribution of EC covariance to the mean growth rate species 1, the invader. We know, a priori, that the mean growth rate of the resident, species 2, must be 0,  $\bar{r}_2 = 0$ , but equation (1) also implies that

$$\frac{N_2(t+1)}{N_2(t)} = (1-\delta) + \delta N \frac{B_2(t)}{B_1(t)N_1(t) + B_2(t)N_2(t)}.$$
 (5)

Setting  $N_2 = N$  and  $N_1 = 0$  then gives

$$\frac{N_2(t+1)}{N_2(t)} = (1-\delta) + \delta = 1 \tag{6}$$

so

$$E(\ln(\frac{N_2(t+1)}{N_2(t)})) = 0, (7)$$

as expected. Again, following REF, we also define

$$\bar{r}_2^{\#} = \mathrm{E}(\ln[(1-\delta) + \delta \exp(b_2^{\#} - b_2)]),$$
 (8)

where  $b_2^{\#}$  is distributed in the same way as  $b_2$ , but is independent of it and of  $b_1$ . Thus  $\bar{r}_2 - \bar{r}_2^{\#} = -\bar{r}_2^{\#}$  is the contribution of EC covariance to the mean growth rate of species 2, the resident. And so

$$\Delta I = (\bar{r}_1 - \bar{r}_1^{\#}) - (\bar{r}_2 - \bar{r}_2^{\#}) = \bar{r}_1 - \bar{r}_1^{\#} + \bar{r}_2^{\#}$$
(9)

has been defined in terms of expected values of elementary expressions of the random variables  $(b_1, b_2)$ ,  $(b_1^{\#}, b_2)$ , and  $(b_2^{\#}, b_2)$ .

Having already specified that  $b_1$  (and therefore also  $b_1^{\#}$ ) is distributed as  $N(\mu_1, \sigma^2)$ , and that  $b_2$  (and therefore also  $b_2^{\#}$ ) is distributed as  $N(\mu_2, \sigma^2)$ , we know, using  $\Sigma$  as notation for a covariance matrix that

$$\left(b_1^{\#}, b_2\right) \sim N\left(\left(\mu_1, \mu_2\right), \Sigma\right) \tag{10}$$

and

$$(b_2^{\#}, b_2) \sim N((\mu_2, \mu_2), \Sigma)$$
 (11)

where

$$\Sigma = \begin{pmatrix} \sigma^2 & 0\\ 0 & \sigma^2 \end{pmatrix}. \tag{12}$$

Thus the difference  $b_1^{\#} - b_2$  that occurs in the expression for  $\bar{r}_1^{\#}$  (4) is a normally distributed random variable with mean  $\mu_1 - \mu_2$  and variance  $2\sigma^2$ . Thus

$$\bar{r}_1^{\#} = \mathrm{E}(\ln[(1-\delta) + \delta \exp(u)]),\tag{13}$$

where  $u \sim N(\mu_1 - \mu_2, 2\sigma^2)$ . Likewise, the difference  $b_2^{\#} - b_2$  in (8) is a normally distributed random variable with mean  $\mu_2 - \mu_2 = 0$  and variance  $2\sigma^2$ , so

$$\bar{r}_2^{\#} = \mathrm{E}(\ln[(1-\delta) + \delta \exp(u)]),\tag{14}$$

where now  $u \sim N(0, 2\sigma^2)$ . The expression (3) for  $\bar{r}_1$  can also be further simplified, in a similar way, when we are in the symmetric tail association case considered in section 2. In that case,

$$(b_1, b_2) \sim N((\mu_1, \mu_2), \Sigma)$$
 (15)

where now

$$\Sigma = \begin{pmatrix} \sigma^2 & \rho \\ \rho & \sigma^2 \end{pmatrix} \tag{16}$$

and rho = put invalue was determined as in section 2. Therefore, the expression  $b_1 - b_2$  that occurred in 3, in the symmetric tail association case, is a normally distributed random variable with mean  $\mu_1 - \mu_2$  and variance

$$var(b_1 - b_2) = cov(b_1 - b_2, b_1 - b_2)$$
(17)

$$= cov(b_1, b_1) + cov(b_2, b_2) - cov(b_1, b_2) - cov(b_2, b_1)$$
(18)

$$=2\sigma^2 - 2\rho. \tag{19}$$

Thus, again only in the symmetric tail association case,

$$\bar{r}_1 = \mathcal{E}(\ln[1 - \delta + \delta \exp(u)]),\tag{20}$$

where here  $u \sim N(\mu_1 - \mu_2, 2\sigma^2 - 2\rho)$ . As for all we know there is no simplicifaction of the expression 3 for  $\bar{r}_1$  in the left and right-tail association cases.

Thus for in summary,

$$\bar{r}_1 = \mathrm{E}(\ln[1 - \delta + \delta \exp(u)]), u \sim N(\mu_1 - \mu_2, 2\sigma^2 - 2\rho),$$
 (21)

for the symmetric case, and

$$\bar{r}_1^{\#} = \mathrm{E}(\ln[1 - \delta + \delta \exp(u)]), u \sim N(\mu_1 - \mu_2, 2\sigma^2),$$
 (22)

$$\bar{r}_2^{\#} = \mathrm{E}(\ln[1 - \delta + \delta \exp(u)]), u \sim N(0, 2\sigma^2).$$
 (23)

We next use the expressions to develop methods to estimate  $\bar{r}_1$  and  $\Delta I$  for any given parameters  $\delta, \mu_1, \mu_2, \sigma$ .

### 4 Estimating $\bar{r}_1$ and $\Delta I$

First, for a large integer M, carry out the following steps once:

- 1. Generate left-tail assocated noise  $(\tilde{b}_{l1}^{(i)}, \tilde{b}_{l2}^{(i)})$ , i = 1, ..., M, as described in the section 2. Hence  $\tilde{b}_{l1}^{(i)}$  and  $\tilde{b}_{l2}^{(i)}$  are distributed as N(0, 1).
- 2. Generate right-tail associated noise  $(\tilde{b}_{r1}^{(i)}, \tilde{b}_{r2}^{(i)})$ , i = 1, ..., M, via the analogous procedure. Again,  $\tilde{b}_{r1}^{(i)}$  and  $\tilde{b}_{r2}^{(i)}$  are distributed as N(0, 1).
- 3. Generate M points  $\tilde{u}_i$ , i = 1, ..., M from a standard normal distribution.

Next, given values of parameters  $\delta, \mu_1, \mu_2$ , and  $\sigma$ , proceed as follows to get estimates of  $\bar{r}_1, \bar{r}_1^{\#}, \bar{r}_2^{\#}$ , and  $\Delta I$ .

- 1. Estimate  $\bar{r}_1$  for the left-tail associated case as  $\hat{r}_1 = \text{mean}_i(\ln[1-\delta+\delta\exp(b_{l1}^{(i)}-b_{l2}^{(i)})])$  where  $b_{l1}^{(i)} = \sigma \tilde{b}_{l1}^{(i)} + \mu_1$  and  $b_{l2}^{(i)} = \sigma \tilde{b}_{l2}^{(i)} + \mu_2$ . The standard error of this estimate is  $\operatorname{se}(\hat{r}_1) = \frac{\operatorname{sd}_i(\ln[1-\delta+\delta\exp(b_{l1}^{(i)}-b_{l2}^{(i)})])}{\sqrt{M}}$ , where  $\operatorname{sd}_i(\cdot)$  is standard deviation.
- 2. Estiate  $\bar{r}_1$  for the left-tail associated case as  $\hat{r}_1 = \text{mean}_i(\ln[1-\delta+\delta\exp(b_{r1}^{(i)}-b_{r2}^{(i)})])$  where  $b_{r1}^{(i)} = \sigma \tilde{b}_{r1}^{(i)} + \mu_1$  and  $b_{r2}^{(i)} = \sigma \tilde{b}_{r2}^{(i)} + \mu_2$ . The standard error of this estimate is  $\text{se}(\hat{r}_1) = \frac{\text{sd}_i(\ln[1-\delta+\delta\exp(b_{r1}^{(i)}-b_{r2}^{(i)})])}{\sqrt{M}}$ .
- 3. Estimate  $\bar{r}_1$  in the symmetric tail association case as  $\hat{r}_1 = \text{mean}_i(\ln[1-\delta+\delta\exp(u_i)])$ , where  $u_i = \sqrt{(2\sigma^2 2\rho)}\tilde{u}_i + \mu_1 \mu_2$ . The standard error of this estimation is  $\text{se}(\hat{r}_1) = \frac{\text{sd}_i(\ln[1-\delta+\delta\exp(u_i)])}{\sqrt{M}}$ .
- 4. Estimate  $\bar{r}_1^{\#}$  (for all three tail-assocaition cases) as  $\hat{r}_1^{\#} = \text{mean}_i(\ln[1 \delta + \delta \exp(u_i)])$ , where  $u_i = \sqrt{2\sigma^2}\tilde{u}_i + \mu_1 \mu_2$ . The standard error is  $\text{se}(\hat{r}_1^{\#}) = \text{sd}_i \frac{\ln[1 \delta + \delta \exp(u_i)]}{\sqrt{M}}$ .
- 5. Estimate  $\bar{r}_2^{\#}$  (for all three tail-assocaition cases) as  $\hat{r}_2^{\#} = \text{mean}_i(\ln[1 \delta + \delta \exp(u_i)])$ , where  $u_i = \sqrt{2\sigma^2}\tilde{u}_i$ . The standard error is  $\text{se}(\hat{r}_2^{\#}) = \text{sd}_i \frac{\ln[1 \delta + \delta \exp(u_i)]}{\sqrt{M}}$ .
- 6.  $\hat{\Delta I} = \hat{r}_1 \hat{r}_1^\# + \hat{r}_2^\#$ , estimated separately for the left-tail associated, right-tail associated and symmetric noise cases. We obtained conservative standard error estimates by adding the standard error of the estimates of  $\hat{r}_1, \hat{r}_1^\#$ , and  $\hat{r}_2^\#$ .

For large enough M, standard error should be very small. Since random variables are generated once only, computation of these quantitaties for a large number of parameter sets should be fast.

# 5 Additional quantities influencing invasion success

Not only does the expected value  $\bar{r}_1$  influence the capacity for species 1 to invade where rare, but so do other aspects of the distribution of

$$r_1 = \ln[1 - \delta + \delta \exp(b_1 - b_2)].$$
 (24)

We here elaborate how some other aspects of the distribution of  $r_1$  were quantified, for our three tail association cases and for any of our parameters  $\delta, \mu_1, \mu_2, \sigma$ .

First, we considered  $sd(r_1)$ , the standard deviation. If this is large enough, then  $r_1$  can occasionally be positive even if  $\bar{r}_1$  is strongly negative, and this invasion can occur under the right environmental circumstances.

We also considered the probability  $P[r_1 > 0]$ , which is, explicitly, the probability that environmental variables that permit invasion. We have

$$P[r_1 > 0] = P[1 - \delta + \delta \exp(b_1 - b_2) > 1]$$
(25)

$$= P[\exp(b_1 - b_2) > 1] \tag{26}$$

$$= P[b_1 > b_2],$$
 (27)

so this was computed for each considered parameter set of  $\delta, \mu_1, \mu_2, \sigma$ , and for each of our three tail association cases.

We also consider the mean value of the possible part of the distribution of  $r_1$ ,  $E(r_1|r_1 > 0)$ . This characterizes how quickly invasion may happen, when it happens, with larger values corresponding to faster invasion. If it takes several time steps for the population of the invader to rise from negligible level at which species 1 is a noticeable presence in the community, then environmental conditions must be suitable for invasion for several sequential time steps. Thus large values of  $E(r_1|r_1 > 0)$  should also correspond to a greater probability of invasion because they should correspond to faster invasions and therefore to reduced need for sequential periods of suitable environmental conditions.

Finally, for a few choices of parameters  $\delta$ ,  $\mu_1$ ,  $\mu_2$ ,  $\sigma$ , we displayed the whole distribution of  $r_1$ , values for each of our tail association cases, to make visual comparisons.

### 6 Symmetries and parameter reduction

The quantities we consider to address invasion prospects for the weaker competitor, species 1 (see sections 3 and 5) depend only on  $\mu_1 - \mu_2$  and not, independtly, on  $\mu_1$  and  $\mu_2$ , and also are the same for our left-and right-tailed association cases. We prove these statements in this section.

Equations 21 - 23 obviously depend only on  $\mu_1 - \mu_2$ , and not independently on  $\mu_1$  and  $\mu_2$ , since only  $\mu_1 - \mu_2$  appears in these expressions if  $\mu_1$  or  $\mu_2$  appear at all. Equation 3 is  $\bar{r}_1$  in the asymmetric tail association cases. But letting  $\beta_1 = b_1 + \eta$  and  $\beta_2 = b_2 + \eta$  and substituting into 3, we get

$$\bar{r}_1 = \mathrm{E}(\ln[1 - \delta + \delta \exp(\beta_1 - \eta - (\beta_2 - \eta))]) \tag{28}$$

$$= E(\ln[1 - \delta + \delta \exp(\beta_1 - \beta_2)]). \tag{29}$$

And so altering the mean of both  $b_1$  and  $b_2$  distributions by the same amount has no affect of  $\bar{r}_1$ , and thus  $\bar{r}_1$  in the asymmetric tail associations also depends only on  $\mu_1 - \mu_2$  and not independily on  $\mu_1$  or  $\mu_2$ . In section 5, we introduce several other metrics. These are all based on the distribution

$$r_1 = \ln[1 - \delta + \delta \exp(b_1 - b_2)].$$
 (30)

But, again making the substitutions  $\beta_1 = b_1 + \eta$  and  $\beta_2 = b_2 + \eta$ , we can see via the same resoning as above that the whole distribution  $r_1$  depends only on  $\mu_1 - \mu_2$ , and not on  $\mu_1$  and  $\mu_2$  independently, for all three of our tail association cases.

To see that our various metrics are the same for out left- and right-tail associated noise processes, let  $(b_1, b_2)$  denote our left-tail associated random variable with parameters  $\mu_1, \mu_2, \sigma$ . Then define  $\beta_1 = -b_2 + \mu_1 + \mu_2$ ,  $\beta_2 = -b_1 + \mu_1 + \mu_2$ . It is easy to see that  $E(\beta_1) = \mu_1$ ,  $E(\beta_2) = \mu_2$ ,  $\operatorname{sd}(\beta_1) = \operatorname{sd}(\beta_2) = \sigma$ , so  $\beta_1$  and  $\beta_2$  are normally distributed. From there it is easy to see that  $\beta_1$  and  $\beta_2$  are distributed in the same wat as our right-tail associated noise with parameter  $\mu_1, \mu_2$ , and  $\sigma$ . Making the substitutions  $b_2 = -\beta_1 + \mu_1 + \mu_2$  and  $b_1 = -\beta_2 + \mu_1 + \mu_2$  in 30, we get

$$r_1 = \ln[1 - \delta + \delta \exp(-\beta_2 + \mu_1 + \mu_2 - (\beta_1 + \mu_1 + \mu_2))]$$
(31)

$$= \ln[1 - \delta + \delta \exp(\beta_1 - \beta_2)]. \tag{32}$$

And since  $(\beta_1, \beta_2)$  is distributed in the same way as our right-tail associated noise, this proves all metrics based on the distribution of  $r_1$  (30) are the same for left- and right-tail associated noise.

### 7 E and C definitions

The lottery model is given by

$$N_i(t+1) = (1-\delta)N(t) + \delta N \frac{B_i(t)N_i(t)}{B_1(t)N_1(t) + B_2(t)N_2(t)}.$$
(33)

REF also defines  $E_i=B_i$  and  $C_1=C_2=\frac{B_1N_1+B_2N_2}{\delta N}$ . Then in the invader-resident scenario which defines the invader to be essentially zero and  $N_2=N$ ,  $C_1=C_2=\frac{B_2}{\delta}$ . The growth rate equation relates the two variables of E and C by

$$\bar{r}_i = \mathcal{E}(\ln(1 - \delta + \frac{E_i}{C_i})). \tag{34}$$

By substituting the definitions,

$$\bar{r}_i = \mathrm{E}(\ln(1 - \delta + \frac{B_i}{B_2/\delta})) \tag{35}$$

$$= E(\ln(1 - \delta + \delta \frac{B_i}{B_2})) \tag{36}$$

The null growth rate of species i is computed by setting both E and C at their means.

$$\epsilon_i^0 = \ln(1 - \delta + \frac{\bar{E}_i}{\bar{C}_i}) \tag{37}$$

$$= \ln(1 - \delta + \delta \frac{\bar{B}_i}{\bar{B}_2}) \tag{38}$$

The contribution of variance E in to the IGR is computed by setting C to its mean and letting E vary subtracted by the null.

$$\epsilon_i^E = \ln(1 - \delta + \frac{E_i}{\bar{C}_i}) - \epsilon_i^0 \tag{39}$$

$$= \ln(1 - \delta + \delta \frac{B_i}{\overline{B}_2}) - \epsilon_i^0 \tag{40}$$

$$\bar{\epsilon}_i^E = \mathcal{E}(\epsilon_i^E) \tag{41}$$

Similarly, the contribution of variance C in to the IGR is computed by setting E to its mean and letting C vary subtracted by the null.

$$\epsilon_i^C = \ln(1 - \delta + \frac{\bar{E}_i}{C_i}) - \epsilon_i^0 \tag{42}$$

$$= \ln(1 - \delta + \delta \frac{\bar{B}_i}{B_2}) - \epsilon_i^0 \tag{43}$$

$$\bar{\epsilon}_i^C = \mathcal{E}(\epsilon_i^C) \tag{44}$$

The contribution of both E and C varying to the IGR is computed by letting both variables vary subtracted by the null and the contributions of only one variable varying.

$$\epsilon_i^{EC} = \ln(1 - \delta + \delta \frac{B_i}{B_i}) - [\epsilon_i^0 + \epsilon_i^E + \epsilon_i^C]$$
(45)

$$\bar{\epsilon}_i^{EC} = \mathbb{E}(\ln(1 - \delta + \delta \frac{B_i}{B_j})) - [\epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C]$$
(46)

So,

$$\bar{r}_i = \epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C + \bar{\epsilon}_i^{EC}. \tag{47}$$

But some of  $\bar{\epsilon}_i^{EC}$  comes from covariance between E and C and some comes from both varying independently.

$$\bar{\epsilon}_i^{(E\#C)} = \mathrm{E}(\ln(1-\delta + \frac{E_i}{C_i^\#})) - [\epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C]$$
(48)

$$= \operatorname{E}(\ln(1 - \delta + \delta \frac{B_i}{B_2^{\#}})) - \left[\epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C\right]$$
(49)

$$\bar{\epsilon}_i^{(EC)} = \bar{\epsilon}_i^{EC} - \bar{\epsilon}_i^{(E\#C)} \tag{50}$$

$$= \operatorname{E}(\ln(1 - \delta + \frac{E_i}{C_i})) - \left[\epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C\right]$$
(51)

$$-\left[\mathrm{E}(\ln(1-\delta+\frac{E_i}{C_i^{\#}}))-\left[\epsilon_i^0+\bar{\epsilon}_i^E+\bar{\epsilon}_i^C\right]\right]$$
(52)

$$= E(\ln(1 - \delta + \delta \frac{B_i}{B_2})) - \epsilon_i^0 - \bar{\epsilon}_i^E - \bar{\epsilon}_i^C$$
(53)

$$-\operatorname{E}(\ln(1-\delta+\delta\frac{B_i}{B_2^{\#}})) + \epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C$$
(54)

$$= \mathrm{E}(\ln(1 - \delta + \delta \frac{B_i}{B_2})) - \mathrm{E}(\ln(1 - \delta + \delta \frac{B_i}{B_2^{\#}}))$$

$$(55)$$

(56)

# 8 Decomposition

To quantify the contribution of different drivers to the difference in growth rate between the invader and the resident, the amount variance due to that driver is considered. We consider the contributions of the null growth rate,  $\epsilon^0$ , the contribution of variance in E (environment),  $\bar{\epsilon}^E$ , the contribution of the variance in C (competitive pressure),  $\bar{\epsilon}^C$ , the contribition of E and C co-varying  $\bar{\epsilon}^{(EC)}$ , and the the contribition of E and C varying, but independently,  $\bar{\epsilon}^{(E\#C)}$ , for the invader and the resident. The difference between invader and resident is computed term by term to get a full decomposition as follows,

$$\bar{r}_1 - \bar{r}_2 = \Delta^0 + \Delta^E + \Delta^C + \Delta^{(EC)} + \Delta^{(E\#C)},$$
 (57)

where each  $\Delta$  denotes a drivers contribution the the invader growth rate subtracted by the drivers contribution to the resident's growth rate.

The null growth rate is computed as the growth rate when both drivers (E and C) are set at their mean. Recalling the growth rate equation from equation 3,

$$\Delta^0 = \epsilon_1^0 - \epsilon_2^0 \tag{58}$$

$$= \ln(1 - \delta + \delta \frac{B_1}{\overline{B}_2}) - \ln(1 - \delta + \delta \frac{B_2}{\overline{B}_2}) \tag{59}$$

$$= \ln(1 - \delta + \delta \frac{\bar{B}_1}{\bar{B}_2}) - 0. \tag{60}$$

(61)

The contribution of variance in E to a species growth rate is computed by letting E vary and setting C to its mean, subtracted by the null. The contribution of variance in C to a species' growth rate is computed in an analogous way, but reverse.

$$\Delta^E = \bar{\epsilon}_1^E - \bar{\epsilon}_2^E \tag{62}$$

$$= \left[ \mathbb{E}(\ln[1 - \delta + \delta \frac{B_1}{\bar{B}_2}]) - \epsilon_1^0 \right] - \left[ \mathbb{E}(\ln[1 - \delta + \delta \frac{B_2}{\bar{B}_2}]) - \epsilon_2^0 \right]$$
 (63)

$$= \mathrm{E}(\ln[1 - \delta + \delta \frac{B_1}{\overline{B}_2}]) - \epsilon_1^0 - \mathrm{E}(\ln[1 - \delta + \delta \frac{B_2}{\overline{B}_2}])$$

$$\tag{64}$$

(65)

$$\Delta^C = \bar{\epsilon}_1^C - \bar{\epsilon}_2^C \tag{66}$$

$$= \left[ E(\ln[1 - \delta + \delta \frac{B_1}{B_2}]) - \epsilon_1^0 \right] - \left[ E(\ln[1 - \delta + \delta \frac{B_2}{B_2}]) - \epsilon_2^0 \right]$$
 (67)

$$= E(\ln[1 - \delta + \delta \frac{B_1}{B_2}]) - \epsilon_1^0 - E(\ln[1 - \delta + \delta \frac{B_2}{B_2}])$$
 (68)

(69)

The contribution of E and C both varying but not together is computed by letting both terms vary but decoupling any association by substituting in a new independent varibable for one of the varibales. Here we use C. The term is subtracted by the previous contributions.

$$\Delta_1^{(E\#C)} = \bar{\epsilon}_1^{(E\#C)} - \bar{\epsilon}_2^{(E\#C)} \tag{70}$$

$$= \left[ \mathbb{E}(\ln[1 - \delta + \delta \frac{B_1}{B_2^{\#}}]) - [\epsilon_1^0 + \bar{\epsilon}_1^E + \bar{\epsilon}_1^C] \right] - \left[ \mathbb{E}(\ln[1 - \delta + \delta \frac{B_2}{B_2^{\#}}]) - [\epsilon_2^0 + \bar{\epsilon}_2^E + \bar{\epsilon}_2^C] \right]$$
(71)

(72)

The contribution of E and C co-varying is the storage effect. Computed by,

$$\Delta^{(EC)} = \bar{\epsilon}_1^{(EC)} - \bar{\epsilon}_2^{(EC)}. \tag{73}$$

Where,

$$\bar{\epsilon}_i^{(EC)} = \bar{\epsilon}_i^{EC} - \bar{\epsilon}_i^{(E\#C)} \tag{74}$$

$$= \operatorname{E}(\ln(1 - \delta + \delta \frac{B_i}{B_i})) - [\epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C]$$
(75)

$$-\operatorname{E}(\ln(1-\delta+\delta\frac{B_i}{B_j^{\#}})) + [\epsilon_i^0 + \bar{\epsilon}_i^E + \bar{\epsilon}_i^C]. \tag{76}$$

By substituting these expansions into 57, we get,

Recall from main text that the goal of this research is to investigate the implications of extreme events and thus asymmetric tail associations on coexistence. Hence, we compare IGR and mechanism values for each noise type. Because only association structure and not means and standard deviation is differ across noise types, different noise types will not result in differences in any of the decomposition terms outside of the storage effect term. All other terms do not consider the associative relationship between the two variables. The null growth grate is a constant that depends on the mean of both variables, the contribution of variance in one variable only depends on that one variable scaled by the mean of the other, and the varying but independent term while it does consider both variable they are set to be completely uncorrelated. These four terms will not differ across noise types.

### 9 new decomposition term

A new decomposition term was proposed to quantify the effect of asymmetric associations to coexistence. Since asymmetry only differs in the storage effect term,  $\bar{\epsilon}^{(EC)}$ , the contribution of asymmetry associations between the species will be a further decomposition.

$$\bar{\epsilon}^{(EC)} = \bar{\epsilon}^{(EC)} - \bar{\epsilon}^{(EC_0)} \tag{77}$$

The contribution of asymmetry to the storage effect is the observed storage effect subtracted by a null storage effect if the association between species was completely symmetrical. The descrition of  $\bar{\epsilon}^{(EC)}$  is given in section 3 and equations 9 and 21-23.

$$\bar{\epsilon}^{(EC_0)} = \bar{r}_1 - \bar{r}_1^{\#} + \bar{r}_2^{\#},\tag{78}$$

where  $\bar{r}_1, \bar{r}_1^{\#}$  and  $\bar{r}_2^{\#}$  are in the symmetric case. In our model,

$$\bar{\epsilon}^{(EC_0)} = E(\ln[1 - \delta + \delta \exp(u_1)]) - E(\ln[1 - \delta + \delta \exp(u_1^{\#})]) + E(\ln[1 - \delta + \delta \exp(u_2^{\#})]), \tag{79}$$

where  $u_1 \sim N(\mu_1 - \mu_2, 2\sigma^2 - 2\rho)$ ,  $u_1^{\#} \sim N(\mu_1 - \mu_2, 2\sigma^2)$ , and  $u_2^{\#} \sim N(0, 2\sigma^2)$ 

\*Note that the contribution of asymmetry to storage effects is not the same as the storage effect that we computed above for asymmetric cases.

In generalized terms, this further decomposition could be applied to test for contributions of asymmetry between any two variables. Here we tested the asymmetry between  $b_1$  and  $b_2$ . Why did we not look at E and C? Do they have to be normally distributed?

This break down would only work if the variables are normally distributed. Thus one can convert their distribution to normal to impliment this decomposition.