

# Relationships in the extremes and their influence on competition and coexistence

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## Abstract

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## 1 Introduction

## 2 Theory

For pedagogical clarity, we develop each step of the theory both for a simple classical model, the lottery model, and in general. The model is as follows. Letting  $N_i(t)$  denote the 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 a mortality rate, and  $B_i(t)$  is the fecundity 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 proportion to the reproductive outputs of the two species that year. For each  $i$ , we assume the random variables  $B_i(t)$  are independent and identically distributed (iid) through time. We let  $B_i = \exp(b_i)$ , where  $(b_1, b_2)$  is some bivariate random variable with the properties that  $b_i$  is normally distributed with mean  $\mu_i$  and variance  $\sigma^2$ . We denote  $\text{cov}(b_1, b_2)$  by  $\rho$ . However, we do *not* assume that  $(b_1, b_2)$  is a bivariate normal distribution. We will consider various distributions of  $(b_1, b_2)$  with the above properties, corresponding to symmetric and asymmetric tail association cases. We assume without loss of generality that  $\mu_1 \leq \mu_2$ , so that species 1 is the weaker competitor. Note that  $N$  is constant through time.

Modern coexistence theory (REFS) and its recent computational extensions (Ellner *et al.*, 2016, 2019) quantify the contributions of different mechanisms to species coexistence. But we show in Sup Mat section X that, for purely temporal variation, only one mechanism relates to tail associations: storage effects. We here define storage effects abstractly and then for the lottery model, using an approach and notation similar to that of Ellner *et al.* (2016) and Ellner *et al.* (2019).

## 3 Methods

## 4 Results

## 5 Discussion

## References

- Ellner, S., Snyder, R. & Adler, P. (2016). How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters*, 19, 1333–1342.
- Ellner, S., Snyder, R., Adler, P. & Hooker, G. (2019). An expanded modern coexistence theory for empirical applications. *Ecology Letters*, 22, 3–18.