

Supplementary Information

A Model analysis

Our model is defined by the finite rate of increase λ_{jt} ,

$$\lambda_{jt} = (1 - G_j)s_j + \frac{G_j Y_j D_t}{C'_{jt}} = G_j(D_t, C'_{jt}). \quad (\text{A.1})$$

Our analysis is based upon the growth rate

$$r_{jt} = \log \lambda_{jt} = g_j(D_t, C'_{jt}). \quad (\text{A.2})$$

To quantify mechanisms of coexistence, we make a quadratic approximation to long-term low-density growth rate \bar{r}_i , which is defined by

$$\bar{r}_i = \overline{\log \lambda_i}, \quad (\text{A.3})$$

where the subscript i is reserved for the growth rate of a low-density ‘invader’ species, in the presence of an established resident species r .

Equilibril values

We make an approximation about equilibril values of environmental and competitive response. These values are equilibril in the sense that

$$\lambda(D^*, C_j'^*) = 1. \quad (\text{A.4})$$

There is a whole continuum of equilibril values that will satisfy this condition. Since disturbance affects both species in the same manner, we set

$$D^* = \bar{D} \quad (\text{A.5})$$

This results in the following equation for $C_j'^*$, which is the amount of competition that allows a species to maintain a constant density in a constant environment.

$$(1 - G_j)s_j + \frac{G_j Y_j \bar{D}}{C_j'^*} = 1 \quad (\text{A.6})$$

$$C_j'^* = \frac{G_j Y_j \bar{D}}{1 - (1 - G_j)s_j} \quad (\text{A.7})$$

In biological terms, equation A.7 tells us what magnitude of competition will cause a species to maintain a constant density in a constant environment. The value of $G_j Y_j \bar{D}$ is the expected number of seeds produced by a single seed over the course of a season. The value $1 - (1 - G_j)s_j$ is the number of seeds that are lost from the seedbank, either by germination or death. Thus, the expression for $C_j'^*$ indicates that if competition exceeds this ‘replacement rate’, a species will decline.

Growth in Constant Environment

With the choice of equilibril values described above, a species’ long-term low-density growth rate in a constant environment is described by

$$\bar{r}'_i = -\mathcal{C}_i^{-i*}, \quad (\text{A.8})$$

where \mathcal{C}_i^{-i*} is the amount (standardized by its effect on growth rate) of competition that an invader experiences due to a resident population at equilibrium. Note the superscript $-i$ is used to denote the absence of invader species i . In this model, we have

$$\mathcal{C} = -\log \lambda_j(D^*, C) = -\log \left\{ (1 - G_j)s_j + \frac{G_j Y_j D^*}{C'_{jt}} \right\}. \quad (\text{A.9})$$

Table 1: List of symbols

symbol:	definition
λ_{jt}	: Finite rate of increase
r_{jt}	: Growth rate, $r_{jt} = \log \lambda_{jt}$
G_j	: germination rate
s_j	: seedbank survival
Y_j	: seed yield
α_{jk}	: competitive effect of species k on species j
D_t	: disturbance process
X_j	: number of seeds of species j

The competitive effect of the resident on the invader is $C_i'^{-i*} = \alpha_{ir} C_r'^*$, which leads to

$$\bar{r}'_i = \log \left\{ (1 - G_i) s_i + \frac{G_i Y_i D^*}{\alpha_{ir} C_r'^*} \right\} \quad (\text{A.10})$$

$$= \log \left\{ (1 - G_i) s_i + \frac{G_i Y_i D^*}{G_r Y_r D^*} \frac{1 - (1 - G_r) s_r}{\alpha_{ir}} \right\} \quad (\text{A.11})$$

Rearranging allows us to see under what conditions a species can grow from low density, i.e. $\bar{r}'_i > 0$. This will be the case whenever

$$(1 - G_i) s_i + \frac{G_i Y_i}{G_r Y_r} \cdot \frac{1 - (1 - G_r) s_r}{\alpha_{ir}} > 1, \quad (\text{A.12})$$

$$\frac{G_i Y_i}{1 - (1 - G_i) s_i} > \alpha_{ir} \frac{G_r Y_r}{1 - (1 - G_r) s_r} \quad (\text{A.13})$$

Biologically, inequality A.13 shows that an invader can grow from low density if its ratio of seeds produced to seedbank loss is greater than that of the resident's, when weighted by the resident's competitive effect, α_{ir} . Also we can see from this expression that coexistence is impossible in a constant environment, unless both species have competitive effects $\alpha_{ir} < 1$.

A.1 Mechanisms

As shown in section A, coexistence is impossible in a constant environment whenever one species' $\alpha_{ij} > 1$. However, when disturbance acts to create temporal heterogeneity, variation-dependent mechanisms of coexistence arise.

In the present investigation, the storage effect ΔI is small, often an order of magnitude smaller than other contributions to \bar{r}_i . As such, the storage effect has little effect on coexistence, and it is not included in the following expressions for \bar{r}_i . The dominant mechanism of coexistence is relative nonlinearity of competition, denoted ΔN . We follow the methods of Chesson (1) to quantify magnitude of relative nonlinearity for each species. The approach is based upon a quadratic approximation in terms of standardized variables \mathcal{E}, \mathcal{C} , defined by:

$$\mathcal{E}_j = g_j(D, C_j'^*) \quad (\text{A.14})$$

$$\mathcal{C}_j = -g_j(D^*, C_j') \quad (\text{A.15})$$

With this notation, we can write:

$$\bar{r}_i = \Delta E - \Delta C, \quad (\text{A.16})$$

where

$$\Delta E = \mathcal{E}_i - q_{ir}\mathcal{E}_r \quad (\text{A.17})$$

$$\Delta C = \mathcal{C}_i - q_{ir}\mathcal{C}_r \quad (\text{A.18})$$

$$(\text{A.19})$$

and the quantity q_{ir} measures the effect of resident competition on invader competition, that is

$$q_{ir} = \left. \frac{\partial \mathcal{C}_i^{-i}}{\partial \mathcal{C}_r^{-i}} \right|_*, \quad (\text{A.20})$$

where $|_*$ indicates evaluation at equilibril values. For our model, we compute

$$q_{ir} = \frac{\frac{G_i Y_i}{\alpha_{ir} G_r Y_r}}{\frac{G_i Y_i}{\alpha_{ir} G_r Y_r} (1 - (1 - G_r) s_r) + (1 - G_i) s_i}. \quad (\text{A.21})$$

Lastly, the terms contributing to ΔC that are due to resident competition at equilibrium are denoted \mathcal{C}_i^{-i*} . If we write invader competition as a function of resident competition $\mathcal{C}_i^{-i} = f(\mathcal{C}_r^{-i})$, then $\mathcal{C}_i^{-i*} = f(0)$, since residents by definition have zero net growth at equilibrium. In our model, we have

$$\mathcal{C}_i^{-i*} = -\log \left\{ \frac{G_i Y_i}{\alpha_{ir} G_r Y_r} (1 - (1 - G_r) s_r + (1 - G_i) s_i) \right\} \quad (\text{A.22})$$

Using these calculations, we compute relative nonlinearity ΔN via the definition

$$\Delta N = \Delta C - \mathcal{C}_i^{-i*}, \quad (\text{A.23})$$

References

- [1] Chesson P (1994) Multispecies Competition in Variable Environments. *Theoretical Population Biology* 45:227–276.