

Supplementary Material for

Understanding the emergence of contingent and deterministic exclusion in multispecies communities

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A A brief introduction to Modern Coexistence Theory on competitive exclusion

Modern Coexistence Theory (MCT) is widely adopted to study competitive exclusion (Chesson, 2000; Fukami *et al.*, 2016; Ke & Letten, 2018). The canonical formalism of MCT on two-species communities builds upon Lotka-Volterra (LV) competition dynamics. The formulation of two-species LV competition dynamics is written as

$$\begin{cases} \frac{dN_1}{dt} = N_1(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2) \\ \frac{dN_2}{dt} = N_2(r_2 - \alpha_{21}N_1 - \alpha_{22}N_2), \end{cases} \quad (\text{S1})$$

where the variable N_i represents the abundance of species i , the parameters $r_i > 0$ and $\alpha_{ii} > 0$ correspond to the intrinsic growth rate and the self-regulation (or intra-specific competition) of species i , respectively, and $\alpha_{12} > 0$ and $\alpha_{21} > 0$ are the corresponding interspecific competition strengths.

From the LV competition dynamics, MCT defines niche overlap ρ as $\rho = \sqrt{\alpha_{12}\alpha_{21}/\alpha_{11}\alpha_{22}}$, and species average fitness ratio κ_2/κ_1 as $r_2/r_1\sqrt{\alpha_{11}\alpha_{12}/\alpha_{22}\alpha_{21}}$ (Chesson, 2018; Bartomeus & Godoy, 2018). Building upon these two concepts, MCT claims that contingent exclusion arises when

$$\frac{1}{\rho} < \frac{\kappa_2}{\kappa_1} < \rho, \quad (\text{S2})$$

and deterministic exclusion arises when

$$\frac{\kappa_2}{\kappa_1} > \max\left\{\frac{1}{\rho}, \rho\right\} \text{ or } \frac{\kappa_2}{\kappa_1} < \min\left\{\frac{1}{\rho}, \rho\right\} \quad (\text{S3})$$

These conditions are illustrated in Figure 3. Note that we used the effective intrinsic growth rates and competition strength in Figure 3 as we translated the population dynamics of grass species into Equation S1.

B Interpretation of Structural Approach in different theoretical formalisms

The crux of the structural approach is to simplify ecological dynamics as a function of internal and external conditions. In the main text, we have represent external conditions by intrinsic growth rates and represent internal conditions by the competition structure. Here we briefly interpret this representation across several mathematically equivalent but ecologically different theoretical formalism of Lotka-Volterra dynamics. A more detailed discussion can be found in Song *et al.* (2020).

There are three theoretical formalisms of two-species Lotka-Volterra dynamics. The formalism we adopted in the structural approach (which we call r -formalism) is:

$$\begin{cases} \frac{dN_1}{dt} = N_1(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2) \\ \frac{dN_2}{dt} = N_2(r_2 - \alpha_{21}N_1 - \alpha_{22}N_2). \end{cases} \quad (\text{S4})$$

where r_i and α_{ij} are separated.

Modern Coexistence Theory usually adopts another formalism (which we call MCT-formalism):

$$\begin{cases} \frac{dN_1}{dt} = N_1 r_1 (1 - \bar{\alpha}_{11} N_1 - \bar{\alpha}_{12} N_2) \\ \frac{dN_2}{dt} = N_2 r_2 (1 - \bar{\alpha}_{21} N_1 - \bar{\alpha}_{22} N_2). \end{cases} \quad (\text{S5})$$

where $\bar{\alpha}_{ij} = \alpha_{ij}/r_i$. Thus, under the MCT-formalism, r_i and $\bar{\alpha}_{ij}$ are interlinked.

And the third formalism (which we call K -formalism) is:

$$\begin{cases} \frac{dN_1}{dt} = N_1 \frac{r_1}{K_1} (K_1 - N_1 - a_{12} N_2) \\ \frac{dN_2}{dt} = N_2 \frac{r_2}{K_2} (K_2 - a_{21} N_1 - N_2). \end{cases} \quad (\text{S6})$$

where the competition strength is to be standardized by the intraspecific competition, i.e., $a_{ij} = \alpha_{ij}/\alpha_{ii}$.

We first focus on the link between r -formalism and MCT-formalism. The ecological interpretations are fundamentally different in these two formalisms. The reason is that while α_{ij} and $\bar{\alpha}_{ij}$ are both called interaction strengths, they have different **units**: α_{ij} in the r -formalism measures the absolute reduction in the growth rates, while $\bar{\alpha}_{ij}$ in the MCT-formalism measures the relative reduction in the growth rates to the maximum growth rates. The reason why we have adopted the r -formalism is that α_{ij} in the r -formalism is what most empirical studies measure.

We then focus on the link between r -formalism and K -formalism. To establish the equivalence between the r -formalism and the K -formalism, the carrying capacity K_i of species i and the intrinsic growth rates are linked via $K_i = r_i/\alpha_{ii}$. Thus, if we assume that α_{ii} is fixed (which is a common assumption in theoretical and empirical studies), then K_i and r_i would reflect identical biotic or abiotic information.

C Applying the structural approach to the population dynamics of annual and perennial species

C.1 A brief introduction of the structural approach

Here we present a brief, self-contained description of the structural approach in community ecology. A more detailed, technical description can be found in Song *et al.* (2018).

Consider an ecological community with S interacting species governed by some nonlinear population dynamics. Suppose the equilibrium $\{N_j^*\}$ of the community is constrained by a set of linear equations,

$$r_i = \sum_{j=1}^S a_{ij} N_j^*, i = 1, \dots, S \quad (\text{S7})$$

where r_i is referred as the effective intrinsic growth rate and a_{ij} is referred as the effective interaction strength.

Feasibility of the community refers to the situation in which the equilibrium of all species is positive (i.e., $N_j^* > 0$, for all j) (Roberts, 1974). The feasibility domain D_F —the full set of intrinsic growth rates r_i that gives rise to feasibility—is given by (Logofet, 1993; Song *et al.*, 2018):

$$D_F = \{ \mathbf{r} \mid \mathbf{r} = -N_1^* \mathbf{v}_1 - \dots - N_S^* \mathbf{v}_S, \text{ with } N_1^*, \dots, N_S^* > 0 \}, \quad (\text{S8})$$

where $\mathbf{v}_i = \{a_{1i}, \dots, a_{Si}\}$ is the i th column vector of the interaction matrix.

Importantly, the operation of positive scalar multiplication on the column space of the effective competition structure \mathbf{A} does not change the feasibility domain (Song *et al.*, 2018). Specifically, $\mathbf{v}_j \rightarrow c_j \mathbf{v}_j$ when c_j is some positive constant (equivalently, changing the effective competition strength from a_{ij} to $c_j a_{ij}$ for all i) does not change the feasibility domain.

C.2 Annual species

We first apply the structural approach to the population dynamics of annual species. As a reminder, the population dynamics of annual species is written as:

$$N_i(t+1) = \underbrace{N_i(t) g_i \frac{\lambda_i}{1 + \sum_j \alpha_{ij} D_j(t)}}_{\text{germinated seeds under competition}} + \underbrace{N_i(t)(1 - g_i)}_{\text{non-germinated seeds}}, \quad (\text{S9})$$

To perform the feasibility analysis in the structural approach, we focus on the equilibrium $N_i(t+1) = N_i(t)$. The equilibrium condition is equivalent to:

$$N_i(t+1) = N_i(t) \quad (\text{S10})$$

$$\Leftrightarrow N_i(t) g_i \frac{\lambda_i}{1 + \sum_j \alpha_{ij} D_j(t)} + N_i(t)(1 - g_i) = N_i(t) \quad (\text{S11})$$

$$\Leftrightarrow g_i \frac{\lambda_i}{1 + \sum_j \alpha_{ij} D_j(t)} + (1 - g_i) = 1 \quad (\text{S12})$$

$$\Leftrightarrow g_i \frac{\lambda_i}{1 + \sum_j \alpha_{ij} D_j(t)} - g_i = 0 \quad (\text{S13})$$

$$\Leftrightarrow \lambda_i - 1 = \sum_j \alpha_{ij} D_j(t) \quad (\text{S14})$$

Substituting the definition of D_j from Eqn. (2), the equilibrium condition can be equivalently expressed as:

$$\lambda_i - 1 = \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S, \quad i \in \mathcal{A} \quad (\text{S15})$$

C.3 Perennial species

Then we apply the structural approach to the population dynamics of perennial species. As a reminder, the population dynamics of perennial species are written as:

$$N_i^S(t+1) = \underbrace{N_i^A(t) \frac{\lambda_i}{1 + \sum_j \alpha_{ij} D_j(t)}}_{\text{produced seeds from adults}} + \underbrace{N_i^S(t)(1 - g_i)}_{\text{non-germinated seeds}}, \quad (\text{S16})$$

$$N_i^A(t+1) = \underbrace{N_i^A(t) \omega_i}_{\text{survived adults}} + \underbrace{N_i^S(t) \frac{g_i v_i}{1 + \sum_j \beta_{ij} D_j(t)}}_{\text{germinated seeds into adults}}, \quad (\text{S17})$$

C.3.1 Excluding life-history processes in perennial species

When we exclude the life-history processes in perennial species, the equilibrium condition is same as that of annual species (Eqn. S15):

$$\lambda_i - 1 = \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S, \quad i \in \mathcal{P}. \quad (\text{S18})$$

C.3.2 Incorporating life-history processes in perennial species

Without considering the density-dependence in transition from adults to seeds Here we consider the case when the germinated seeds into adults are not under the pressure of competition. Mathematically, $\beta_{ij} = 0$ in Eqn. 4. Specifically, Eqns. 3 and 4 reduce to:

$$g_i N_i^S = N_i^A \frac{\lambda_i}{1 + \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S + \sum_{j \in \mathcal{P}} \alpha_{ij} N_j^A}, \quad (\text{S19})$$

$$N_i^A = N_i^S \frac{g_i v_i}{1 - \omega_i}. \quad (\text{S20})$$

Substituting the expression of N_i^A from Eqn. (S20) into Eqn. (S19), the equilibrium conditions are:

$$g_i N_i^S = N_i^S \frac{g_i v_i}{1 - \omega_i} \frac{\lambda_i}{1 + \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S + \sum_{j \in \mathcal{P}} \alpha_{ij} N_j^S \frac{g_j v_j}{1 - \omega_j}} \quad (\text{S21})$$

Then the equilibrium condition can be equivalently expressed as:

$$\frac{v_i \lambda_i}{1 - \omega_i} - 1 = \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j \left(1 + \frac{v_j}{1 - \omega_j}\right) N_j^S, \quad \text{if } i \in \mathcal{P} \quad (\text{S22})$$

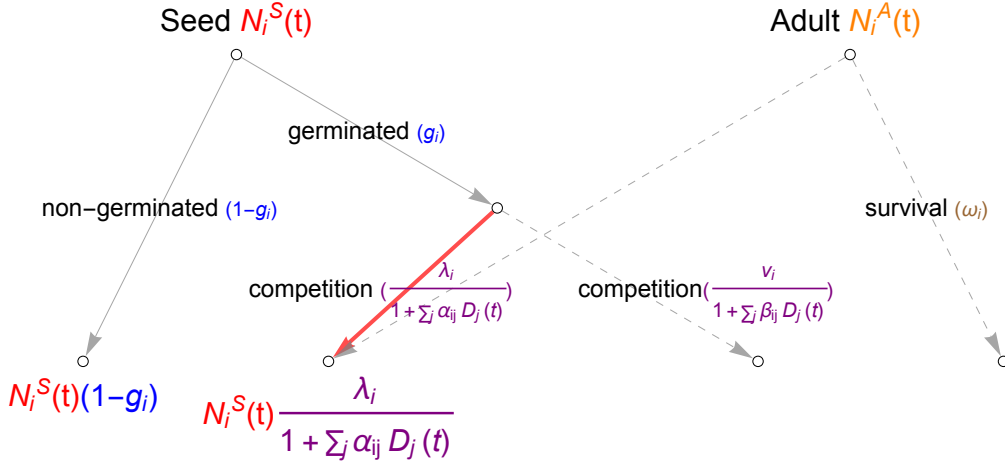


Figure S1: Population dynamics of perennial plant species with their perennial life history processes removed. Gray links (both solid and dashed) represent the ecological transitions of seeds and adults. Here, we remove the adult stage of the perennial species. We remove the dashed links: over-summer survival of adult perennials, over-summer maturation from perennial seedlings into adults, and competition during this transition. The germinated seeds transition directly into seeds in the next year (the red link).

The key difference between Eqn. S18 and S22 is the change of effective parameters:

$$\text{Effective intrinsic growth rate: } \lambda_i - 1 \rightarrow \frac{v_i \lambda_i}{1 - \omega_i} - 1 \quad (\text{S23})$$

$$\text{Effective competition strength: } \alpha_{ij} g_j \rightarrow \alpha_{ij} g_j \left(1 + \frac{v_j}{1 - \omega_j}\right) \quad (\text{S24})$$

With the effective parameters according to the transformations listed in Eqns. S23 and S24, we would have a system of equations with exactly the same dynamics as the original annual/plant dynamics.

As we have discussed in the beginning of this section, multiplication on the column space of competition strength ($a_{ij} \rightarrow c_i a_{ij}, \forall j$) does not affect the feasibility domain. Here, $c_i = 1$ for annual species while $c_i = (1 + \frac{v_j}{1 - \omega_j})$ for perennial species. Thus, the feasibility domain remains the same with or without transitions.

Note that this result does not imply that the feasibility would not change with or without transitions. As a reminder, the community is feasible if and only if the effective intrinsic growth rates are inside the feasibility domain. Here, the effective intrinsic growth rates change from $\alpha_{ij} g_j$ to $\alpha_{ij} g_j (1 + \frac{v_j}{1 - \omega_j})$. Thus, feasibility (determined by both intrinsic growth rates and competition structure) may change even though the feasibility domain (determined only by the competition structure) does not change.

C.3.3 Incorporating life-history processes in perennial species

Considering the density-dependence in transition from adults to seeds Here we consider the case when the seeds and adults face the same level of competition. Mathematically, $\alpha_{ij} = \beta_{ij}$.

Specifically, Eqns. 3 and 4 reduce to:

$$g_i N_i^S = N_i^A \frac{\lambda_i}{1 + \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S + \sum_{j \in \mathcal{P}} \alpha_{ij} N_j^A} \quad (\text{S25})$$

$$N_i^A (1 - \omega_i) = N_i^S \frac{g_i v_i}{1 + \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S + \sum_{j \in \mathcal{P}} \alpha_{ij} N_j^A} \quad (\text{S26})$$

Substituting the expression of N_i^A from Eqn. (S26) into Eqn. (S25), the equilibrium conditions are:

$$g_i N_i^S = \sqrt{\frac{v_i}{\lambda_i (1 - \omega_i)}} g_i N_i^S \frac{\lambda_i}{1 + \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S + \sum_{j \in \mathcal{P}} \alpha_{ij} \sqrt{\frac{v_j}{\lambda_j (1 - \omega_j)}} g_j N_j^S} \quad (\text{S27})$$

Then the equilibrium condition can be equivalently expressed as:

$$\sqrt{\frac{\lambda_i v_i}{1 - \omega_i}} - 1 = \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j \left(1 + \sqrt{\frac{v_j}{\lambda_j (1 - \omega_j)}}\right) N_j^S, \text{ if } i \in \mathcal{P} \quad (\text{S28})$$

Similarly, we have the changes of effective parameters from Eqn. S18 to Eqn. S28,

$$\text{Effective intrinsic growth rate: } \lambda_i - 1 \rightarrow \sqrt{\frac{\lambda_i v_i}{1 - \omega_i}} - 1 \quad (\text{S29})$$

$$\text{Effective competition strength: } \alpha_{ij} g_j \rightarrow \alpha_{ij} g_j \left(1 + \sqrt{\frac{v_j}{\lambda_j (1 - \omega_j)}}\right) \quad (\text{S30})$$

β_{ij} is the same for all species (i.e., whether $j \in \mathcal{A}, \mathcal{P}^S, \mathcal{P}^A$)

$$g_i N_i^S = N_i^A \frac{\lambda_i}{1 + \sum_{j \in \mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \alpha_{ij} g_j N_j^S + \sum_{j \in \mathcal{P}} \alpha_{ij} N_j^A} \quad (\text{S31})$$

$$N_i^A (1 - \omega_i) = N_i^S \frac{g_i v_i}{1 + \sum_{j \in \mathcal{A}} \beta_{ij} g_j N_j + \sum_{j \in \mathcal{P}} \beta_{ij} g_j N_j^S + \sum_{j \in \mathcal{P}} \beta_{ij} N_j^A} \quad (\text{S32})$$

D Disentangling sources of environmental stress

Here we apply the methods from (Song *et al.*, 2020) to disentangle the effects of parameter perturbations on species pairs. In general, a species pair exhibits a trade-off between the structural stability (tolerance) in competition strength and in intrinsic growth rates. Figure S2 illustrates this trade-off, which is the same for both coexistence and priority effects (Song *et al.*, 2020).

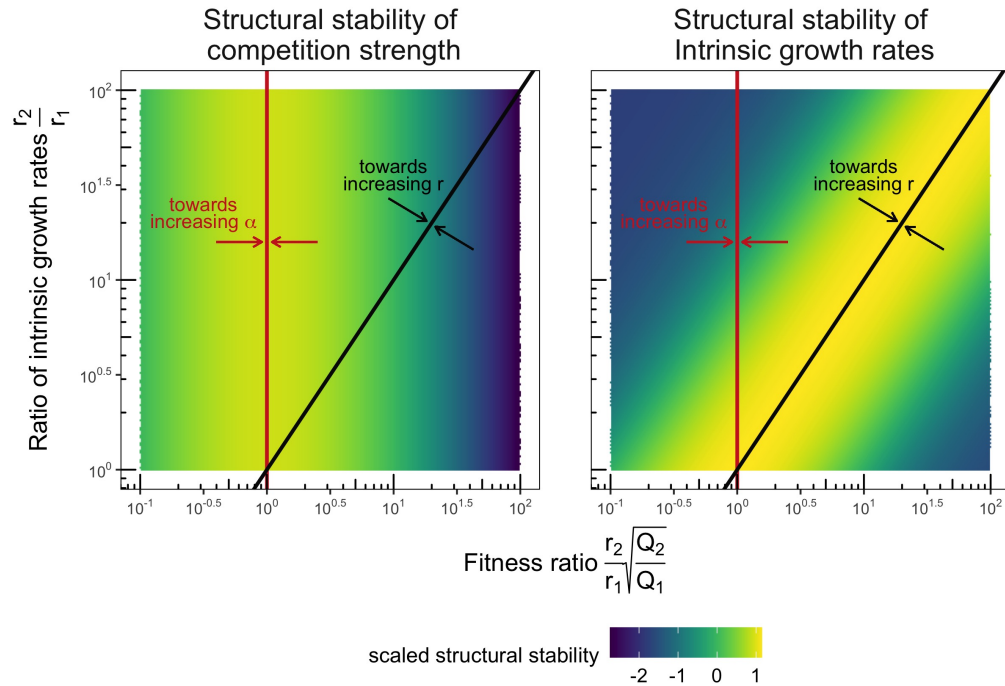


Figure S2: **Trade-off between structural stability in competition strength and in intrinsic growth rates.** The structural stability in competition strength is increased following the red arrows, and is maximized on the red line (i.e. species average fitness equivalence). The structural stability in intrinsic growth rates is increased following the black arrows, and is maximized on the black line (i.e., species average fitness ratio equals to the ratio of intrinsic growth rates). The color represents the scaled structural stability, where the yellow indicates high while the purple indicates low.

Applying this method to species pairs in the grassland community, Figure S3 shows that: (1) The perennial pairs are robust to both parameter perturbations in intrinsic growth rates and in the competition strength. (2) The annual pairs are more likely to persist under parameter perturbations in the competition strength but not in the intrinsic growth rates. (3) The mixed pairs of one annual and one perennial are robust to changes in intrinsic growth rates only when we exclude the life history processes, but are robust to changes in competition strength only when we incorporate life history processes.

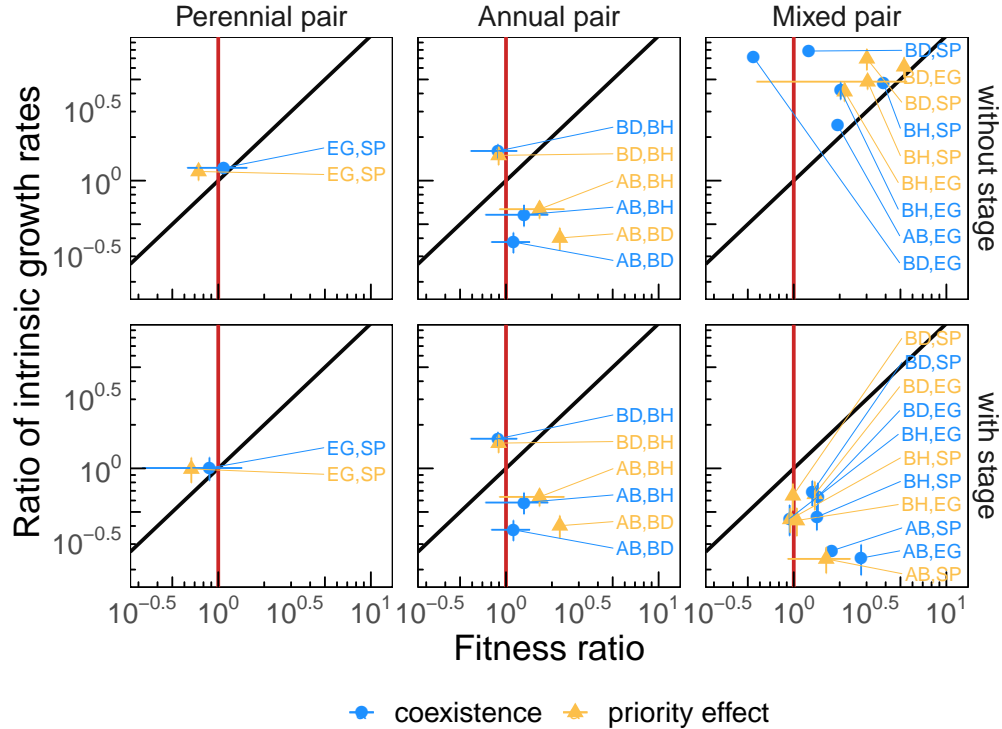


Figure S3: **Community persistence under environmental (parameter) perturbations.** Here we focus on the structural stability (robustness) of coexistence and priority effects to parameter perturbations. As Figure S2 shows, the structural stability in competition strength increases when the system pair is closer to the red line, while the structural stability in intrinsic growth increases when the system pair is closer to the black line. For the perennial pair (EG & SP; left panels), they maximize both the structural stability in competition strength and in intrinsic growth rates, regardless whether the stage dependency is considered. This result is consistent with the fact that they are native species coexisting for a long time. Then for the annual pairs (middle panels), they tend to maximize the structural stability in competition strength instead of that in intrinsic growth rates. Because the annual species do not have stage dependency, the two panels are exactly the same. Then, for the mixed pairs with one annual and one perennial (right panels), they tend to maximize the structural stability in intrinsic growth rates when the stage dependency is not considered (top), while they maximize the structural stability in competition strength when the stage dependency is considered (bottom). Thus, the stage dependency makes the perennials more vulnerable to parameter perturbations in competition strength (while the annuals have been adapted to these kinds of perturbations). The blue dots denote the pairs exhibiting priority effects, while the orange triangles denote the pairs exhibiting priority effects. The error bars represent two standard deviations.

E Effects of life-history processes

Figure S4 is a remake of Figure 3 in the main text except that all the species pairs are shown individually.

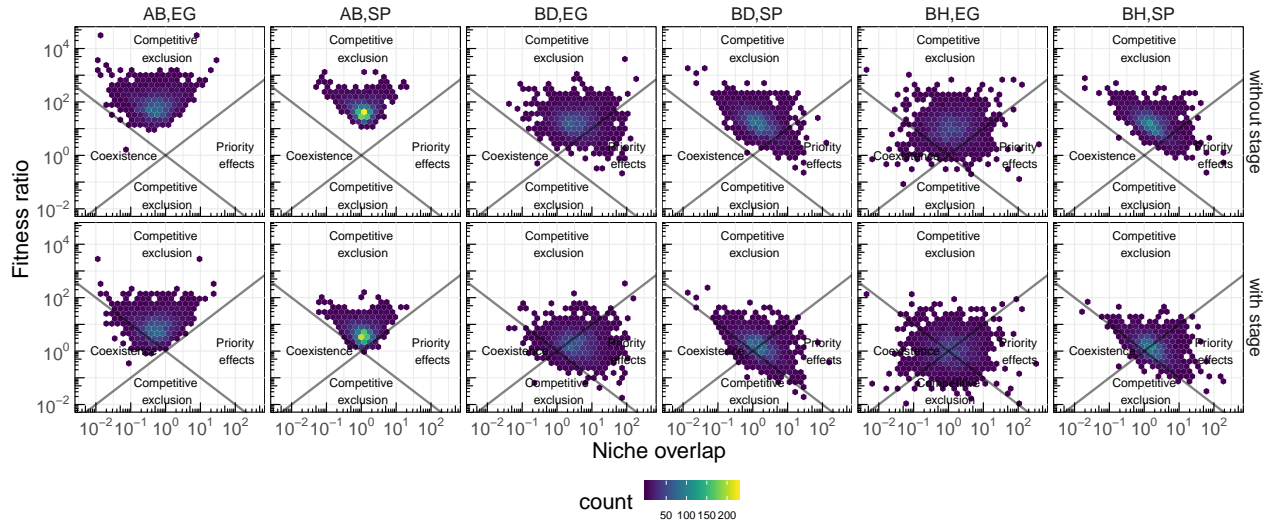


Figure S4: This figure is identical to Figure 3 except species pairs are shown separately.

Figure S5 shows the transition probability of community dynamics for a given ecological community between excluding and incorporating perennial life history processes. Note that there is zero transition probability from coexistence to contingent exclusion. The reason is that changing the effective intrinsic growth rates cannot change the system from coexistence to priority effect, or vice versa (Song *et al.*, 2020).

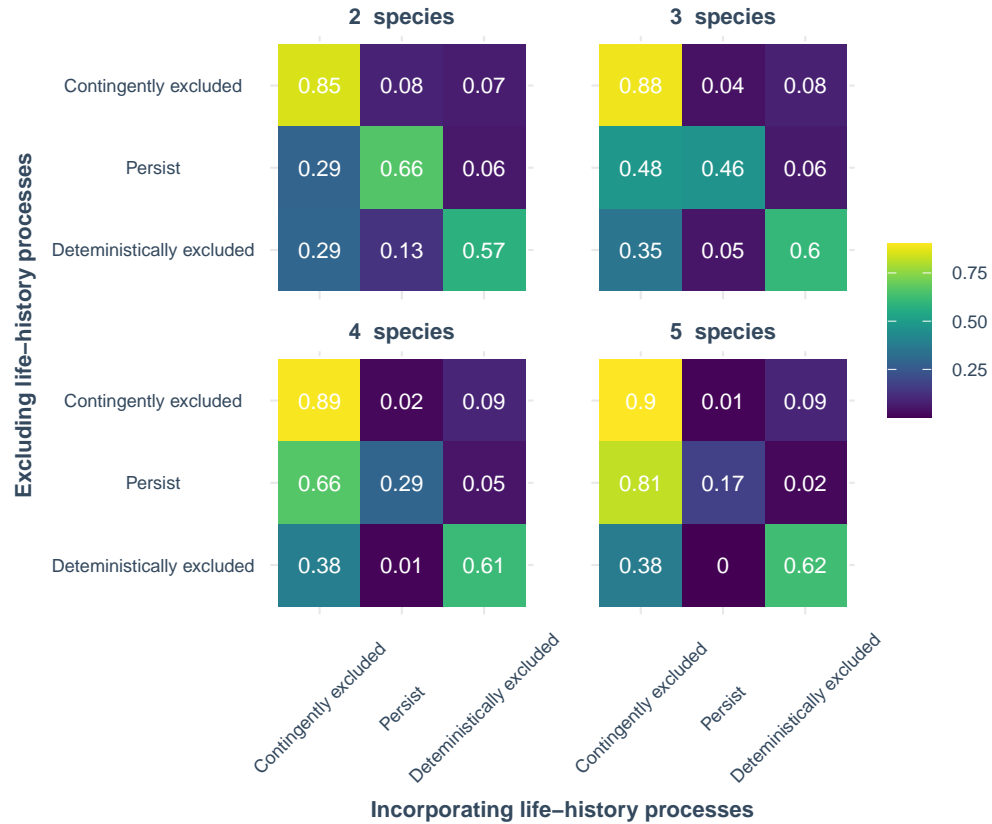


Figure S5: **The frequency and prevalence of contingent exclusion decreases as a function of community size.** We show the transition matrix of community dynamics between excluding (rows) and including (columns) life-history processes as a function of community size. Each element corresponds to the conditional probability (expressed as frequency) of having a particular dynamics by incorporating life-history processes (e.g., contingent exclusion including life-history, first column) given that the system started in a given dynamics excluding life-history processes (deterministic exclusion, third row). The matrices show that the prevalence (starting and remaining) of contingent exclusion (first element) decreases in general with community size. The matrices also show that the incidence (starting from deterministic exclusion—note that coexistence never leads to contingent exclusion) of contingent exclusion also decreases with community size.

F Effects of community size

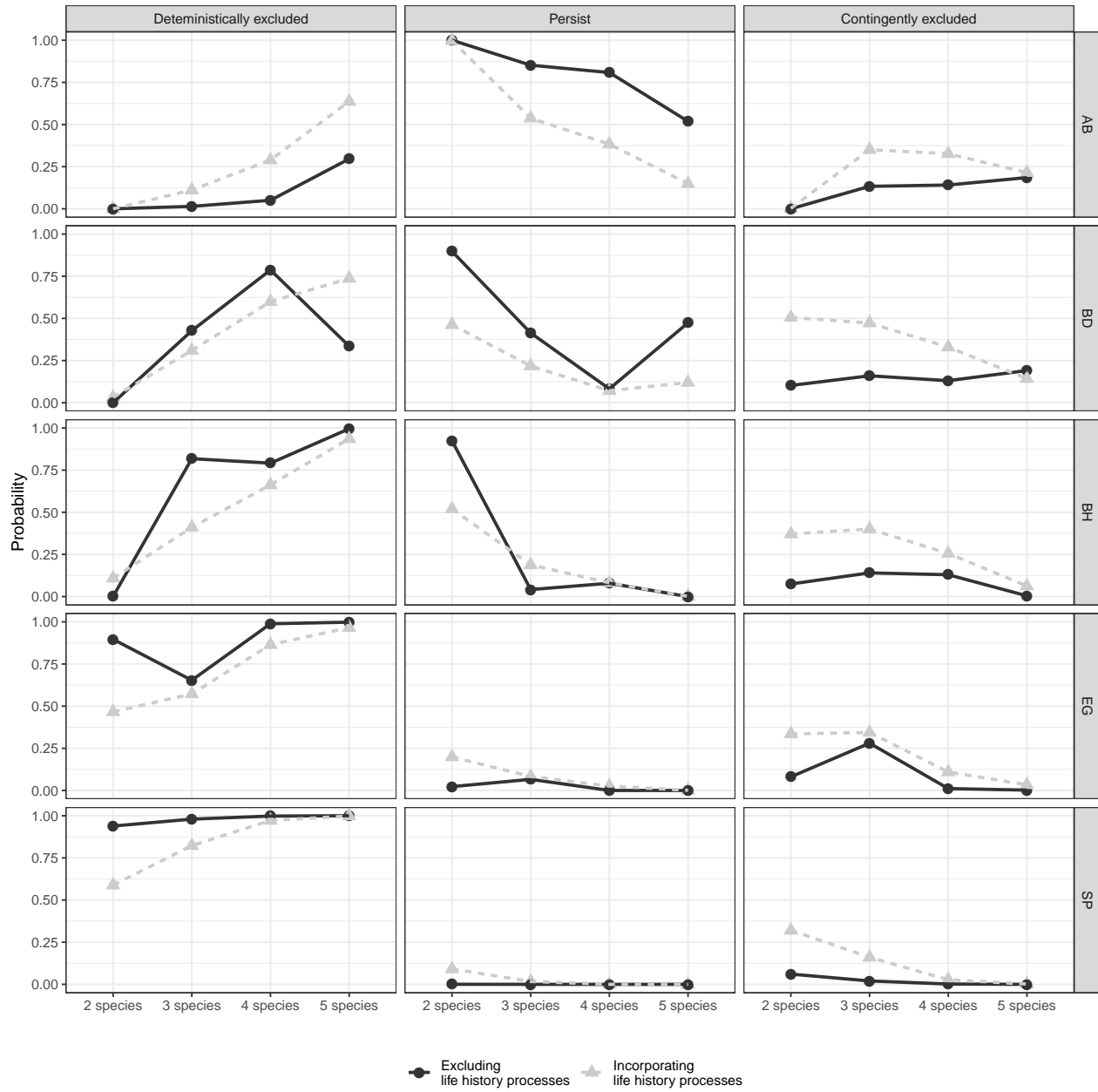


Figure S6: This figure is a remake of Figure 4 in the main text except that the probability is now shown in a scatter plot instead of in a bar plot.

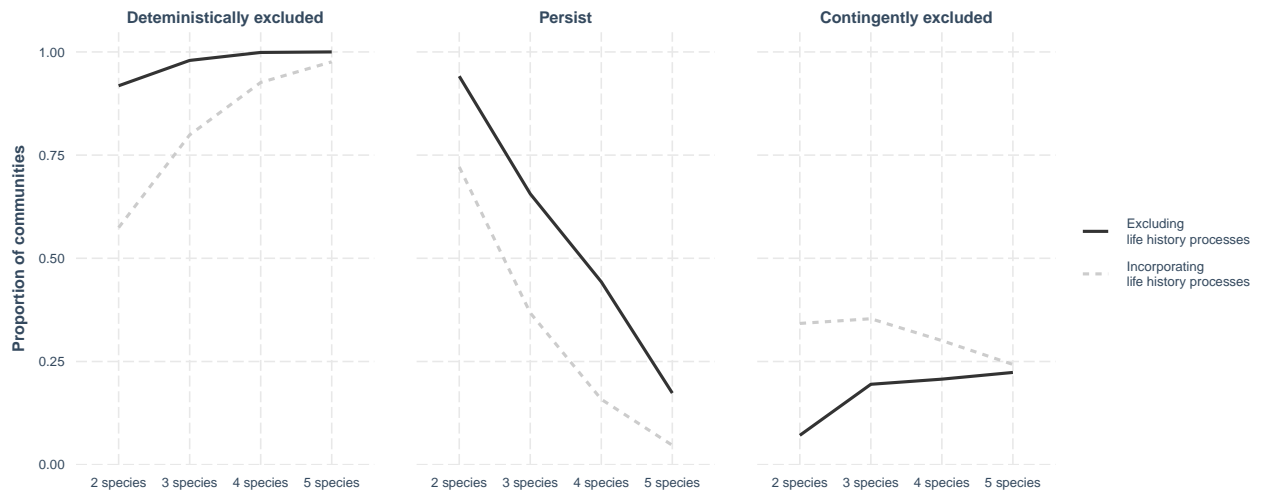


Figure S7: We study the proportion of communities that has at least one species demonstrating the three qualitative outcomes.

G Effects of competition structure

Here we perform additional simulations to test the robustness of Figure 5.

We changed the distribution of inter-specific interaction from uniform distribution to half-normal distribution ($|N(0, 1)|$). See Figure S8.

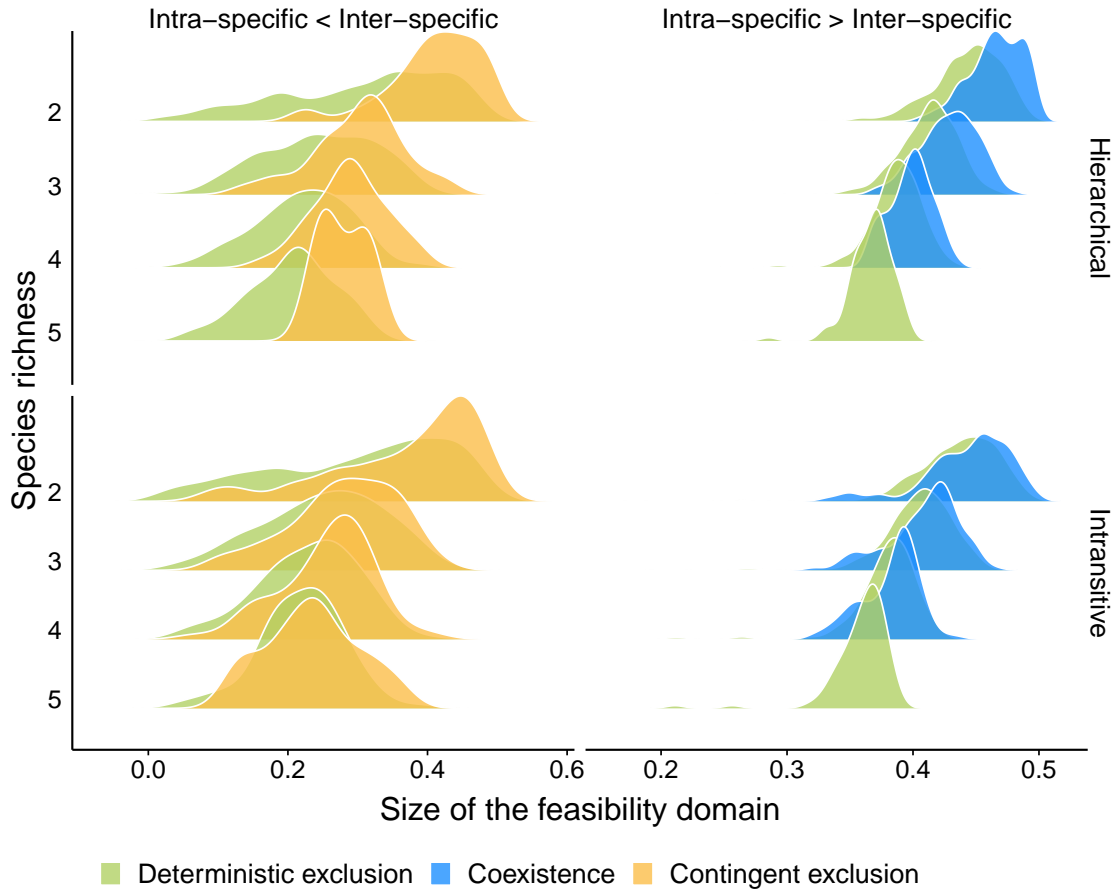


Figure S8: Same as Figure 5 except that the interspecific interactions are drawn from a half-normal distribution. Specifically, this figure shows the theoretical expectations about how competition structure affects the patterns of competitive exclusion. We show model-generated communities with different competition structures. We use two structural combinations: (i) communities with either a low (intraspecific < interspecific) or high (intraspecific > interspecific) intraspecific competition, and (ii) communities with either a hierarchical or intransitive competition structure. We find that the competition structures with weaker intraspecific competition, regardless of being hierarchical or not, produce qualitatively the same patterns as the empirical patterns shown in Panel (B) in Figure 5.

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