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Coexistence theory and the frequency-dependence of priority effects

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Priority effects are commonly used to describe a broad suite of phenomena capturing the influence of species arrival order on the diversity, composition and function of ecological communities. Several studies have suggested reframing priority effects around the stabilizing and equalizing concepts of coexistence theory. We show that the only compatible priority effects are those characterized by positive frequency-dependence, irrespective of whether they emerge in equilibrium or non-equilibrium systems.

The order in which species arrive in a locality can have lasting impacts on the diversity, composition and function of ecological communities[1,2]. This phenomenon, frequently referred to as priority effects, historical contingency or founder control[3], was originally explored analytically through Lotka–Volterra competition models[4,5]. In these simple models, priority effects emerge when the growth rate of each species is a positive function of its relative abundance, which results in the emergence of alternative stable states (panel a of the figure in Box 1). From a theoretical perspective, the term priority effect is synonymous with any process generating alternative stable states[6]; however, over time its usage has broadened to encompass a wider suite of phenomena, including those lacking multiple attractors. Several studies have subsequently raised the prospect of reorganizing priority effects around the stabilizing and equalizing concepts of coexistence theory[7–9]. Here, we identify the unrecognized problems and promise of such an endeavour. In particular, we demonstrate that the only compatible priority effects are those characterized by positive frequency-dependence (PFD).

According to coexistence theory, species can coexist when the fitness differences between them are smaller than their niche differences, where the former compares overall adaptedness to a shared environment and the latter captures overlap in resource usage in space and time[10]. This is equivalent to stating that each species exhibits negative frequency-dependence (NFD), that is, reduced growth as a function of its own relative abundance in a community. For a two-species Lotka–Volterra competition model this can be summarized via the inequality

$$\rho < \frac{f_2}{f_1} < 1/\rho \tag{1}$$

where the niche overlap, ρ, is equal to '1 − niche difference' and is bounded between 0 and 1, and f_2/f_1 is the fitness ratio (panels b,c of the figure in Box 1). It follows that we can differentiate between two classes of coexistence mechanisms: the equalizing mechanisms that reduce the fitness difference and the stabilizing mechanisms that reduce niche overlap.

In addition to being ecologically intuitive, the bounding of the niche overlap between 0 and 1 has statistical provenance in Chesson's original definition as the correlation between the resource utilization functions of species in MacArthur's consumer–resource model[11]. More recently, however, Chesson[12] provided a convenient formula for the niche overlap in terms of the Lotka–Volterra competition coefficients, α_{ij}. Specifically

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} \tag{2}$$

Whether a given ρ generates NFD depends on the fitness difference between competing species, but it is clear from this formulation that ρ is bounded by 0 and 1 only when the product of the intraspecific coefficients is greater than the product of the interspecific coefficients. When the reverse is true, ρ takes values greater than 1, and the system exhibits priority effects giving rise to two alternative stable states, depending on the initial density of the species (panels a,b of the figure in Box 1).

At first glance, $\rho > 1$ is at odds with both intuitive and statistical interpretations of the niche overlap, and it becomes even more nonsensical when cast as a negative niche difference $(1 - \rho)$. However, this break with convention operationalizes the criteria for PFD, that is, the analytical definition of priority effects, as the inverse of the stable coexistence inequality (panel b of the figure in Box 1)[9]:

$$\rho > \frac{f_2}{f_1} > 1/\rho \tag{3}$$

we rename the niche difference $(1-\rho)$ as the stabilization potential to avoid the semantic challenges of referring to a negative niche difference, we see from equation (3) that any mechanism that reduces the fitness ratio, or further decreases the stabilization potential below zero (that is, further increases $\rho > 1$), will increase the probability of priority effects. Thus, similar to stable coexistence, we recognize that stable priority effects are also jointly controlled by both stabilizing and equalizing mechanisms. Note that the stabilization potential diverges around zero such that values above zero represent the stabilization potential for coexistence, whereas values below zero represent the stabilization potential for priority effects, that is, the strength of the attractor towards alternative stable states (panel b of the figure in Box 1). Our terminology is different from recent heuristic translations of priority effects into coexistence theory, where the decrease in niche differences (the stabilization potential) below zero has been referred to as destabilization[7,8]. However,

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Box 1 | Coexistence and priority effects in a Lotka–Volterra competition model

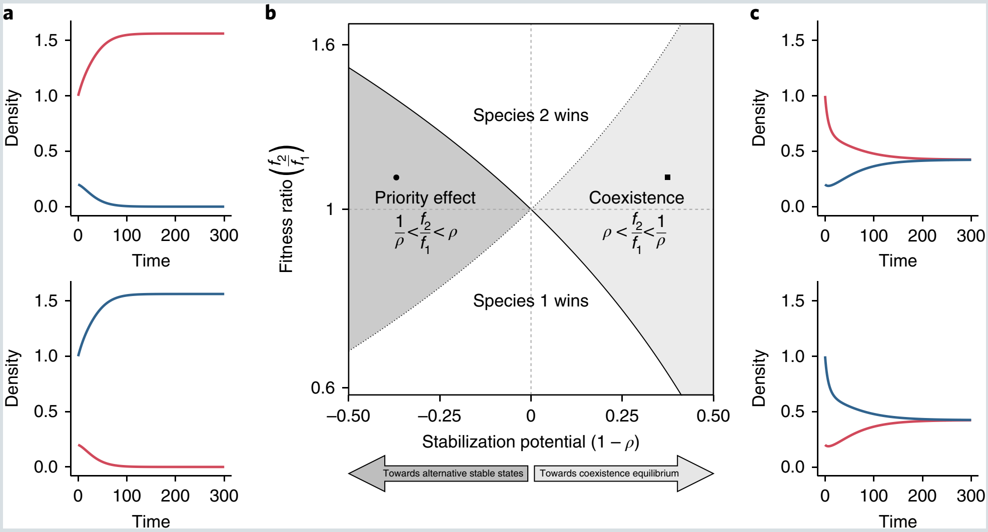
Whether coexistence or priority effects emerge in a two-species Lotka–Volterra competition model depends on the relative magnitude of intra- and interspecific competition. Consider the following Lotka–Volterra model:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - a_{11} N_1 - a_{12} N_2) \tag{5}$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - a_{21} N_1 - a_{22} N_2) \tag{6}$$

The intrinsic growth rate, r_1 and r_2, of each species is negatively affected by intraspecific (α_{11} and α_{22}) and interspecific competition (α_{12} and α_{21}). The two species coexist in a stable state with positive densities if $\alpha_{11} > \alpha_{21}$ and $\alpha_{22} > \alpha_{12}$, that is, when intraspecific competition exceeds interspecific competition. Under this scenario, each species exhibits NFD because an increase in its abundance leads to a larger negative impact on itself. Alternatively, when interspecific effects exceed intraspecific effects, that is, $\alpha_{11} < \alpha_{21}$ and $\alpha_{22} < \alpha_{12}$, each species exhibits PFD and an increase in its abundance results in a larger negative impact on the competitor. This leads to priority effects in the form of alternative stable states. The community trajectory is attracted to one of the two monoculture equilibriums, dominated by either N_1 or N_2, depending on the initial abundance of the two species.

The relationship between the competition coefficients and competition outcome can be directly mapped to the parameter space of the stabilization potential ($1-\rho$, x axis) and the fitness ratio (f_2/f_1, y axis) (panel b; see Main text). The solid ($f_2/f_1 = \rho$) and dotted ($f_2/f_1 = 1/\rho$) boundaries partition the parameter space into four distinct regions, each representing different outcomes of competition. The light grey area on the right ($\rho < f_2/f_1 < 1/\rho$) indicates parameter combinations that result in stable coexistence. This requires ρ to be bounded between 0 and 1, which is guaranteed when intraspecific competition is stronger than interspecific competition. The dark grey area on the left ($1/\rho < f_2/f_1 < \rho$) indicates the parameter space such that $\rho > 1$, resulting in priority effects.



Coexistence and priority effects in a Lotka–Volterra competition model. **a–c**, The community trajectories demonstrating priority effects (**a**) and stable coexistence (**c**). The dynamics in **a** and **c** correspond to the position of the black circle and black square, respectively, in **b**. In **b**, the x axis represents the stabilization potential ($1-\rho$) and the y axis represents the fitness ratio, f_2/f_1; the solid and dotted lines represent the boundary where f_2/f_1 equals ρ and $1/\rho$, respectively. The upper and lower white areas indicate the regions where parameter combinations result in the dominance of species 2 (blue) and 1 (red), respectively; the right light grey and the left dark grey areas indicate regions of stable coexistence and priority effects, respectively (parameter values and starting values provided in the Supplementary Information). All units are arbitrary.

although the coexistence attractor becomes unstable, multiple community attractors become dynamically stable. Therefore, we favour conceptualizing destabilization as any process that causes the stabilization potential to approach zero from values above or below zero (Fig. 1e).

A classic example of priority effects emerging from PFD is from Tilman's 1982 monograph[13]. Using the approach taken by Letten et al.[9] to derive the niche overlap and the fitness ratio from Tilman's consumer–resource model, PFD-generated priority effects can be partitioned into stabilizing and equalizing components. This partitioning is achieved by translating Tilman's model into a Lotka–Volterra form, which allows for the competition coefficients in terms of consumer–resource parameters to be derived. From there we can explore the effect of modifying mechanistic parameters on the stabilization potential using equation (2) and the fitness ratio using the companion formula[12,14] (full derivation provided in the Supplementary Information):

$$\frac{f_2}{f_1} = \sqrt{\frac{a_{11} a_{12}}{a_{22} a_{21}}} \tag{4}$$

In Fig. 1a, NFD and coexistence occur due to a combination of (1) intersecting ZNGI (the set of resource concentrations at which the growth of the species balances the mortality) indicating a trade-off in the competitive fitness of the two species for two substitutable resources (R) where the red species benefits more from R_2 and the blue species from R_1; (2) consumption vectors (relative rates at which resources are depleted via consumption) that are directed towards the favoured resource of each species, such that the red

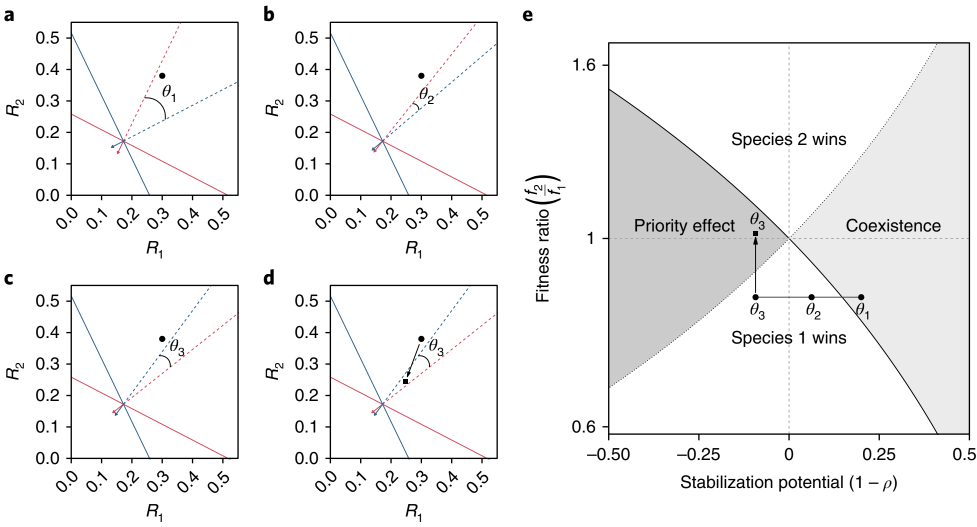


Fig. 1 | Effect of changing the consumption vector of species and the supply ratio of two resources in a consumer–resource model on the fitness ratio and stabilization potential (niche difference) of coexistence theory. a–d, The solid red and blue lines represent the zero net growth isocline (ZNGI) for each species (species 1 and 2, respectively); the solid lines with arrow heads are the respective consumption vectors; the dashed lines are the inverse of the vectors; and the black circles and squares represent two different resource supply ratios. The red species benefits more from consuming R_2, while the blue species benefits most from R_1, as indicated by its lower intercept. In **a**, red and blue species coexist, in **b** and **c**, red excludes blue; in **d**, priority effects lead to the monodominance of either red or blue. **e**, The *x* axis represents the stabilization potential ($1-\rho$); the *y* axis represents the fitness ratio (f_2/f_1); and the right and left grey areas indicate the coexistence and priority effect regions, respectively. The angles given by θ_{1-3} in **a–d** correspond to the respective θ_{1-3} in **e**. Note that the *y* axis is a logarithmic scale. Analytical treatment and simulation parameters are provided in the Supplementary Information.

species consumes more R_2 and vice versa, which is a prerequisite for intraspecific feedbacks being greater than interspecific feedbacks; and (3) a resource supply point (resource availability the system would return to in the absence of consumption) with an intermediate resource ratio, which ensures neither species is overly advantaged by an imbalanced abundance of their favoured resource[9,15]. As the angle between the consumption vectors declines to θ_2 (Fig. 1b), the stabilization potential also declines. The outcome is competitive exclusion when the stabilization potential falls below the fitness ratio (Fig. 1e). Once the consumption vectors cross and begin to diverge, each species consumes more of its competitor's favoured resource (θ_3; Fig. 1c), setting up the conditions for PFD. However, if the fitness difference remains sufficiently large, the outcome will still be exclusion, irrespective of arrival order (Fig. 1e). If the resource supply shifts to a more balanced ratio (Fig. 1d), the fitness inequality is reduced and priority effects emerge (Fig. 1e). The species that arrives first reduces the resource level of its competitor's favoured resource below the competitor's R^*, which is the minimum resource concentration required to maintain a positive growth rate and is denoted by the intercept of the ZNGI with the resource axis. The result is that the late-arriving competitor is unable to invade.

The above results demonstrate that priority effects are a function of both the stabilization potential and the fitness inequality, and that only the subset of phenomena commonly referred to as priority effects are compatible with coexistence theory. In particular, compatible phenomena are limited to those that generate PFD and are therefore consistent with the original definition derived from the Lotka–Volterra model[6]. This is not to say that PFD is unique to systems exhibiting point equilibria. For example, the coexistence-affecting mechanism relative nonlinearity can generate PFD when species that benefit from fluctuations in the intensity of competition also exacerbate those fluctuations[16]. In Fig. 2, two species with nonlinear functional responses exhibit negative average invader growth rates when competing for a logistically growing resource. As the resident, blue is able to draw resource levels below red's R^* and therefore prevent red from invading; however, at sufficiently high initial density, red generates large resource fluctuations that blue is unable to control. Nevertheless, in a system that precludes the emergence of PFD or NFD, and hence the emergence of a non-zero stable attractor, the stabilization potential term is unquantifiable. This criterion, however, wholly or partially excludes a number of phenomena lacking multiple attractors, which for heuristic reasons are often included under the umbrella of priority effects (see examples in Fukami[2]). We briefly consider two of these phenomena below.

When applying coexistence theory to study priority effects, it is important to recognize that PFD can emerge from negative or positive density dependence, that is, facilitation. However, while conceptually compatible with coexistence theory, the analytical tools currently available (equation (2)) cannot be leveraged to interpret the facilitative dynamics because negative α_{ij} in the Lotka–Volterra framework would generate unbounded population densities. Facilitation, of course, cannot go on forever and coexistence theory may still provide insight when negative density dependence starts to operate[17]. However, unless constrained by specific model designs, the formulas can only be applied to PFD emerging from negative density dependence.

An alternative form of positive density dependence sometimes characterized as a priority effect is an Allee effect[6]. For species exhibiting an Allee effect, there is a density threshold dividing two alternative stable states, such that above which the population persists and below which the population goes extinct. The alternative stable states arise from endogenous mechanisms at the population level, and are therefore distinct from priority effects that emerge at the community level driven by species interactions. Thus, while Allee effects can effect community composition if interspecific interactions maintain species below their Allee threshold, they occur independently of the frequency of a species in a community.

Finally, the notion of priority effects has also been usefully applied to understand the effects of arrival order on successional dynamics. In these instances, differences in initial abundance can

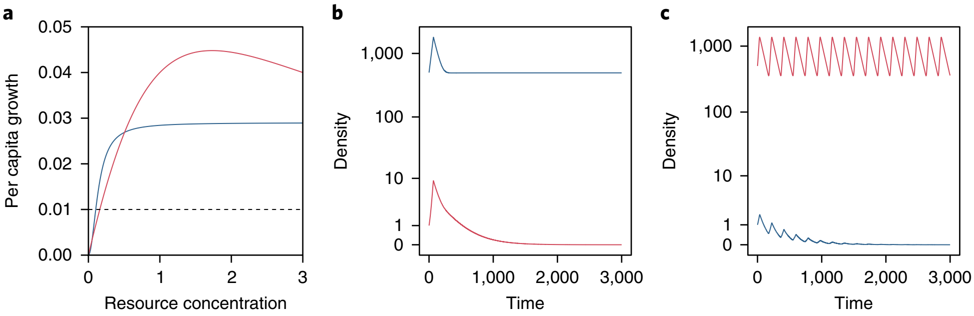


Fig. 2 | PFD emerges from endogenously generated resource fluctuations. a–c, Blue is the better competitor at low resource levels and also suppresses fluctuations in the resource to its own advantage; red is the better competitor at moderate resource levels and, because of a highly nonlinear functional response due to inhibited growth at high resource levels, generates fluctuations in the resource to its own advantage (**a**). When each species begins at a sufficiently higher density than its competitor, it is able to prevent its competitor from invading (**b**,**c**). Simulation parameters provided in the Supplementary Information. All units are arbitrary.

cause compositional trajectories to vary through time, even though they may all eventually converge on the same community state. Such 'alternative transient states'[18] can also be observed in naturally ephemeral microbial systems, such as those that develop in floral nectar or woody debris, where the final state might be the local extinction of all community members following the exhaustion of available resources. The trajectories of these communities, which are an outcome of resource pre-emption, may have downstream impacts on pollinator preference and decomposition rates and therefore undoubtedly reflect ecological phenomena with meaningful consequences for ecosystem function. Furthermore, it may be relevant to consider these processes with respect to stabilizing mechanisms operating at some larger temporal or spatial scales. Nevertheless, treated independently of their broader spatio-temporal context, there is little scope or rationale to bring coexistence theory to bear on such phenomena.

Interest in coexistence theory has been growing steadily, but to date the overwhelming emphasis has been on the underlying stabilizing mechanisms giving rise to NFD and stable coexistence. We have illustrated the most accessible approach to incorporating priority effects mediated through PFD into this body of theory. When priority effects emerge from positive density dependence or occur in transient systems, it is currently unclear how to analytically connect them to coexistence theory.

Methods

PFD in an equilibrium system. We first provide an example of PFD emerging from resource competition in an equilibrium system (Fig. 1). To this end, we take Tilman's original consumer–resource model (see p. 270 of ref. [13]), where two consumers, N_1 and N_2, are competing for two perfectly substitutable resources, R_1 and R_2. The dynamics of this system can be described as follows:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t}=r_1N_1\left[\frac{w_{11}R_1+w_{12}R_2-T_1}{k_1+w_{11}R_1+w_{12}R_2-T_1}\right]-DN_1 \tag{7}$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t}=r_2N_2\left[\frac{w_{21}R_1+w_{22}R_2-T_2}{k_2+w_{21}R_1+w_{22}R_2-T_2}\right]-DN_2 \tag{8}$$

$$\frac{\mathrm{d}R_1}{\mathrm{d}t}=D\,(S_1-R_1)-c_{11}N_1-c_{21}N_2 \tag{9}$$

$$\frac{\mathrm{d}R_2}{\mathrm{d}t}=D\,(S_2-R_2)-c_{12}N_1-c_{22}N_2 \tag{10}$$

Here, r_i represents the maximum population growth rate for species i ($i=1$ or 2) and D represents the constant mortality of the consumers and turnover rate of resources. The per capita resource consumption rate of consumer N_i on resource R_j ($j=1$ or 2) is represented by c_{ij}, whereas w_{ij} represents a weighting factor that converts availability of R_j into its value for consumer N_i. Following a Monod growth model, k_i is the half-saturation constant for N_i resource consumption, and T_i is the minimum amount of total resource required for N_i to grow. Finally, S_1 and S_2 represent the resource supply concentrations for R_1 and R_2, respectively. For this model, we define the consumption vectors for consumer i on the two substitutable resources as a vector with elements (c_{i1}, c_{i2}), and the supply point can be expressed as a point with coordinates (S_1, S_2).

We used the approach implemented in Letten et al.[9] to translate changes in the parameters of Tilman's consumer–resource model[13] into changes to the stabilization potential ($1-\rho$) and fitness ratio (f_2/f_1) of coexistence theory (see Supplementary Information for detailed mathematical treatment). In brief, we solved the coexistence equilibrium of a consumer–resource model and rearranged it algebraically to a form comparable to the equilibrium of a two-species Lotka–Volterra competition model (Box 1,equations (5) and (6)). We then quantified the stabilization potential and fitness ratio based on equations in the main text. For our specific model, we can express these two components of coexistence theory as follows:

$$\rho=\sqrt{\frac{a_{12}a_{21}}{a_{11}a_{22}}}=\sqrt{\frac{\left(c_{22}+c_{21}\frac{w_{11}}{w_{12}}\right)\left(c_{12}+c_{11}\frac{w_{21}}{w_{22}}\right)}{\left(c_{12}+c_{11}\frac{w_{11}}{w_{12}}\right)\left(c_{22}+c_{21}\frac{w_{21}}{w_{22}}\right)}} \tag{11}$$

$$\frac{f_2}{f_1}=\sqrt{\frac{a_{11}a_{12}}{a_{22}a_{21}}}=\frac{\left(S_2+\frac{w_{21}}{w_{22}}S_1-B_2\right)}{\left(S_2+\frac{w_{11}}{w_{12}}S_1-B_1\right)}\sqrt{\frac{\left(c_{12}+c_{11}\frac{w_{11}}{w_{12}}\right)\left(c_{22}+c_{21}\frac{w_{11}}{w_{12}}\right)}{\left(c_{22}+c_{21}\frac{w_{21}}{w_{22}}\right)\left(c_{12}+c_{11}\frac{w_{21}}{w_{22}}\right)}} \tag{12}$$

where

$$B_1=\left[\frac{D\,(k_1-T_1)+r_1T_1}{w_{12}\,(r_1-D)}\right] \tag{13}$$

and

$$B_2=\left[\frac{D\,(k_2-T_2)+r_2T_2}{w_{21}\,(r_2-D)}\right]\left(\frac{w_{21}}{w_{22}}\right) \tag{14}$$

We varied the per capita consumption rates, c_{ij}, of the species and the supply point to study the effects of changing consumer–resource parameters on stabilization potential and fitness ratio. See Supplementary Information for detailed parameter values.

PFD in a non-equilibrium system. Next, we provided an example of PFD emerging through the coexistence-affecting mechanism relative nonlinearity. In this example, our model consists of two consumers competing for a single logistically growing resource. One species has a type-3 functional response (blue in Fig. 2), given by:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t}=N_1\left(\mu_{\max_1}\frac{R^2}{Ks_1+R^2}-d\right) \tag{15}$$

The other species (red in Fig. 2) has a modified Monod (type-2) functional response with inhibition at high resource levels:

$$\frac{dN_2}{dt} = N_2\left(\mu_{\max_2}\frac{R}{Ks_2 + R + \frac{R^2}{Ki}} - d\right) \quad (16)$$

Here, N_i is the population density of consumer i ($i = 1$ or 2), $\mu_{\max_i}$ is the maximum growth rate, Ks_i is the half-saturation constant, R is the density/concentration of resource, d is the density independent mortality rate and Ki is the inhibition term unique to the second species.

Time series simulations were run with the LSODA solver using the deSolve package v1.20[19] in R v3.4.2. To study PFD, we started the simulation with different initial population sizes. See Supplementary Methods for detailed parameter values.

Data availability

All simulated data was generated by R language. All code used for this study is available at https://github.com/pojuke/CoexistPFD and upon request from the corresponding author.

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References

1. Chase, J. M. *Oecologia* **136**, 489–498 (2003).
2. Fukami, T. *Annu. Rev. Ecol. Evol. Syst.* **46**, 1–23 (2015).
3. Slatkin, M. *Ecology* **55**, 128–134 (1974).
4. Lewontin, R. C. *Brookhaven Sym. Biol.* **22**, 13–24 (1969).
5. May, R. M. *Math. Biosci.* **12**, 59–79 (1971).
6. Petraitis, P. *Multiple Stable States in Natural Ecosystems* (Oxford Univ. Press, Oxford, 2013).
7. Mordecai, E. A. *Ecol. Monogr.* **81**, 429–441 (2011).
8. Fukami, T., Mordecai, E. A. & Ostling, A. *J. Veg. Sci.* **27**, 655–657 (2016).
9. Letten, A. D., Ke, P.-J. & Fukami, T. *Ecol. Monogr.* **87**, 161–177 (2017).
10. Chesson, P. *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
11. Chesson, P. *Theor. Popul. Biol.* **37**, 26–38 (1990).
12. Chesson P. & Leemans, R. in *Ecological Systems* (ed. Leemans, R.) 223–256 (Springer, New York, 2013).
13. Tilman, D. *Resource Competition and Community Structure* (Monographs in Population Biology Vol. 17, (Princeton Univ. Press, Princeton, 1982).
14. Chesson, P. & Kuang, J. J. *Nature* **456**, 235–238 (2008).
15. Chase, J. & Leibold, M. *Ecological Niches: Linking Classical and Contemporary Approaches* (Univ. Chicago Press, Chicago, 2003).
16. Chesson, P. *J. Biol. Dynam.* **3**, 149–163 (2009).
17. Schreiber, S., Yamamichi, M. & Strauss, S. Preprint at *bioRxiv* https://doi.org/10.1101/161919 (2017).
18. Fukami, T. & Nakajima, M. *Ecol. Lett.* **14**, 973–984 (2011).
19. Soetaert, K., Petzoldt, T. & Setzer, R. W. *J. Stat. Softw.* **33**, 1–25 (2010).

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Author contributions

P.-J.K. and A.D.L. conceived the study, performed the analysis and wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Software and code

Policy information about availability of computer code

Data collection	Not applicable, simulated data generated by R language
Data analysis	Simulations performed in R language. All code used for this study are available at https://github.com/pojuke/PFD and are available on request.

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Study description	Priority effects are commonly invoked to describe a broad suite of phenomena capturing the influence of species arrival order on the diversity, composition and function of ecological communities. Several studies have suggested reframing priority effects around the stabilizing and equalizing concepts of coexistence theory. We show that the only compatible priority effects are those characterized by positive frequency dependence, irrespective of whether they emerge in equilibrium or non-equilibrium systems.
Research sample	Not applicable as all analyses use simulated data
Sampling strategy	Not applicable as all analyses use simulated data
Data collection	Not applicable as all analyses use simulated data
Timing and spatial scale	Not applicable as all analyses use simulated data
Data exclusions	Not applicable as all analyses use simulated data
Reproducibility	All code used for this study are available at https://github.com/pojuke/PFD and are available on request.
Randomization	Not applicable as all analyses use simulated data
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☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
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☒	☐ Animals and other organisms
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Methods

n/a	Involved in the study
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☒	☐ MRI-based neuroimaging