Title: Bridging Theory and Experiments of Priority Effects

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Abstract

Although priority effects play a key role in structuring natural communities, considerable confusion and uncertainty remain about when and how they affect different ecological systems. Reviewing previous empirical studies, we show that most of the confusion arises because the term priority effect is often used indiscriminately without considering the various underlying mechanisms or the temporal scales at which they operate. Traditional theory has focused on a single mechanism that applies to a subset of natural systems, revealing a troublesome disconnect between theory and experiments. We propose a new framework that categorizes the different mechanisms of priority effects into two functional groups. We show how this unifying framework allows ecologists to predict the consequences of priority effects across diverse natural systems.

Glossary

Community assembly: The process that track changes in species number, identity, and abundance in an ecological community.

Historical contingency: Scenarios when the order and timing of any biotic or abiotic events affect community assembly. Priority effects can be drivers of historical contingency, but not all historical contingencies are driven by priority effects.

Generation time: The length from an individual's birth to the completion of reproduction.

Phenology: Seasonal timing of important life history events, e.g., breeding, migration, germination, leaf out, and recovery from hibernation.

Positive frequency dependence: The species with a higher frequency in the community has a higher population growth rate, as opposed to negative frequency dependence (population growth is limited by a higher frequency).

Priority effects: Scenarios where the effect of species on each other depends on their relative arrival times.

Season: A period marked by environmental changes. Seasons often refer to spring, summer, fall, and winter, but they can also describe a period with suitable habitats, e.g., when ephemeral ponds have water. Communities often reassemble at the beginning of the season.

The outcome of species interaction often depends on the temporal sequence of community assembly. This phenomenon termed the priority effect is common across a wide range of taxa and ecosystems [1–4]. By altering species interactions, they can affect species coexistence and competitive dominance [5,6], or lead to alternative stable states [7]. As a consequence, priority effects play a key role in driving biodiversity patterns [8,9] and ecosystem functioning [10–12]. Despite the long history of priority effects in community ecology, they are still understudied, and uncertainty remains about when and how they affect various ecological systems [7]. Much of this uncertainty arises because priority effects are still typically treated as a "black box" and used indiscriminately to describe any relationship between the temporal sequence of arrival orders and changes in the outcomes of interactions or community states, without considering the variety of underlying mechanisms. Over time, this has led to a troublesome disconnect between empirical and theoretical research on priority effects, leading to confusion, misconceptions, and seemingly conflicting findings about when and how priority effects influence natural populations and communities. Resolving this uncertainty is not only essential to understand the dynamics and composition of natural communities, but also key to predicting how communities will change in the future as climate change is reshuffling the phenologies of species worldwide.

Here, we provide a conceptual framework to understand, interpret, and predict the consequences of priority effects across different systems. We start by synthesizing empirical and theoretical studies, then discuss how accounting for the different mechanisms of priority effects and the time scales at which they operate can overcome discrepancies across studies. We then propose a general framework that classifies the wide range of mechanisms into two categories (types) of priority effects and discuss how this framework can help explain

discrepancies across empirical and theoretical studies. Finally, we explain how these different mechanisms can be quantified in empirical studies and integrated into community models to predict priority effects across different temporal and organizational scales and discuss future directions.

Unpacking Priority Effects: Mechanisms and Scales

The concepts at the heart of priority effects were first introduced almost a century ago [13], with the term itself being almost half a century old [14]. The term "priority effects" has been subsequently used in many occasions and systems in which this phenomenon has been detected: bacteria and single-cell fungi [3,9,15–17], macroscopic fungi [18,19], protists and planktons [8,20,21], insects [1,5,22], terrestrial plants [2,23], amphibians [4,24] and fish [25,26]. However, these and other studies often differ in the underlying mechanisms and the organizational and temporal scale at which priority effects are measured.

A Multitude of Mechanisms

The biological mechanisms of documented priority effects are often either unknown, indirectly inferred, or appear specific to a given study system (Appendix I). For instance, in many microbial systems, priority effects are only indirectly inferred by linking changes in community composition to differences in the timing of arrivals; while they are sometimes attributed to factors like resource preemption [27] or phylogenetic relatedness [28,29], the specific mechanisms are often unknown. Other studies in microbial systems point to more resolved mechanisms such as sugar concentration or environmental pH [3,17]. In coral reef fish, priority effects often arise because first arrivers become more aggressive toward later arrivers

[25,26,30]. Early arriving individuals of intertidal invertebrates prevent the colonization of late arrivers by physically blocking the highly limited substrate surface [31]. In dragonfly and damselfly communities, priority effects can be driven by intraguild predation because early arrivers gain a size advantage that allows them to prey on smaller late arrivers [22,32]. In plants, priority effects can arise from a range of different mechanisms, including competition for light [33] or pollinators [34], and plant-soil feedback (e.g., via shifts in microbiome or allelopathy) [35]. In host-pathogen systems, priority effects between two parasites co-infecting the same host can be mediated via an immune response of the host (e.g., cross-immunity) [36–38]. These and other examples highlight the multitude of mechanisms that can drive priority effects (Appendix I).

A Dichotomy of Temporal Scales

Given the diversity of study systems, it is not surprising that priority effects have been studied at different temporal scales with most falling into two distinct groups: studies that last only one generation or less vs. studies that last for many generations. In our review of the literature, we found that out of 136 experimental studies, 56 (41.2%) lasted more than five generations of focal organisms, while 64 (47.1%) lasted for only one generation or less (Box 1). The two distinctive groups of experiments reveal a clear dichotomy in the research on priority effects.

A closer inspection of these studies indicates that this dichotomy largely reflects differences in the life history of focal organisms. Studies that focused on organisms with relatively long generation times, such as plants and amphibians [1,23,24,39] usually last less than one generation, and the manipulated differences in arrival times are usually less than the

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length of their full life cycle (Box 1). Here, arrival times reflect species phenology (i.e., seasonal timing within a year), and these studies largely focus on changes in traits (morphology, development or survival rates, etc.) of individuals and test specific biological mechanisms that cause priority effects [22,26,40]. But since they only last for one generation or less, they cannot directly measure the long-term consequences of priority effects. The latter can only be inferred when the experimental data is fitted to models of population dynamics [41,42].

On the other hand, studies on organisms with short generation times such as zooplankton and microbes focus on population and community dynamics and thus often run for tens to hundreds of generations [3,43,44]. In these studies, arrival times between species typically differ by multiple generations which allows them to study the long-term consequences of priority effects on communities (e.g., alternative stable states) [9,20,45]. However, because of the fast generation time, they typically do not infer or isolate the relative importance of specific underlying mechanisms.

Thus, there is a clear dichotomy of temporal scales across empirical studies with very different research questions. This is problematic because the temporal scale of an experiment is typically linked to the specific biological mechanisms causing priority effects (Appendix I). In addition, both groups measure very different response variables that are recorded at different scales (individual- vs. population-level). Therefore, patterns or mechanisms identified in studies that focus on the individual short-term (within one generation) scale may not emerge or be relevant for dynamics and patterns observed in studies on long-term community dynamics.

The Gap between Theoretical Framework and Empirical Studies

Early theoretical work on priority effects can be traced back to the classic competition

models first introduced by Lotka and Volterra in the 1920s [46,47]. They showed that when two species in the community limit each other more than themselves then the outcome of competition is determined by the relative abundance of competitors and the system exhibits alternative stable states [48]. Analyzing this framework, Gause [49] came to the conclusion that "the development of a definite biological system is conditioned not only by its state at a given moment, but that the past history of the system exerts a powerful influence together with its present state". In short: the development of a community depends on its history. This idea was quickly picked up to explain priority effects in natural systems, by arguing that whichever species arrives earlier can gain a numerical advantage and thus exclude the other, leading to different final community states. Recent work has shown how this type of priority effect also emerges in models using modern coexistence theory [50–52] (Box 2).

Although intuitive and practical, this traditional body of theory and its recent extension has one key caveat: it focuses on one single mechanism. Specifically, it assumes that priority effects arise from a shift between alternative stable states driven by a change in the relative numerical abundances (frequencies) of species (see Box 2 for full description). This focus on one single mechanism sharply contrasts with the multitude of mechanisms that have been identified in empirical studies over the past decades (Appendix I), and naturally raises the question: to which empirical studies does this theory apply?

We can answer this question by focusing on the key requirements for this type of priority effect to occur (Box 2): (1) early arrival must provide the species with a numerical advantage when the interaction starts, (2) the combination of interaction coefficients needs to ensure positive frequency dependence to promote alternative stable states, and (3) the inter- (and intra-) specific per-capita interactions and demographic rates of species are fixed and independent of

arrival times and sequence. The last condition effectively decouples arrival time from species interactions. It highlights that timing only matters when early arrival also ensures a numeric advantage, but the numeric advantage does not necessarily require early arrival. In fact, many studies simulate this type of "priority effect" without manipulating the arrival times and instead simply start experiments with an initial numeric advantage [9,53,54].

A closer inspection of empirical studies on priority effects quickly reveals that these conditions are met in some studies but not in most. Systems with short generation times such as zooplankton or microbial community are the most likely to meet these conditions. In these systems, arrival times are typically separated by multiple generations, giving the early arriver enough time to reproduce, eventually outnumbering late arrivers [3,20]. However, per-capita effects are often not quantified in these studies and still could change between arrival times, e.g., due to habitat modification, phenotypic plasticity, or rapid evolution [17,55,56].

In contrast, most short-term studies documenting priority effects in empirical systems with longer generation times such as terrestrial plants, fish, and amphibians, do not satisfy these conditions. First, differences in arrival times are often too short (less than a generation) for a numerical advantage through reproduction, and many experiments keep initial densities constant across arrival time treatments. Second, interactions in these systems are often not constant but change with the timing of arrival. Early arrival advantages caused by aggression [25,26], behavioral interference [24,57], and plant-soil feedback [35,40,58,59] are all mediated by a change of specific traits that alter the interaction between the early and the late arriver. Furthermore, studies in insects, vertebrates, and plants quantify these changes in per-capita interaction effects with relative arrival time [2,39,60]. These changes in demographic rates with relative arrival time are common (Appendix I), and they represent a mechanism of priority

effects that is fundamentally different from numerical priority effects. Thus, the traditional theory does not capture the full diversity of priority effects observed in natural systems and hence cannot be applied to interpret or predict the long-term effects of these different priority effects. This gap between theory and empirical work clearly highlights current limitations and the need for a conceptual framework that captures this diversity of mechanisms.

Bridging the Gap: A Unifying Framework of Priority Effects

Here, we propose a new categorization of priority effects to bridge the gap between theory and nature and provide a unified conceptual framework of priority effects that can be applied across different empirical systems. We suggest to group mechanisms of priority effects into two general types: "numeric" priority effects and "trait-mediated" priority effects (Table 1). Here we follow the original meaning and previous reviews [7] by defining "priority effects" to describe scenarios where the *effect of species on each other depends on their relative arrival times*.

We define priority effects arising from positive frequency dependence as *numeric*: in these cases, the early arriver obtains a higher relative frequency through reproduction, leading to a priority effect that is further maintained by positive frequency dependence. Numeric priority effects represent the priority effects in traditional competition models and have the same requirements (Box 2).

On the other hand, we define priority effects that arise when differences in arrival times alter the traits of species as *trait-mediated*. Here, the early-arriving advantage arises from changes in per-capita parameters of species (e.g., per-capita interaction coefficients or other demographic rates; Box 3). Trait-mediated priority effects thus relax the assumption of constant

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parameters in traditional models on numeric priority effects and changes in arrival times lead to concurrent changes of key parameters that determine the outcome of interactions, e.g., the fitness ratio and stabilization potential of competing species. Depending on the original and shifted position of the interaction, this may simply mean a change in the relative frequencies of coexisting species, or a dramatic shift, e.g., from stable coexistence to competitive exclusion or vice versa (Box 3). This sets them fundamentally apart from numerical priority effects, which arise from shifting between two alternative stable states, but the outcome (i.e., possible states) of the system is always fixed and independent of arrival times. Unlike numeric priority effects, trait-mediated priority effects are possible for any combination of competition parameters, and they can arise within a generation and therefore help explain priority effects in empirical systems with longer-generation times where arrival times are separated by less than a generation.

Why It Matters

Applying this framework extends previous approaches in several important ways:

(1) It bridges the gap between theory and empirical work by providing a straightforward pathway to integrate a diversity of mechanisms observed in natural systems into theoretical models (Box 3), allowing researchers to critically evaluate and test the role of priority effects across a much wider range of natural systems.

(2) It helps to reconcile the dichotomy between experiments on systems with short and long generation times and of long vs. short durations by differentiating between the two mechanisms that operate at different time scales (Box 1).

(3) Priority effects arising from different mechanisms have fundamentally different

consequences for the dynamics of a system (Box 4). Differentiating between mechanisms is therefore essential to understanding and predicting how a system will respond to changes in the temporal structure (e.g., phenological shifts) or other types of perturbations. For instance, restoring a system that exhibits alternative stable states due to numeric priority effects requires very different management strategies than a system driven by trait-mediated priority effects. Identifying the underlying mechanism also helps to resolve potential contradicting results among empirical studies (e.g., alternative dispersal-diversity relationships [8,9,61–64]).

(4) Finally, the framework unifies and expands previous conceptual and mathematical frameworks. For instance, the definition of numeric vs. trait-mediated priority effects is closely related to the niche-based categorization of priority effects [7,27]. If the early arriver modifies the environment such that it changes the probability of the late arriver successfully establishing itself (niche modification *sensu* [7]), this change occurs via a shift in the demographic traits of the second arriver as a function of arrival time, i.e., trait-mediated priority effects. However, if the early arriver occupies the niche space of the late arriver, e.g., by resource exploitation (niche preemption), then priority effects could arise from both numeric and trait-mediated mechanisms (Box 4).

The framework can even be expanded to an evolutionary time scale. If one species arrives early enough for local adaptation to occur, it could dominate the habitat and prevent other species or even ancestral conspecifics from colonizing, i.e., the monopolization effect [55,65–68]. At extremely large temporal scales, evolution can lead to a "phylogenetic priority effect": early-arriving taxa could diversify and dominate in the local community [69–71]. These evolutionary priority effects can be categorized as extreme cases of trait-mediated priority effects: the difference in arrival times is so long that certain traits of the early arriver

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change permanently.

Looking Forward

Realistic Models of Priority Effects

Our classification framework emphasizes the importance of biological realism in research on priority effects, especially in theoretical studies. Models that do not capture the key mechanisms driving population and community dynamics cannot accurately predict how they change over time or respond to perturbations. Thus, a realistic model of priority effects should include two key components: a base competition model, and a function that describes how interacting species traits change with relative arrival times. Integrating both mechanisms allows one to capture the diversity of priority effects in natural systems and helps to isolate individual and synergistic effects of arrival times within and across generations (Box 4).

This integration comes with new opportunities and challenges. Different mechanisms typically operate at different time scales (e.g., within vs. between generations). How models capture these different time scales will ultimately depend on the life history of species, which is directly related to the temporal scales of arrival time differences (Box 1). Previous studies suggest an easy implementation on annual systems by modeling interaction coefficients (or other traits) as a function of arrival times (e.g., the competition-phenology function [72]; Box 3), which allows researchers to maintain much of the original model structure and analytical tools for analyses. However, this approach does not easily extend to systems where arrival times vary across years, but interactions last over multiple generations within years. The latter systems require different types of model formulations, like size/stage-based models or agent-based models [73,74]. Importantly, these hybrid approaches have already started to

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reveal how the importance of priority effects for the long-term dynamics of communities can depend on the life history of species. For instance, trait-mediated priority effects are likely to play a major role in the population dynamics of annual species but may be less important the more generations per year a system exhibits [73]. In addition, variations in arrival times are widespread in nature (e.g., between years and patches [75,76]), and individual and combined effects of different types of priority effects could lead to different community dynamics and biodiversity patterns [63,64,77]. We hope that our framework will stimulate a range of new theoretical studies that will shed new light on the different consequences of priority effects across biological systems.

Better Quantification of Different Priority Effects

Traditionally, studies focused on the detection of priority effects by comparing dynamics that arise from different arrival orders (e.g., early vs. late treatment; Box 1). The problem with this approach is that it is unreliable to detect the potential for priority effects. For instance, with numeric priority effects, the early arriving species may or may not exclude the later arriver, depending on whether it had enough time to increase in relative frequency to gain a numeric advantage (Box 4). Therefore, the community dynamics depend on not only the arrival *order*, but also the specific arrival *time*.

Therefore, we suggest that future experimental research should aim to characterize priority effects across a wide range of arrival times to quantify how interactions or outcomes scale with relative arrival time (e.g., the competition-phenology function). This would allow the experiment to uncover an accurate phenomenological representation of priority effects in the focal system. The range of arrival times should scale with the life history of species to capture

differences in arrival times that cover at least one generation (or length of a life stage). Relative arrival times can either be directly manipulated or simulated by competing different combinations of stages/size classes of species [2,22,39]. The effect of timing can then be measured by vital rates such as survival, growth rate, and fecundity. For systems without apparent size- or stage-mediated competition, such as most organisms with short generation times or continuous reproduction (bacteria, fungi, protists), interspecific competition coefficients can be directly evaluated from invasion growth rates [3,78]. Differences in arrival times may nevertheless allow the early arriver to establish a numeric advantage in these systems, potentially requiring crossing different initial frequencies of each species to the gradient of arrival times. The quantified competition-phenology relationship can then be used to model long-term community dynamics under other conditions.

Although the competition-phenology function is a powerful tool to characterize priority effects, it is phenomenological and cannot detect the potential underlying biological mechanism, such as size-mediated predation, resource competition, or environmental factors. Additional measurements on other parameters, such as functional traits, demographic parameters, or behavioral assays, are required to identify the exact mechanism of priority effects in a system. Different arrival times are also likely to influence intraspecific competition in some systems with distinct ontogeny [79–81]; therefore, characterizing the relationship between intraspecific competition and arrival time might also be necessary.

Concluding Remarks

Temporal- and seasonal-explicit ecology remains one of the understudied frontiers in community ecology [72,82]. We show that by accounting for the specific mechanisms that link

the relative arrival time of species to their interactions, we can extend our current theoretical framework of priority effects to cover a much wider range of taxa and ecological conditions. Our temporal-explicit framework provides new paths for modeling priority effects and highlights the need for new experimental designs that manipulate arrival times at finer temporal scales. We hope that this framework marks the first step in considering timing in classic and burgeoning concepts in ecology, including but not limited to phenotypic plasticity [56,83,84], metacommunity theory [63,64,77], alternative assembly paths [85,86], and higher-order interactions [87,88] (Outstanding Questions). Resolving and predicting species interactions in a temporally explicit context will not only help us to better understand the dynamics and structure of natural communities, but it is also essential to predict how natural communities will respond to climate change.

Outstanding Questions

1. How can we extend the current framework of timing of interactions and trait-mediated priority effects to multispecies communities with higher-order interactions?

2. How can phenological shifts and changes in species' life cycles (e.g., reproduction timing, number of generations per year) work in concert to affect species interactions under climate change?

3. How do different mechanisms of priority effects contribute to alternative paths of community composition?

4. How diverse is the shape of competition-phenology function in nature and what factors are driving this diversity?

5. How can intraspecific variation and phenotypic plasticity affect the consequences of priority effects?

6. How does rapid evolution among interacting species affect the magnitudes and consequences of priority effects?

7. How do different mechanisms of priority effects contribute to the biodiversity, stability, and ecosystem functioning in nature?

Table 1. Comparing numeric with trait-mediated priority effects.

	Trait-mediated	Numeric
Timing affects…	Interaction strength	Population size
Per-capita effect…	Depends on difference in arrival time	Constant, independent of arrival time
Depends on initial density?	No	Yes
Outcome of competition changes…	Continuously along the gradient of arrival times	Abruptly depending only on the arrival order
Potential outcomes of competition	Competitive exclusion, positive frequency dependence, or coexistence; may include shifts in relative abundance	Competitive exclusion
Scale of differences in arrival times comparing to the time of one generation	Difference in arrival times usually within one generation	Difference in arrival times usually longer than one generation

Box 1. Empirical studies of priority effects: a literature review

We compiled 140 empirical studies of priority effects (see Appendix II for methods). Despite the diverse study systems in our list of experiments, most studies were conducted on terrestrial plants (58/140, or 41.4%). Among all experiments, 39 (27.9%) did not explicitly manipulate arrival times but rather used initial community composition or length of natural colonization as proxies. Even among the remaining 101 studies that considered arrival time as a treatment, only 30 used a temporal gradient rather than a simple early/late arrival treatment (Figure 1).

We further calculated the proportion of studies with durations of less or equal to one generation (defined by the emergence of adults or reproduction within the experimental period), 1-5 generations, or more than five generations. We omitted four studies using taxa that are significantly different in life histories (e.g., insects and fungi). About half of the 136 studies (64, 47.1%) were conducted over a time span of less than or equal to one generation, but the other half lasted more than five generations of focal taxa (56, 41.2%). These results represented the slow- and fast-generating systems often used in experiments on priority effects. Indeed, all studies spanning less than five generations (80, 58.8%) were conducted on terrestrial/aquatic plants, amphibians, fish, and slow-generating insects (e.g., odonates), all of which require weeks to years for development and reproduction. In contrast, most studies spanning more than five generations were conducted on fast-generating microbial communities, protists, planktons, and fast-generating insects (e.g., aphids), with a small fraction of long-term studies on terrestrial plant communities (9, 6.6%). These results clearly indicate that the current body of experimental work on priority effects is strongly biased towards two extremes: short-term studies on systems with long generation times and long-term studies on systems with very short

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generation times (Figure 2).

In addition to system selection and experimental design, priority effects are also measured in diverse ways. The most common response variables include community composition [45], functional traits [28,29], demographic rates such as growth, survival, and fecundity [2,39,58], and ecosystem function [18,89], but studies can also measure highly specific responses such as aggression, site occupancy [26,30,90], and in coinfection experiments, pathogen load and host response [37,91]. These measurements in part highlight the importance of priority effects in nature, but also increase the difficulty of generalizing, quantifying, and comparing the consequences of priority effects across systems.

Box 2. Mathematical representations of numeric priority effects

Consider a simple Lotka-Volterra competition model:

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

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

(Eqn. B1).

Analytically, numeric priority effects represent a definitive outcome of pairwise competition under the modern coexistence theory framework, defined by two key parameters, fitness ratio $(f_2/f_1 = \sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{22}\alpha_{21}}})$ and stabilization potential $(1 - \rho = 1 - \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}})$ [51]. Coexistence requires that the fitness ratio should be smaller than the stabilization potential, i.e., $\rho < f_2/f_1 < 1/\rho$ [52]. Numeric priority effects requires that the reverse is true, i.e., $\rho > f_2/f_1 > 1/\rho$. If the stabilization potential is larger than the fitness ratio, both species cannot invade the other when rare, and the early arriver maintains its numeric advantage by positive population growth [50,51]. Therefore, this type of priority effect is particularly likely in species that have similar niches, essentially providing a mathematical formulation of the concept of "niche pre-emption" that has been proposed previously as a key mechanism of priority effects [7,27]. With a large body of literature providing methods for quantifying competition coefficients, fitness, and niche differences [78,92] this theoretical framework allows the parameterization of competition models from experimental data to test and critically evaluate the role of priority effects on long-term structure of natural communities [6,41].

Visually, competition outcomes can be represented by a "coexistence space", where the fitness ratio is on the y-axis and stabilization potential is on the x-axis (Figure 3). Each pairwise interaction can therefore be mapped as a point of this plane and falls into one of the

three outcomes: competitive exclusion, coexistence, and (numeric) priority effects.

Note that the framework of numeric priority effects does not prohibit key parameters of the competition model, such as interspecific competition coefficients, to change with relative arrival times, if the calculated fitness ratio and stabilization potential still satisfy $\rho > f_2/f_1 > 1/\rho$. However, the majority of models and experiments that parameterize these models assumes constant interspecific competition coefficients [3,42,50,51].

Box 3. Mathematical representations of trait-mediated priority effects

Trait-mediated priority effects assume a change in species interaction with their timing. This is often modeled by a shift in interspecific competition coefficients α_{12} and α_{21}, although other demographic rates (intrinsic growth rates, intraspecific competition, or mortality) may also contribute to this change. Specifically, the interspecific competition is defined as a function of their relative arrival time, $\Delta p_{12} = p_2 - p_1$; the Lotka-Volterra model therefore becomes:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - f_{12}(\Delta p_{12}) N_2)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 - f_{21}(\Delta p_{21}) N_1)$$

(Eqn. B2).

The key to the difference between numeric and trait-mediated priority effects is termed the interaction-phenology function (or competition-phenology function, since priority effects are mostly studies in competitive systems), $\alpha_{12} = f(\Delta p_{12})$, because it links per capita strength of species interactions directly to their relative (typically seasonal) timing of arrival within a generation [72]. Although the few empirical studies that quantified $f(\Delta p_{ij})$ all support a nonlinear relationship [2,39,60] (Figure 4), the function could also have other shapes. For instance, if species interaction only depends on whether another species is previously present, not how long it has been present (e.g., patch memory [63]), then $f(\Delta p_{12})$ could take the form of a piecewise function (Figure 4). When the competition-time function is constant, i.e., $f(\Delta p_{12}) = \alpha_{12}$ for all Δp_{12}, then species interactions are not linked with relative arrival times, and the model simply collapses to a model with only numeric priority effects (Figure 4). By accommodating a wide range of competition-phenology relationships, this method of modeling

priority effects is versatile and can be used to parameterize any empirical system.

Because both the fitness ratio and stabilization potential depend on interspecific competition coefficients, they become functions of Δp_{12} as well:

$$f_2/f_1 = \sqrt{\frac{\alpha_{11}f_{12}(\Delta p_{12})}{\alpha_{22}f_{21}(\Delta p_{21})}}$$

$$1 - \rho = 1 - \sqrt{\frac{f_{12}(\Delta p_{12})f_{21}(\Delta p_{21})}{\alpha_{11}\alpha_{22}}}$$

(Eqn. B3)

Therefore, any change in the relative timing of species would shift the position of the species pair in the coexistence space. For instance, when $\Delta p_{12} = 0$ species 1 and 2 could coexist (point D in Figure 3), but when species 1 arrives earlier ($\Delta p_{12} > 0$) the corresponding fitness ratio and stabilization potential may shift to point C, or species 1 wins. Note that these shifts may not necessarily lead to observable changes in competition outcomes (for instance, a shift within the coexistence region), but whether that counts as a trait-mediated priority effect depends on the working definition of priority effects: the arrival order changes either the outcome of species interaction (by which it would not be a trait-mediated priority effect) or the species interaction itself (by which it would).

Box 4. How resource competition could lead to priority effects from numeric and trait-mediated mechanisms

Here, we illustrate the utility of our framework by unpacking a common mechanism of priority effects, resource competition [7]. In this system, the early-arriver advantage could result from the higher abundance and subsequent population growth by positive frequency dependence (i.e., numeric priority effects [93]). For instance, within the microbiome hosted by a single polyp of *Hydra vulgaris*, one strain of bacteria gains dominance by a higher initial abundance [94]. However, the early-arriver advantage could also arise from changes in traits of individuals (trait-mediated priority effects). For instance, the early arriver might have a larger size compared to the late arriver. This could lead to higher feeding rates in amphibians [24,95] or an advantage in light competition in plants [33]. In these cases, size is the trait that changes as the two species arrive at different times.

To quantitatively capture the above examples, we analyzed a modified, discrete-time version of the consumer-resource model used by Ke and Letten [51], where two consumer species compete for a shared resource. We modeled consumers with an annual cycle, and arrival times were allowed to vary within a year vary between species. We assume a higher feeding rate of the earlier arriver within a year. Therefore, the early-arriver advantage in this model could arise from: (1) resource preemption by the early arriver, which is a numeric mechanism that leads to positive frequency dependence; (2) change in resource uptake rates, which is a trait-mediated mechanism. See Appendix III for model and simulation details.

Without trait-mediated priority effects, the two species display positive frequency dependence: a species wins if it arrives early over several years (Figure 5A), regardless of the within-year arrival times (phenology) of the two species (Figure 5C). However, with

trait-mediated priority effects, both arrival times within and across years matter: while one species could gain an advantage by establishing itself several years earlier than the other, it could still be excluded if it emerges late within a year (Figure 5B, 5D). These results highlight that: (1) one common biological mechanism of priority effects, resource competition, can be driven by either numeric or trait-mediated mechanisms, or a combination of both; (2) numeric and trait-mediated priority effects are not mutually exclusive and can synergistically determine long-term population dynamics; (3) population dynamics could be affected by arrival times both within a year and across years, which has important implications for empirical systems with different life histories.

Figure Captions

Figure 1. Manipulation of time in experiments and the dichotomy of time scales of experimental systems. (A) Results from the literature review show that 39 out of 140 experiments (27.9%) did not manipulate the arrival times of species. (B) Results from the literature review show the dichotomy of temporal scales among experiments: all studies spanning less than five generations were conducted on slow-generating systems (e.g., plants, amphibians, fish), while most studies spanning more than five generations were conducted on fast-generating systems (e.g., microbial communities, protists, planktons), with a small fraction of long-term studies on terrestrial plant communities.

Figure 2. Differences in arrival times in fast- and slow-generating systems. (A) Conceptual figure showing priority effects in fast-generating systems, where the difference in arrival times spans several generations. (B) Conceptual figure showing priority effects in slow-generating systems, where the difference in arrival times is less than a generation.

Figure 3. Numeric and trait-mediated priority effects in a coexistence space. The coexistence space is often used to map species interactions with measurements of stabilizing mechanism (stabilizing potential on x-axis) and equalizing mechanisms (fitness ratio on y-axis). Numeric priority effects, as defined by positive frequency dependence, are represented by a region where $\rho > f_2/f_1 > 1/\rho$ (point A). Trait-mediated priority effects are defined by changes in interaction strengths due to changes in arrival times, represented by arrows. Note that a trait-mediated priority effect does not necessarily lead to exclusion; a shift from exclusion to coexistence (points C to D), or in relative abundance of species is also a trait-mediated priority effect.

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Figure 4. Examples of competition-phenology functions that assume an early arriver advantage. In all panels, relative arrival time $(\Delta p) > 0$ means species 2 arrives first, and $\Delta p < 0$ means species 1 arrives first. (A) Competition coefficients do not change with relative arrival times. (B) Competition coefficients change continuously with relative arrival times. (C) Competition coefficients change abruptly with relative arrival times.

Figure 5. A model with both numeric and trait-mediated priority effects. (A) Population dynamics when species 1 establishes several years earlier than species 2; species 1 has a higher density, showing a numeric priority effect. (B) Population dynamics when species 1 establishes several years earlier than species 2 but emerges later than species 2 within a year; despite species 1's numeric priority effect, species 2 has a higher feeding rate by emerging earlier within a year, displaying a trait-mediated priority effect over species 1. (C) Without trait-mediated priority effects, the relative emergence time within a year (Δp) does not affect competition outcomes. (D) With both numeric and trait-mediated priority effects, both the relative arrival time over years (years early on the y-axis) and within a year (Δp on the x-axis) affect competition outcomes.

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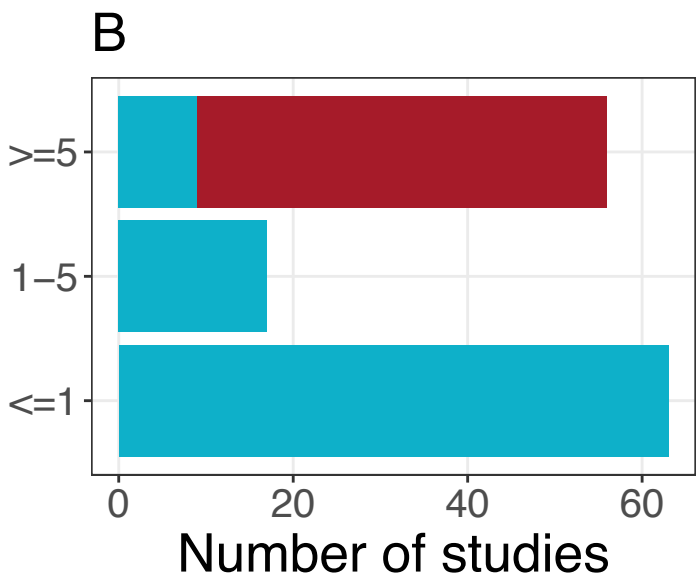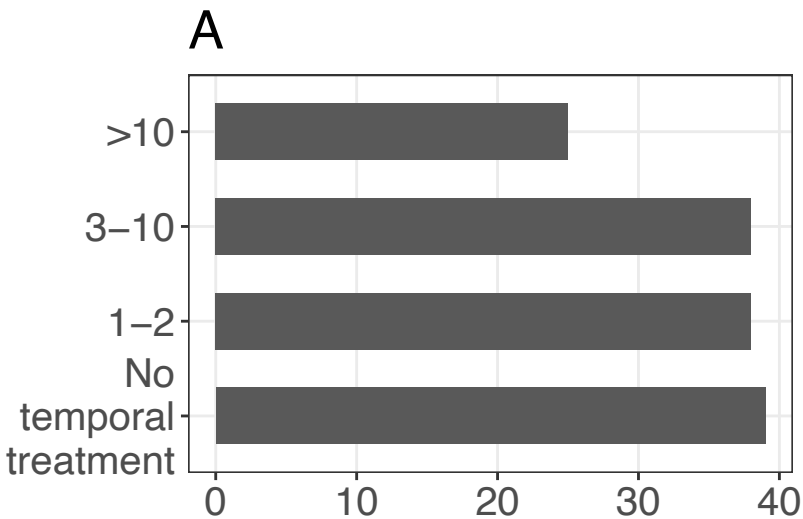
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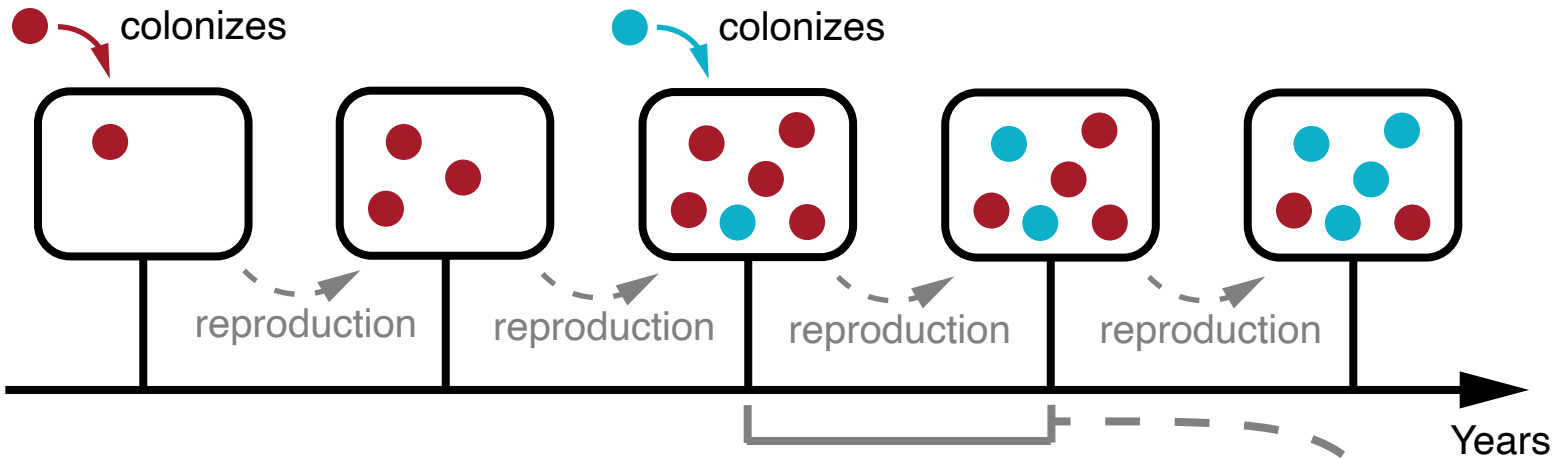[95] Lawler SP, Morin PJ. Temporal overlap, competition, and priority effects in larval anurans. Ecology 1993;74:174–82. https://doi.org/10.2307/1939512.

A. Arrivals across years (sequence of colonization)

colonizes

colonizes

reproduction   reproduction   reproduction   reproduction

Years

B. Arrivals within a season (sequence of phenology)

emerges   emerges   Time within a year