




















Review

# Priority effects transcend scales and disciplines in biology

J.T. Stroud <sup>1,\*</sup>, B.M. Delory <sup>2,3,\*</sup>, E.M. Barnes <sup>4</sup>, J.M. Chase <sup>5,6</sup>, L. De Meester <sup>7,8,9</sup>, J. Dieskau <sup>5,10</sup>, T.N. Grainger <sup>11</sup>, F.W. Halliday <sup>12</sup>, P. Kardol <sup>13,14</sup>, T.M. Knight <sup>5,15,16</sup>, E. Ladouceur <sup>5,6</sup>, C.J. Little <sup>17</sup>, C. Roscher <sup>5,18</sup>, J.M. Sarnel <sup>19</sup>, V.M. Temperton <sup>2</sup>, T.L.H. van Steijn <sup>19</sup>, C.M. Werner <sup>20</sup>, C.W. Wood <sup>21</sup>, and T. Fukami <sup>22,\*</sup>

Although primarily studied through the lens of community ecology, phenomena consistent with priority effects appear to be widespread across many different scenarios spanning a broad range of spatial, temporal, and biological scales. However, communication between these research fields is inconsistent and has resulted in a fragmented co-citation landscape, likely due to the diversity of terms used to refer to priority effects across these fields. We review these related terms, and the biological contexts in which they are used, to facilitate greater cross-disciplinary cohesion in research on priority effects. In breaking down these semantic barriers, we aim to provide a framework to better understand the conditions and mechanisms of priority effects, and their consequences across spatial and temporal scales.

## Priority effects: moving beyond community ecology

**Priority effects** (see [Glossary](#)), whereby arrival order influences **community assembly**, can be a powerful driver of ecological **community structure** [1–3]. Priority effects can be facilitative ([Box 1](#)), but most research has focused on the role of inhibitory species interactions [4] in which early-arriving or initially abundant species negatively affect the immigration, establishment, or abundance of late-arriving species through **niche preemption** and/or **niche modification** [5]. Although primarily studied by community ecologists, patterns consistent with priority effects have been observed in a wide variety of biological contexts ([Figure 1](#)). However, these phenomena have often been described using a range of different terms ([Table 1](#)). This diversity of perspectives can promote a greater range of discoveries, but a lack of conceptual cohesion because of differences in language can also hinder our understanding of priority effects as a broader biological phenomenon.

Here, we review the diverse fields where priority effects are relevant and identify outstanding research questions. We mainly focus on **inhibitory priority effects** as it has been the primary focus of most studies. We aim to help accelerate progress in future research on priority effects in two complementary ways. First, we seek to empower researchers currently studying priority effects by encouraging drawing on insights, conclusions, and research approaches used in other biological fields. Second, we aim to inspire biologists who do not currently study this concept explicitly to explore the role that priority effects may play in their own study systems.

## A history in community ecology

Ecologists have recognized **historical contingency** in community assembly for the past century [2]. Following early descriptive studies, the development of a theoretical framework in the mid-to-late 20th century [1] formulated one form of historical contingency – the role that priority effects can play in driving variation in species diversity among ecological communities formed from the

## Highlights

The effects of species on one another sometimes depend on the order in which they arrive at a local site. This historical contingency, termed priority effects, can have a major influence on the assembly and functioning of ecological communities.

Although historically studied within community ecology, phenomena consistent with priority effects appear in a variety of biological scenarios and across a wide range of spatial and temporal scales, but are referred to by many different but related terms.

There exists a fragmented communication landscape between studies of priority effects across these disparate biological subfields, which is stifling a conceptual unification of how, when, and why priority effects occur.

Our review provides a launchpad for developing a unified framework across a broad range of ecological contexts.

<sup>1</sup>School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA

<sup>2</sup>Institute of Ecology, Leuphana University Lüneburg, Lüneburg, Germany

<sup>3</sup>Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, The Netherlands

<sup>4</sup>Thomas H. Gosnell School of Life Sciences, Rochester Institute of Technology, Rochester, NY 14623, USA

<sup>5</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

<sup>6</sup>Institute of Computer Science, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany



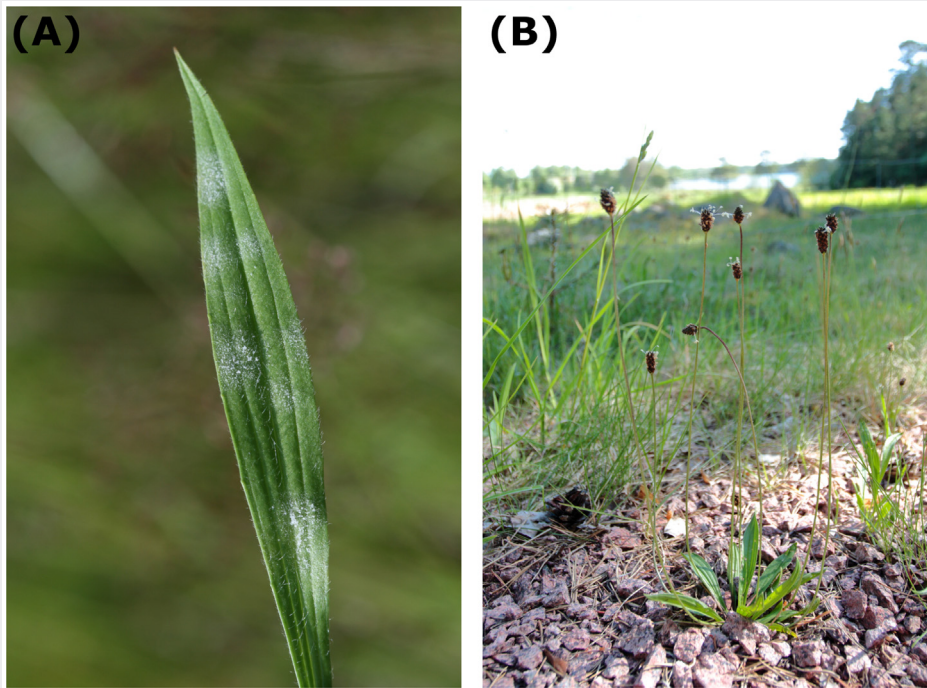
### Box 1. Going beyond inhibition: facilitative priority effects

Competition is one of many mechanisms involved in species coexistence and community assembly [5]. Positive interactions can also lead to contingency in community assembly. For example, **facilitative priority effects** can occur when a species performs better in the presence of particular established residents [2,97]. For facilitative priority effects to occur during community assembly, the positive effects of niche modification by early-arriving species must outweigh the negative effects associated with the early uptake of essential resources that become less available to later-arriving species (niche preemption [2]). Although facilitation effects have been implicated in many ecoevolutionary contexts from ecological succession to macroevolutionary dynamics [98], it remains unknown how common and strong these facilitative priority effects are in nature [99,100].

For example, for plant communities in harsh environments such as deserts, increased shading by shrubs can facilitate herbaceous annuals by ameliorating the local microclimate and making it more favorable to more drought-sensitive species [101]. Species immigrating into the community can also benefit from soil nutrient enrichment by early colonizers, which can take place via the exudation of nutrient-mobilizing compounds by plant roots or by an increase in soil nitrogen availability produced by free-living plant-associative N<sub>2</sub>-fixing bacteria [102].

Facilitative priority effects have also been detected in microbial and host-associated systems. In microbial communities, cases of syntrophy – in which early-arriving species break down complex molecules into smaller molecules that can then be taken up and used by other microbes – have been found in both infant gut microbiota [45] and marine microbial communities [103]. Facilitative priority effects can also drive the assembly of parasite communities, for example, on host plants (Figure 1). Indeed, early infection by some parasite strains can increase the susceptibility of host plants to future infection by altering their physiology or immunity [99].

These few examples show that the perception that priority effects can only lead to the exclusion or suppression of later-arriving species is incomplete. It also challenges the narrow definition of priority effects used in some ecological theories, such as Tilman's consumer-resource model (R\*) and modern coexistence theory, in which priority effects are strictly inhibitory and occur when an early arriver prevents the establishment of a late arriver as a result of positive frequency-dependence of population growth [104]. Future research should aim to better integrate facilitative priority effects into ecological theories (see Outstanding questions).



Trends in Ecology & Evolution

**Figure 1. Community assembly and priority effects in a host-associated community.** In host-associated communities, and especially among plant hosts, strong within-host interactions between coinfecting parasites can drive local priority effects. For example, early-establishing strains of the powdery mildew, *Podosphaera plantaginis* (A), on leaves of the host plant, *Plantago lanceolata* (B), can facilitate infection by later-arriving strains, which are less likely to establish in their absence [99]. Photo credits: Mikko Jalo, Anna-Liisa Laine.

<sup>7</sup>Leibniz Institut für Gewässerökologie und Binnenfischerei (IGB), Müggelseedamm 310, 12587 Berlin, Germany

<sup>8</sup>Institute of Biology, Freie Universität Berlin, Königin-Luise-Strasse 1–3, 14195 Berlin, Germany

<sup>9</sup>Laboratory of Aquatic Ecology, Evolution, and Conservation, Katholieke Universiteit Leuven, B-3000 Leuven, Belgium

<sup>10</sup>Department of Geobotany and Botanical Garden, Martin-Luther University, Germany

<sup>11</sup>Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada

<sup>12</sup>Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, USA

<sup>13</sup>Department of Forest Mycology and Plant Pathology, Swedish University of Agricultural Sciences, 750 07 Uppsala, Sweden

<sup>14</sup>Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 90183 Umeå, Sweden

<sup>15</sup>Department of Community Ecology, Helmholtz Centre for Environmental Research (UFZ), Halle (Saale), Germany

<sup>16</sup>Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

<sup>17</sup>School of Environmental Science, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

<sup>18</sup>Department of Physiological Diversity, Helmholtz Centre for Environmental Research (UFZ), Leipzig, Germany

<sup>19</sup>Department of Ecology and Environmental Science, Umea University, 901 87 Umea, Sweden

<sup>20</sup>Department of Environmental Science, Policy, and Sustainability, Southern Oregon University, Ashland, OR 97520, USA

<sup>21</sup>Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

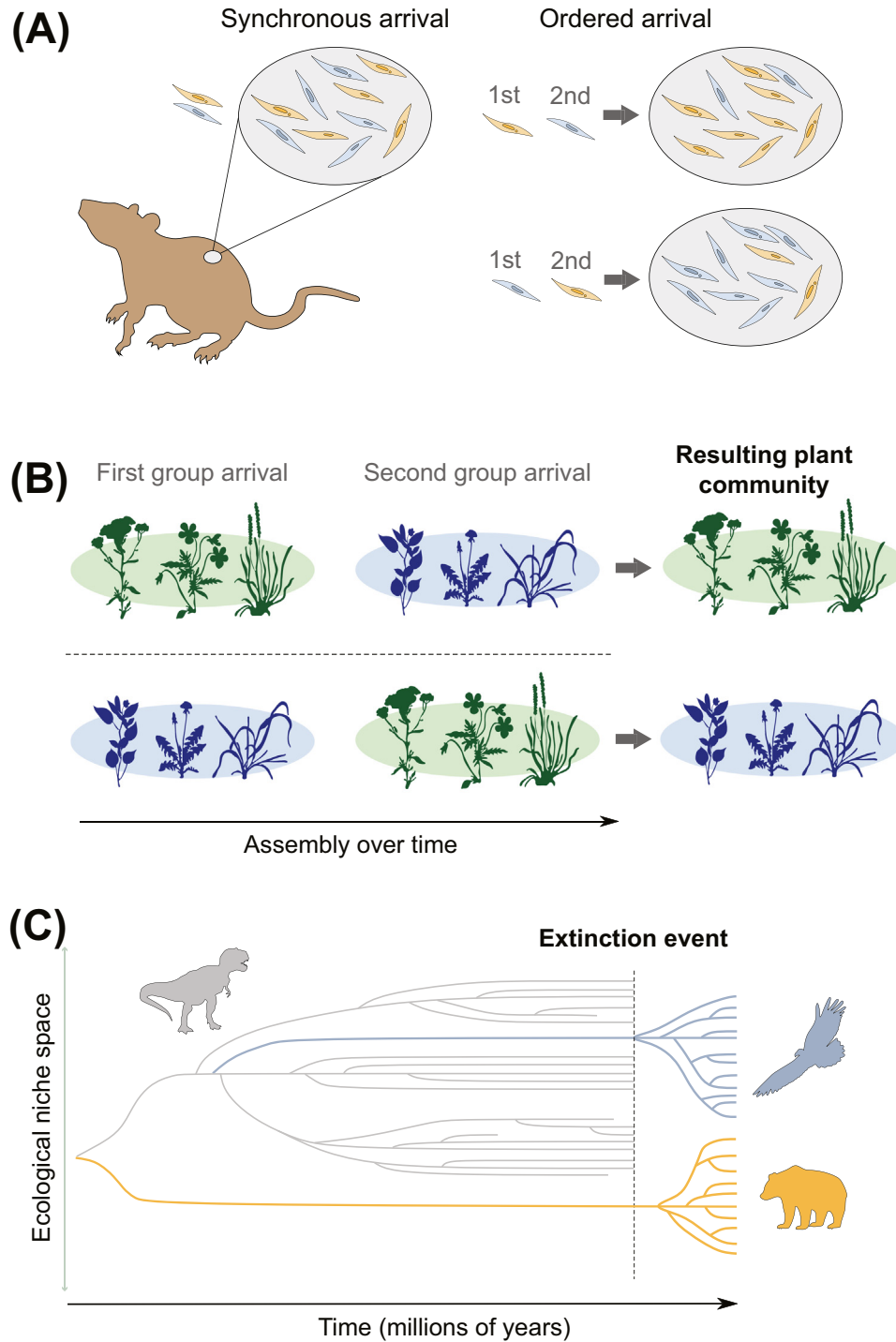
<sup>22</sup>Departments of Biology and Earth System Science, Stanford University, Stanford, CA 94305, USA

\*Correspondence:

[stroud@gatech.edu](mailto:stroud@gatech.edu) (J.T. Stroud),

[b.m.m.delory@uu.nl](mailto:b.m.m.delory@uu.nl) (B.M. Delory), and

[fukamit@stanford.edu](mailto:fukamit@stanford.edu) (T. Fukami).



**Glossary**

**Alternative stable states:** different historical sequences of species entering a local area leads to different final community compositions.

**Community assembly:** the generation of local communities through immigration of species from the regional species pool.

**Community composition:** the identity of species present in a community.

**Community structure:** the composition of a community, including the number of species and their relative abundances.

**Facilitative priority effect:** when a species that arrives first positively affects the establishment, growth, or reproduction of a species arriving later.

**Historical contingency:** the effect of the order and timing of past events on community assembly.

**Inhibitory priority effect:** when a species that arrives first negatively affects the establishment, growth, or reproduction of a species arriving later.

**Monopolization:** evolution-mediated priority effect at the population or community level.

**Niche modification:** early-arriving species change the types of niches available within a local site, and consequently affect the identities of late-arriving species that can colonize the community.

**Niche preemption:** earlier-arriving species reduce resource availability such that species arriving later are limited in their ability to survive and reproduce.

**Priority effects:** phenomena in which the effects of species on one another depend on the arrival order of species into a local site.

**Regional species pool:** the set of species that could potentially colonize and establish within a local community or patch.

**Stochasticity:** the variability in intrinsic demographic processes or extrinsic environmental conditions that affect community assembly.

Figure 1. Priority effects transcend spatial, temporal, and biological scales. (A) Inhibitory priority effects of malarial strains during infection: for example, early-arriving malarial strains can limit the infectious efficacy of later-arriving strains in infected mice [36]. (B) Inhibitory priority effects in the assembly of local or regional communities: for example, early-arriving

(Figure legend continued at the bottom of the next page.)

Table 1. Terms related to priority effects and examples of their use<sup>a</sup>

Terms related to priority effects	Biological subfields where terms are used (with example studies)
Alternative stable states, alternative equilibria	Restoration ecology [61,62], community ecology [63,64]
Colonization/invasion/biotic resistance	General ecology [65,66], restoration ecology [67], community ecology [68], immunology [69,70], invasion biology [25]
Cross-immunity, cross-protection, induced resistance	Immunology [71,72], disease ecology [73,74]
Founder control, founder effect	Community ecology [75,76], evolutionary ecology [51], population genetics [51]
Home-field advantage	Conservation biology [77], invasion ecology [19], ecosystem ecology [28]
Lottery-based assembly	Microbial ecology [78], general ecology [79,80]
Monopolization	Evolutionary ecology [51,52]
Mutual non-invasibility	General ecology [81,82]
Niche incumbency, incumbency effects	Paleobiology [53,83], macroecology [84], macroevolution [85,86], community ecology [27]
Niche filling	Macroevolution [83,87]
Niche preemption	Macroevolution [87], community ecology [88]
Positive frequency-dependence (modern coexistence theory)	Theoretical ecology [89], experimental ecology [9]
Preemptive competition	Paleobiology [90], entomology [79], immunology [70]
Priming	Disease ecology [91,92], chemical ecology [93]
Prior-residence advantage	Population biology [94], community ecology [95]

<sup>a</sup>Biological phenomena consistent with 'priority effects' have been studied using a wide range of terms. We review here the terms used in different subfields of biology. Reflecting the traditional focus, most of the terms included concern inhibitory priority effects, but some terms (e.g., alternative stable states) are used broadly to include both inhibitory and facilitative priority effects.

same **regional species pool** (i.e., **alternative stable states** [6]). In accordance with trends in community ecology at the time [7], interspecific competition for limiting resources was considered to be the primary mechanism for many of these priority effects which occur when the per capita strength of interspecific competition exceeds that of intraspecific competition [1]. Consequently, the majority of research on priority effects has centered on their inhibitory roles, whereby early-arriving species negatively affect the establishment or abundance of subsequent immigrant species, primarily through exploitative competition [8]. Inhibitory priority effects are also a central component of the modern coexistence theory [9] – a framework for understanding how species niche and fitness differences can promote coexistence and maintain species diversity. More recently, there has been a greater appreciation that other types of biotic interactions can also lead to similar ecological patterns (e.g., plant–soil feedbacks [10,11]).

### Priority effects transcend scales and disciplines

We suggest that more cross-pollination between studies of priority effects would accelerate progress in our understanding of priority effects and their wider influence on community assembly and ecosystem functioning (Box 2). To foster cross-pollination, we offer a twofold approach: first,

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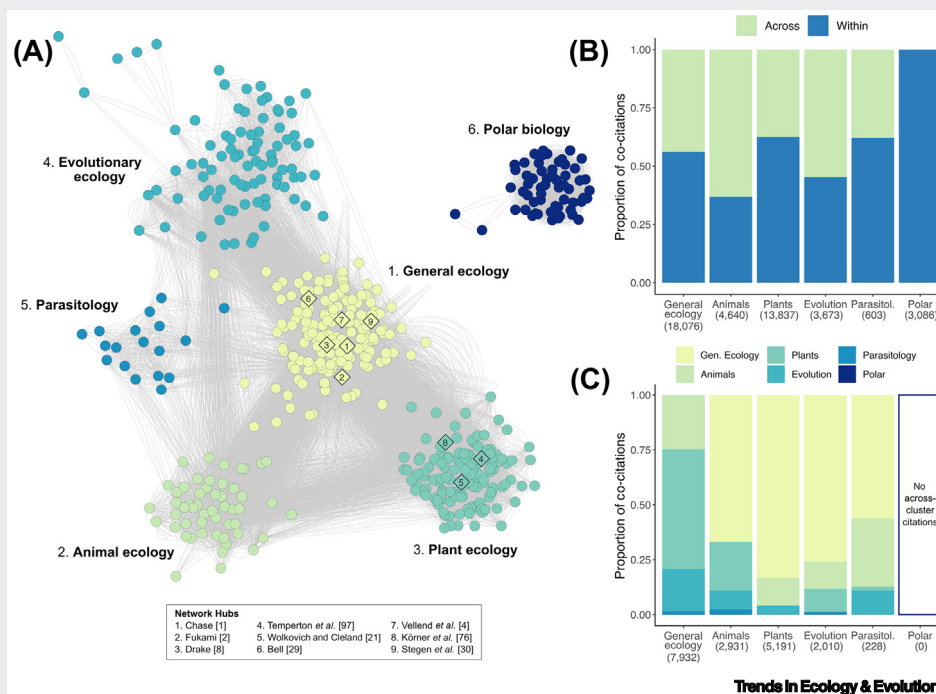
species can limit the invasion or establishment success of later-arriving species [96]. (C) Inhibitory priority effects have also been suggested to influence macroevolutionary dynamics: for example, extensive diversification of some clades may occur following the removal of incumbent clades that occupy similar ecological niches, demonstrated here by the rapid diversification of birds and placental mammals following the Cretaceous–Paleogene mass extinction of non-avian dinosaurs and other archosaurs [53]; this illustration has been conceptually simplified for illustrative purposes.

### Box 2. Information transfer between priority effects studies

Although priority effects are attracting an increasingly diverse range of research attention, a lack of cohesion among studies – likely driven by the absence of a well-resolved semantic framework (Table 1) – has stifled a broader biological understanding of this phenomenon. To quantitatively explore trends in the transfer of information between studies on priority effects, we conducted a co-citation network analysis of studies related to priority effects ( $n = 902$ ; see 'Co-citation network analysis' in the supplemental information online). A co-citation analysis measures how frequently two studies are cited together in a publication, and a network algorithm identifies clusters of studies that have more within-cluster than between-cluster shared citations (alternative algorithm analyses are given in Figure S1).

Taken together, our co-citation analysis demonstrates inconsistent cohesion among studies of priority effects and related topics across disparate biological subfields (Table 1). It highlighted several large clusters that correspond to major biological disciplines which operate with varying degrees of research connectivity to each other (Figure 1). Specifically, the analysis revealed four disciplines with relatively well-connected citations, which we call (1) general ecology, (2) animal ecology, (3) plant ecology, and (4) evolutionary ecology (Figure 1). The general ecology cluster is primarily constructed of conceptual, mathematical, and statistical papers of broad ecological relevance, but also contains studies that specialize on specific groups of organisms, mainly bacteria and fungi, which could be due to their amenability for experimental tests of ecological theory. We collectively refer to this well-connected set of four primary clusters (i.e., 1–4; Figure 1) as the super-cluster of research on priority effects and related topics.

Next to the super-cluster, two additional clusters were identified by the co-citation analysis: (5) parasitology, and (6) polar biology (Figure 1). Although parasitology papers are frequently co-cited with studies from the super-cluster, papers from the super-cluster are rarely co-cited with papers from the parasitology literature. Although the term priority effects has been increasingly used in recent parasitological publications, other terms were used traditionally (e.g., immune priming [91]), perhaps explaining this pattern of asymmetric co-citations. In addition, polar biology, as a subfield, seems to have operated almost completely independently from other studies on priority effects and related topics (Figure 1). The reasons for this separation are unclear but could stem from the notion that polar ecosystems are ecologically too unique to inform or be informed by studies conducted elsewhere. Similarly, whether these patterns are specific to research on priority effects or are indicative of a broader pattern of fragmented communication between ecological research fields deserves further comparative analyses.



**Figure 1. Co-citation network analysis highlighting information transfer between studies on priority effects and related topics.** (A) The co-citation network, where circles represent publications, circle colors represent publication clusters identified via the Louvain algorithm, and gray lines represent co-citation of two studies. At the bottom (identified by diamonds in the network) are influential and highly cited papers that serve as network hubs. (B) The proportion of co-citations between studies either within their own cluster or from separate clusters. (C) Breakdown of co-citation patterns and frequency across clusters. In panels (B) and (C) numbers in parentheses represent the total number of co-citations for that cluster.

a literature review highlighting diverse terminologies across subfields consistent with priority effects (Table 1); second, insights from diverse biological subfields conducting research related to priority effects.

### Restoration ecology

Restoration ecology – the science of how to restore degraded, damaged, or destroyed habitats – has long recognized the role of priority effects in determining patterns of community structure [12,13]. In this context, priority effects have been used as a tool for restoration management [14] by manipulating the order of species introductions to inhibit the ecological success of 'undesirable' species in an effort to enhance the success of 'desirable' species [15]. Restoration through human intervention assumes that a system has been degraded and would benefit from actions that accelerate recovery or overcome some type of ecological threshold. Such restoration scenarios have primarily focused on terrestrial plant communities and have often been studied through the semantic frameworks of 'alternative vegetative states', 'hysteresis', and 'invasion resistance' (Table 1). Because these terms are predominantly used in restoration studies, some insights from restoration ecology may be overlooked by biologists outside this subfield.

Although restoration ecology is often focused on terrestrial plants [16], similar scenarios exist in other ecological contexts such as coral reefs [17] (see Outstanding questions). For example, the prior establishment of corals during reef assembly can exhibit strong inhibitory priority effects on competing macroalgae [18], thereby affecting management decisions during coral reef restoration projects [17]. Together, restoration research offers opportunities to study the mechanisms that drive priority effects, and restoration practitioners would value a better understanding of priority effects. A greater synthesis of research on priority effects between restoration biologists and the broader ecology and evolution community would be beneficial, particularly for those who study ecological succession (Box 1). In addition, a better understanding of the long-term transient ecological consequences of priority effects (see Outstanding questions) could be a key contribution from restoration ecology (Box 3).

#### Box 3. On the temporal nature of priority effects

How long should an effect of arrival order on community assembly last for it to qualify as a priority effect? Early work emphasized that communities should remain different for longer than at least one complete turnover of individuals to conclude that the communities are in alternative community states caused by priority effects [105], a condition that is rarely met in experiments with plants and other long-lived organisms [106]. However, how ephemeral is sufficient to be negligible is a tricky question. Many mathematical ecologists would say that we need to wait until the community reaches a stable equilibrium to determine whether priority effects are present. For them, priority effects mean the same thing as the existence of alternative stable states. With this definition, we would not have a priority effect if communities eventually converged on a single common stable state no matter how long it takes for the convergence to occur [107]. This equilibrium-based definition is used because it makes it possible to analyze priority effects mathematically, and not necessarily because the definition is empirically or ecologically relevant [11,108]. Most real communities are influenced by disturbance events that move the communities back to an earlier stage of succession, making it unlikely that a stable state is reached [109]. However, this does not mean that, in the meantime, these transient priority effects cannot have long-lasting ecosystem consequences via, for example, changes in associated communities (e.g., soil microbial and faunal communities in the case of transient priority effects in plant communities). In addition, rapid evolution of species traits during community assembly can change the equilibrium that the community is attracted to [52,110,111], and can potentially act as an additional factor that keeps the community away from any stable equilibrium. Transient priority effects may also have long-lasting consequences by producing different starting conditions that determine community trajectories in response to environmental change, for example anthropogenic stress. Consequently, the strict mathematical definition of priority effects is unlikely to be relevant in understanding community assembly and in applying this understanding to practical issues such as conservation, restoration, and medicine. What is mostly lacking and sorely needed to better understand priority effects is the development of theoretical predictions and empirical tests regarding the long-term transient dynamics of community assembly, and not only equilibrium outcomes [11,108]. A recent contribution from Zou and Rudolf [3] discusses some concrete ways in which such development can be accomplished.

### Invasion biology

In the context of species invasions, inhibitory priority effects often operate in two ways, both of which conceptually overlap with restoration ecology (discussed in the section on restoration ecology, above). First, the disturbance of native species provides opportunities for invasive species to establish and gain priority [19], often through the expression of traits associated with strong priority effects [20]. These invasive species can subsequently threaten the persistence and (re)establishment of local species, leading to shifts in **community composition** and ultimately in ecosystem function [21]. For example, in North American prairies, invasive legumes (e.g., *Lespedeza cuneata*) can exhibit strong inhibitory priority effects on multiple native plant species [22], and similar scenarios have been reported for other taxa (e.g., birds [23] and lizards [24]).

Second, inhibitory priority effects can also be beneficial for invasive species prevention and management: earlier-established native species can minimize the establishment success of invaders (commonly termed 'biotic resistance' [25]). These scenarios are well suited for hypothesis testing in an experimental framework. Furthermore, invasive species as 'natural experiments' [26,27] might provide some of the best opportunities to gain an understanding of when, where, how, and why priority effects occur in nature (see Outstanding questions), thereby providing insights for classic eco-evolutionary theory as well as applied value for conservation biology [19].

### Microbial ecology, parasitology, and disease ecology

Evidence is growing for priority effects across many immunological, parasitological, and microbial community studies, but these studies have traditionally used terms such as 'lottery-based assembly', 'cross-immunity', 'immune priming', 'colonization resistance', and 'preemption' (Table 1). Some of these terms are broad (e.g., preemption) whereas others are more specialized (e.g., cross-immunity), and the relevance of these studies may therefore be overlooked by researchers outside these fields. Nevertheless, priority effects in microbial communities can have major ecological consequences, and can drive differences in the structure and function of terrestrial and aquatic ecosystems [28–30] as well as influencing the patterns of microbial community assembly when free-living microbes transfer to associated hosts [31,32]. For this reason, understanding microbial priority effects has high value for biomedical and bioaugmentation applications (see Outstanding questions) such as microbiome transplants, bioinoculants, and probiotics [33]. Similar scenarios in which founder microbes can inhibit the colonization of other symbionts, pathogens, or parasites exist in plant- [34] and animal-associated systems [35]. Similarly, in disease ecology, studies have highlighted that early-arriving pathogens can alter host susceptibility to secondary infection by subsequent pathogens. For example, malarial strain dominance in mice can be predicted by the order of strain inoculation, such that strains that remain rare in simultaneous inoculations can dominate when introduced first [36].

### Polar biology

Although there is a growing community ecology literature on polar ecosystems, most studies operate in apparent isolation from other fields (discussed in Box 2), and few studies explicitly address the role of priority effects in polar environments. Those that do often find evidence for priority effects. For example, variation in the timing of nutrient availability can influence the strength of priority effects during Antarctic bacterial community succession [37]. Similarly, in Antarctic macrobenthic communities, **stochastic** processes have a stronger explanatory effect on the assembly patterns than any environmental factor [38], suggesting historical contingency during community assembly. As these studies show, polar ecosystems represent opportunities for research on priority effects in two ways (see Outstanding questions). First, polar regions generally have a relatively small number of species, which makes them tractable for experimental community ecology. Second, polar environments are changing rapidly in response to contemporary

climate change [39], and therefore provide opportunities to observe community dynamics resulting from species invasions via climate-driven migrations as well as community assembly patterns as climate change generates new habitat types *in situ* [40].

#### Human microbiome ecology

Despite a large research investment in human-associated microbiomes over the past few decades, surprisingly little attention has been paid to the role of priority effects in these systems [33] compared to other microbial systems (discussed in the sections on microbial ecology and food microbiology). The introduction of bacteria intended to restore or maintain a healthy gut microflora, often referred to as probiotics, has been well studied and implemented, but the historical contingency that priority effects cause in microbiome assembly has rarely been considered explicitly in improving the efficacy of probiotics. A small but increasing number of recent studies have suggested strong priority effects for human-associated microbes using mouse models. Most studies focus on a particular bacterium that is of medical significance as a pathogen or a beneficial symbiont (*cf* [32]), such as *Salmonella enterica* serovar [41] and *Clostridium difficile* in the intestine [42], *Helicobacter pylori* in the stomach [43], *Cutibacterium acnes* on the skin [44], and *Bifidobacterium* species in the infant gut [45].

Studies on human microbiomes are limited by the dearth of possibilities for manipulative experiments directly on humans (see Outstanding questions). However, these biomedical studies excel in the presentation of multiple layers of evidence regarding the chemical and genetic mechanisms that underlie microbial priority effects – an uncommon focus of classic community ecology studies on priority effects. Even though some of the methods available for studying medically important microbes are not yet ready to be applied to non-model organisms, these studies provide guidance as to how to gain insights into the mechanisms leading to priority effects in microbial organisms as new methods, particularly gene knockouts and associated tools, become more widely applicable. The combination of these approaches with manipulative experiments that vary inoculation order in model systems is likely to provide experimental designs that are especially promising for understanding the importance of priority effects in host-associated microbiome assembly.

#### Food microbiology

Microbial interactions are responsible for the flavor, aroma, and nutritional value of many fermented food products. Food practitioners can manipulate microbial arrival to create desired taste profiles [46]. For example, liquor flavor has been linked to the arrival order of microbial starters because they differentially modify the niche space to suppress particular species in a two-stage brewing process [47]. Similarly, early inoculation with some bacteria that produce antimicrobial compounds and therefore initiate priority effects through niche modification can enhance flavor and extend the shelf life of cheese and sourdough [48–50]. Nevertheless, most studies on food microbiology in this context have operated independently of knowledge of ecological priority effects. Such situations have been underexploited for research on priority effects, even though food-associated microbial communities offer well-resolved systems to examine how and why priority effects occur, and practitioners have historic knowledge of when, how, and why the use of priority effects has applied value (see Outstanding questions).

#### Eco-evolutionary dynamics

Evolution can influence ecological community assembly if early-arriving species that rapidly adapt to environmental conditions subsequently monopolize local resources and prevent the expansion of later-arriving species through differential biotic interactions (the **monopolization** hypothesis [51]). Monopolization is particularly likely when late-arriving species are maladapted or have



poor dispersal, thereby providing early-arriving species sufficient time for adaptation [51,52]. Evolution-mediated priority effects can also occur intraspecifically, whereby early-arriving genotypes dictate the evolutionary trajectory of the founding population and inhibit the success of subsequent genetic lineages (i.e., founder effects) (see Outstanding questions). Although the ecological significance of microevolutionary dynamics is well supported, incorporating the study of such processes into field studies on priority effects is logistically challenging because one needs to study both the ecological and evolutionary dynamics, and it also faces the problem of inferring processes that operated in the past. A greater synthesis of approaches, combining field studies – which offer valuable insights into how natural processes unfold in the wild – with the experimental power of microcosms or microbial systems will be important to improve our empirical understanding of the relationship between microevolution, priority effects, and community assembly.

### Paleobiology and macroevolution

In the fossil record, episodes of explosive diversification following the removal of ecologically similar species have often been taken as evidence for inhibitory priority effects, commonly termed incumbency effects in paleobiology [53]. For example, following the Cretaceous–Paleogene mass extinction event, birds and placental mammals explosively radiated into a variety of ecological niches that were previously occupied by now-extinct non-avian dinosaurs and other archosaurs [54]. Macroevolutionary priority effects may also occur among members of the same clade [55,56]. For example, following the earlier Permian–Triassic extinction event, marine ammonoids diversified into ecological niches that were previously occupied by clade members which succumbed to the extinction event [57]. Recent attempts to develop theoretical macroevolutionary models have supported these observations from the fossil record. Priority effects can influence niche evolution, speciation, and extinction dynamics, leading to major disparities between evolutionary lineages and higher patterns of metacommunity diversity. Such studies offer insight into the macroevolutionary consequences of priority effects at timescales that exceed classic community ecology, but draw parallels to microbial studies that can operate on analogous timescales if expressed as the number of generations [58]. A greater synthesis of the paleontological literature, which is replete with evidence for incumbency (i.e., priority) effects, but lacks the ability to test ecological hypotheses owing to the retrospective nature of the field [53], with experimental evolution involving organisms with short generation times may provide opportunities for testing and generating new hypotheses (see Outstanding questions). Of course, the focal taxa in paleontological studies and experimental evolution research often have very different life histories, and it is therefore important to exercise caution when extending conclusions from one field to another.

### Concluding remarks: moving forward with cross-disciplinary communication

Our observation of variable communication between studies on priority effects (Box 2) may indicate differences in the spatial and temporal scales of the processes that the studies focus on. For example, restoration and invasion ecology studies are not only conceptually similar but also operate at similar spatial and temporal scales, meaning that similar methods and analyses can be used, further facilitating information transfer between these fields. By contrast, the phenomena studied by some other fields operate at vastly different scales that require disparate approaches, such as paleontological studies and those on microbiomes, parasites, and diseases, and have therefore experienced limited cross-disciplinary communication. In addition, some fields such as polar biology, animal ecology, and plant ecology appear to have limited communication even though studies typically operate on similar spatial and temporal scales. This lack of communication likely represents a rather artificial silo in research and one that would be valuable to bridge. How can we actually bridge such communication gaps between different fields studying priority effects, especially those operating on vastly different spatial and temporal scales? Our

### Outstanding questions

Do priority effects operate in similar or dissimilar ways across different ecosystems?

What are the long-term ecological consequences of priority effects?

To what extent can invasive species serve as 'natural experiments' in contributing to our understanding of priority effects?

How can a better understanding of microbial priority effects lead to practical applications in biomedical and agricultural research, bioaugmentation, and/or disease ecology?

What role do priority effects play during community reassembly under contemporary climate change?

How widespread are priority effects in determining the establishment success of human-associated microbes?

How can knowledge of priority effects application by food practitioners be integrated into the ecological framework of priority effects?

How do intraspecific genetic priority effects (e.g., the founder effect) influence the assembly of multi-species communities?

How can experimental evolution models be used to investigate the role of priority effects in driving macroevolutionary processes?

To what extent and in what ecological contexts do facilitative priority effects influence community assembly?

When do priority effects involve niche preemption versus niche modification?

How does the relative importance of niche preemption versus niche modification vary across systems and scales?

collation of variable terms related to priority effects (Table 1) represents a first step to break down semantic barriers between subfields. In providing a list of appropriate keywords to researchers studying priority effects, we hope that this contribution will provide a launchpad for developing a unified framework across a broad range of ecological contexts.

Experimental approaches continue to offer the strongest means for making causal inferences regarding how and why priority effects occur (see Outstanding questions). However, in situations where an experimental approach is less viable because of the large scales or ethical considerations involved, such as experimental assembly of vertebrate communities, recent advances in estimating historical species distributions provide new ways to investigate how priority effects have operated in the past. For example, new statistical tools to estimate ancestral phylogeographic [59] and ecological network reconstruction [60] provide better estimates for past patterns of community assembly or ecological interactions. Further development of these approaches will help to interpret the processes that led to present-day biodiversity patterns, as well as to forecast future community dynamics following anthropogenic change or disturbance.

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### Author contributions

J.T.S., B.M.D., and T.F. led the writing of the manuscript; E.M.B. and B.M.D. led the co-citation analysis; all authors contributed substantially to concept development.

### Declaration of interests

The authors declare no conflicts of interest.

### Supplemental information

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