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Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects

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Abstract

The order and timing of species immigration during community assembly can affect species abundances at multiple spatial scales. Known as priority effects, these effects cause historical contingency in the structure and function of communities, resulting in alternative stable states, alternative transient states, or compositional cycles. The mechanisms of priority effects fall into two categories, niche preemption and niche modification, and the conditions for historical contingency by priority effects can be organized into two groups, those regarding regional species pool properties and those regarding local population dynamics. Specifically, two requirements must be satisfied for historical contingency to occur: The regional pool contains species that can together cause priority effects, and local dynamics are rapid enough for early-arriving species to preempt or modify niches before other species arrive. Organizing current knowledge this way reveals an outstanding key question: How are regional species pools that yield priority effects generated and maintained?

1. INTRODUCTION

Organisms live in a complex web of interspecific interactions, affecting one another via competition, predation, mutualism, and various other forms of interactions. How do these interactions influence the membership of ecological communities? Although this question has been addressed throughout the past century (Morin 2011), few general principles have emerged (Lawton 1999). Instead, it has become increasingly clear that how species affect one another depends on the particular order and timing in which different species happen to join communities, the phenomenon known as priority effects (Chase 2003). In other words, why species affect one another the way they do in a community can often be understood only by considering the specific history of community assembly (Drake 1991, Petraitis & Latham 1999).

Furthermore, recent work has shown that assembly history can influence not only the structure of communities, such as species richness and composition, but also the functional properties of ecosystems, such as productivity, decomposition, and nutrient and energy flow (Dickie et al. 2012, Körner et al. 2008, Tan et al. 2012). Recent evidence also indicates that assembly history can alter community structure and function by dictating how species interact not only ecologically but also evolutionarily (Fukami et al. 2007, Lee et al. 2012, Urban & De Meester 2009). The ever-increasing scope for historical influences poses a serious challenge to community ecology because, in most cases, relevant historical information is impossible to obtain in adequate detail.

Despite this challenge, progress in understanding communities can be made by asking which instances of community assembly are particularly sensitive to history (Chase 2003, Drake 1991, Long & Karel 2002). In a sense, this question makes community ecology similar to weather forecasting, in which it is difficult to predict precisely when and where a particular event (e.g., a storm) will happen, but it is still feasible to predict the range of possibilities as well as the conditions that make a particular possibility more robust to stochastic historical events. This approach has steadily become popular, and with the growing appreciation that assembly history can be important, an increasing number of attempts have been made over the past decade to understand the conditions for historical contingency in community assembly (Chase 2003, Fukami 2010). In short, when should history matter and when should it not? That is the question that is both essential and feasible to answer.

Nevertheless, trends in the literature indicate that this research has not kept pace with the rapidly growing general interest in community assembly (**Figure 1a**). In contrast to the increasing relative number of papers on other topics in community assembly, such as functional traits and phylogenetic structure (Ackerly & Cornwell 2007, Kraft et al. 2007, Swenson 2013), historical contingency has remained a fairly minor part of the literature to date (**Figure 1b**). The reasons for this trend are unclear, but I suggest that there are two possible, interrelated reasons, one practical and one philosophical. Practically, data on species traits and phylogenies are more readily available than historical data on community assembly, resulting in more papers on these more easily accessible topics. Philosophically, the vagaries of history tend to be viewed as a nuisance that hinders advances in community ecology as a predictive science (Kingsland 1995). It is more tempting to search for deterministic patterns and processes that are amenable to general predictions. Idiosyncrasies of historical contingency make each instance of community assembly appear unique and therefore not understandable within a general predictive framework (Lawton 1999).

The goal of this review article is to provide a way to conceptually organize the various mechanisms and conditions that have been considered for explaining priority effects and their consequences for community structure and function. In doing so, I hope to help bring the study of historical contingency from its current minor status to the mainstream position that it deserves in community ecology. To this end, I first clarify what exactly is meant by historical contingency. I

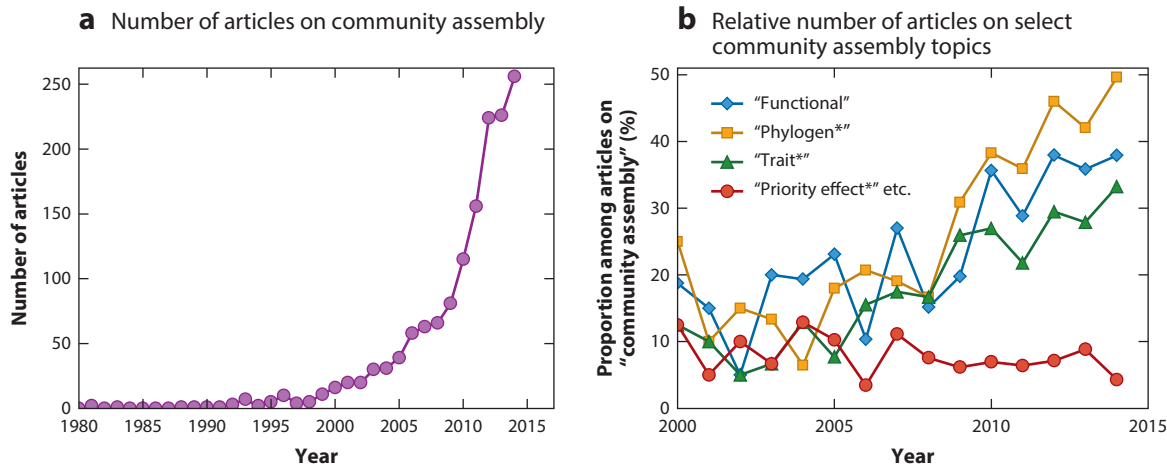


Figure 1

Trends in community assembly research, as reflected in (a) the number of articles published annually and (b) the proportion of those articles written on select topics, including functional, phylogenetic, trait-related, and historical (priority effects, etc.) aspects of community assembly. Note that a single article can address more than one topic; thus, the sum can be greater than 100%. The literature search was conducted using the Web of Science database on June 8, 2015. To find articles that include “community assembly” shown in panel a, the following specifications were used: topic = (“community assembly”), databases = (wos), research domains = (science technology), document types = (article), and research areas = (environmental sciences ecology or biodiversity conservation or plant sciences or entomology or zoology or marine freshwater biology or evolutionary biology or forestry or mycology or fisheries or agriculture or microbiology or paleontology). To find articles on the topics shown in panel b, the same specifications as above were used except that the topic selection was as follows: topic = (“community assembly” and functional), topic = (“community assembly” and trait*), topic = (“community assembly” and phylogen*), or topic = (“community assembly” and (“priority effect*” or “immigration history” or “assembly order” or “assembly history” or “arrival order*” or “order of arrival*” or “assembly sequence*” or “historical contingency*” or “alternative state*” or “alternative stable state*” or “alternative transient state*” or “alternative stable point*” or “alternative community state*” or “multiple stable state*” or “multiple stable point*” or “multiple community state*” or “permanent cycle*” or “heteroclinic cycle*” or “assembly cycle*”).

then suggest that the mechanisms of priority effects that have been considered can be categorized into two types, niche preemption and niche modification (**Figure 2**). Next I organize the conditions that promote priority effects into two classes, those affecting the rate of local population dynamics and those affecting the properties of the regional species pool. Using this organization of current knowledge, I then identify a key question for future research: What factors facilitate the generation and maintenance of a regional species pool under which priority effects occur? I conclude by briefly highlighting the significance of studying historical contingency for applied issues such as conservation, agriculture, and medicine.

2. DEFINITIONS: WHAT IS HISTORICAL CONTINGENCY?

In this article, I define community assembly as the construction and maintenance of local communities through sequential, repeated immigration of species from the regional species pool (Fukami 2010). The regional species pool is defined as “the set of species that could potentially colonize and establish within a community” (Lessard et al. 2012, p. 600). A new round of community assembly is initiated when a disturbance event removes most or all of the individuals in a habitat patch. Examples of habitat patches where community assembly occurs include forest gaps created by a landslide (Walker & Shiels 2013), river floodplains denuded by a flood (Fukami et al. 2013),

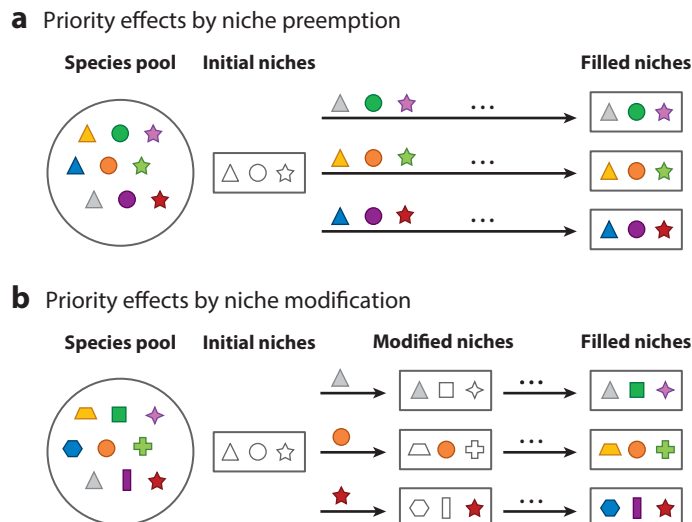


Figure 2

Schematic representation of priority effects by (a) niche preemption and (b) niche modification. Different symbol colors indicate different species. Symbol shapes denote the guilds or functional groups that the species belong to; these groups are delineated on the basis of the requirement component of the species' niches. Open symbols represent vacant niches. Symbols indicated above the arrows represent the arrival order of colonizing species, whereas dots above the arrows represent immigration attempts by unspecified multiple species from the species pool.

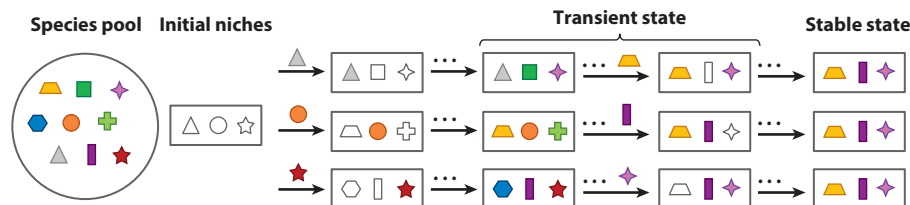
intertidal patches caused by an ice scour (Petraitis & Latham 1999), oceanic islands disturbed by a volcanic eruption (Thornton 1996), newly opened flowers available for microbial colonization of nectar (Peay et al. 2012), and temporary ponds characterized by repeated drought and refilling of water (Chase 2007).

2.1. Historical Contingency and Priority Effects

By historical contingency, I mean the effect of the order and timing of past events on community assembly. Events that cause historical contingency in community assembly can be either abiotic or biotic. Examples of abiotic events are disturbances such as floods, fires, storms, and earthquakes that initiate a new round of community assembly (Crawley 2004) and resource pulses that initiate changes in the trajectory of community assembly (Holt 2008, Nowlin et al. 2008). An example of a biotic event is the arrival of species during community assembly. Although biotic events can be harder to observe or reconstruct than abiotic events, even subtle differences in species arrival history can cause large differences in the structure and function of communities, as effects are amplified over time and space via population growth and interactions. These are the effects termed priority effects, in which the effect of species on one another depends on the order in which they arrive at a site. This historical contingency caused by priority effects is the focus of this article.

Priority effects can be either inhibitory or facilitative, although inhibitory ones, variously called prior-residence advantage, home-field advantage, incumbency effects, and other similar terms (Jablonski & Sepkoski 1996), have received more attention. The priority effect of species A on species B is inhibitory when A affects B more negatively, or less positively, if A arrives before B than if B arrives before A. Conversely, it is facilitative when A affects B more positively if A

a Alternative transient states



b Compositional cycle

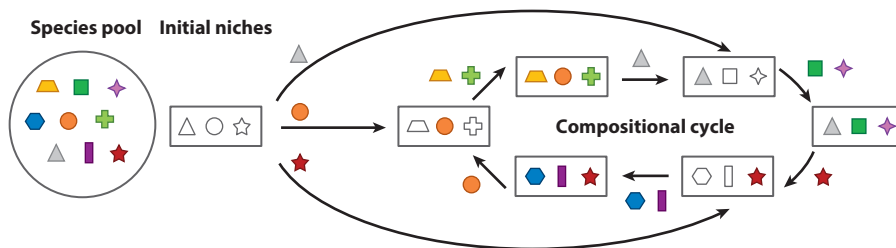


Figure 3

Schematic representation of (a) alternative transient states and (b) the compositional cycle. Symbols are as in Figure 2.

arrives before B than if B arrives before A. This distinction between inhibition and facilitation has an obvious link to inhibition and facilitation in Connell and Slatyer's classic model of succession (Connell & Slatyer 1977). However, Connell and Slatyer's model does not explicitly consider any effect of arrival order per se, whereas priority effects occur only when arrival order matters, so that the outcome cannot be predicted unless arrival order is known.

2.2. Consequences of Priority Effects

There are three types of long-term community-level consequences of priority effects. In all types, local communities diverge in structure and/or function owing to differences in species arrival order even when the communities share the same species pool and the same environmental conditions. First, communities may enter alternative stable states (Beisner et al. 2003, Schröder et al. 2005), in which "different historical sequences of species entering a locality lead to different final community composition" (Chase 2003, p. 489). They are also known by the terms multiple stable states, alternative stable equilibria, multiple domains of attraction, and other similar terms. In this article, I consider a community stable if the locally coexisting species are permanent members of the community and are resistant to colonization by any additional species in the species pool (Law 1999). Once a community enters one of the alternative stable states, it cannot move to another stable state unless heavily disturbed. Alternative stable states result from local species interactions but can have larger, even global, consequences for community structure and function (Staver et al. 2011).

Second, communities may enter alternative transient states (Figure 3a) while undergoing multiple pathways of succession (Donato et al. 2012, Fastie 1995). According to Fukami & Nakajima (2011, p. 974):

[C]ommunities are in alternative transient states when they have not reached a stable state, but vary in structure (e.g., species composition and diversity) and/or function (e.g., total biomass and carbon flux) because of variable immigration history and other stochastic processes, even though they have assembled under the same environmental conditions, have received the same set of species multiple times, and have undergone population dynamics over multiple generations of the species involved. This definition ensures that alternative transient states do not include obvious cases in which communities vary in composition simply because they vary in environmental conditions or species pool or because they are at an early stage of assembly where species composition is inevitably variable.

Although alternative stable states and alternative transient states may seem similar, distinguishing them is important because the conditions under which historical contingency is expected can differ depending on whether the focus is transient or stable states (Fukami & Nakajima 2011, 2013).

Third, communities may enter a compositional cycle (**Figure 3b**), which is a set of species that “occur in a cyclic (or more complex) sequence of communities” (Morton & Law 1997, p. 325). Compositional cycles have also been called permanent endcycles (Morton & Law 1997), cyclic assembly trajectories (Steiner & Leibold 2004), heteroclinic cycles (Schreiber & Rittenhouse 2004), and assembly cycles (Fox 2008). Communities that have entered a compositional cycle are historically contingent because species composition at a given time depends on the past sequence of species arrival. Compositional cycles occur when species engage in, for example, multiple-species predator–prey interactions (Lockwood et al. 1997, Steiner & Leibold 2004) or intransitive interactions in a rock–paper–scissors fashion (Schreiber & Killingback 2013).

I find it helpful to remember that priority effects are distinct from alternative stable states, alternative transient states, and compositional cycles in terms of the timescale considered. According to the definitions given above, for an effect of the order of species arrival to be called a priority effect, it does not have to involve all species in the species pool. In addition, a priority effect can occur either over multiple generations or within a single generation of the species involved. In contrast, alternative stable states, alternative transient states, and compositional cycles are all long-term consequences of priority effects. Thus, for these phenomena to occur, all species must have attempted to colonize the community multiple times, and they also must have undergone population dynamics over multiple generations within the community since the initiation of community assembly.

2.3. Historical Background

To my knowledge, the earliest use of the term priority effects in ecology was by Slatkin (1974), who used the term to apply the idea of underdominant selection in population genetics to understanding species coexistence in community ecology. However, the potential importance of historical contingency in community assembly had been recognized long before that. For example, Gleason (1927) discussed what we now call priority effects as an alternative to Clements’s (1916) then-dominant climax concept of plant succession. Some of the earliest experimental evidence for priority effects was obtained in the United Kingdom in the 1950s (Aspinall 1957, Sagar 1959), although these studies did not become well known. A decade or so later, ecologists in North America began to articulate the concept of alternative stable states as a long-term consequence of priority effects for community structure (Diamond 1975, Gilpin & Case 1976, Lewontin 1969, May 1977). Inspired by Lewontin (1969), Sutherland (1974) conducted an experiment on marine fouling communities, which is now regarded as the pioneering work that popularized the alternative stable states concept. Although this experiment was criticized as being too short to demonstrate the existence of alternative stable states (Connell & Sousa 1983), a subsequent series

of theoretical (Drake 1990, Law & Morton 1993, Lockwood et al. 1997, Post & Pimm 1983) and empirical (Drake 1991, Morin 1984, Robinson & Dickerson 1987, Wilbur & Alford 1985) studies that emphasized long-term consequences of priority effects solidified the view that historical contingency could be substantial in community assembly. It is, however, only over the past decade that the conditions for priority effects and the evolutionary and ecosystem-level consequences of priority effects began to be examined systematically.

3. MECHANISMS: HOW DO PRIORITY EFFECTS WORK?

Now that historical contingency has been defined, I will organize current knowledge on the mechanisms of priority effects. Although various mechanisms have been proposed, it is possible to categorize them into what I will call niche preemption and niche modification.

The term niche has been defined in many ways in ecology. Here I use Chase & Leibold's (2003) definition of niche as "the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita effects of that species on these environmental conditions" (Chase & Leibold 2003, p. 15). This definition views niche as having two components, requirement and impact (Leibold 1995). In my classification of the mechanisms of priority effects (**Figure 2**), I regard niche preemption as occurring between species that are similar in both the requirement and impact components of their niches. In contrast, niche modification occurs between species that have no or little overlap in their requirement components but have an impact component that leads to degradation or facilitation of the requirement component of the other species' niche. I will now elaborate on each.

3.1. Niche Preemption

In niche preemption, species that arrive early reduce the amount of resources (nutrients, space, light, etc.) available to other species and, in doing so, limit the local abundance that can be attained by late-arriving species that need these resources to survive and reproduce (**Figure 2a**). Priority effects are therefore always inhibitory when driven by niche preemption. In strong instances of niche preemption, early-arriving species prevent colonization by late-arriving ones. Founded on the principles of competitive exclusion (Gause 1934) and limiting similarity (MacArthur & Levins 1967), these inhibitory priority effects are hypothesized to be strong when resource use by species greatly overlaps. Some evidence supports this hypothesis. For example, prairie grassland plants that were experimentally introduced to communities of different species composition attained lower abundances if the recipient communities contained species that belonged to the same functional guild (legumes, forbs, C3 grasses, or C4 grasses) as the added species (Fargione et al. 2003). Species of anuran larvae also engage in preemption-driven priority effects through depletion of algal resources (Hernandez & Chalcraft 2012).

Species have to be competitively similar for niche preemption to result in priority effects. Under a strong competitive hierarchy, species arrival order does not matter, as the most competitive species always dominate regardless of history. Competitive similarity, which acts as an equalizing force (*sensu* Chesson 2000), makes the outcome of interspecific competition sensitive to arrival order owing to neutral drift (Hubbell 2001). As such, competitive similarity alone does not ensure stable species composition. Therefore, it can lead to alternative transient states but not alternative stable states. However, additional processes affecting populations can stabilize preemption-driven priority effects and enable alternative stable states. One example is ontogenetic diet shift that can cause predator–prey role reversal among species (Barkai & McQuaid 1988). Local adaptation is

another factor that can stabilize preemption-driven priority effects (De Meester et al. 2002, Urban & De Meester 2009). More generally, anything that causes an Allee effect (e.g., decreased reproduction when a population is small, as is often the case when a new species immigrates to a community) should contribute to stabilizing preemption-driven priority effects (De Roos et al. 2003).

3.2. Niche Modification

In niche modification, early-arriving species change the types of niches available within the local site and, consequently, the identities of late-arriving species that can colonize the community (**Figure 2b**). Thus, priority effects can be inhibitory or facilitative. Niche modification is broadly equivalent to ecosystem engineering (Jones et al. 1994) and niche construction (Odling-Smee et al. 2003). Priority effects by niche modification were originally articulated by Peterson (1984), who described the illustrative example of a species of ghost shrimp that modified the physical conditions of sediments in marine soft-bottom systems and, by doing so, influenced bivalve species' abundances, depending on the shrimp's colonization history relative to the bivalves. Since then, modification-driven priority effects have been indicated in a variety of systems. For example, some plant species make local patches fire prone by litter production, thereby creating niches for fire-resistant species, including themselves, while erasing niches for fire-sensitive species (D'Antonio & Vitousek 1992, Odion et al. 2010, Westoby et al. 1989). Conversely, fire-sensitive species may prevent creation of the niche for fire-resistant species by, for example, keeping local patches moist. More generally, by modifying soil conditions in various ways (Kardol et al. 2007, van de Voorde et al. 2011), plant species can create niches for a different set of plant species, driving communities onto alternative transient trajectories (Fukami & Nakajima 2013). Similarly, in the marine environment, coral- and alga-dominated states, or mussel- and alga-dominated states, have been indicated to represent alternative stable states (Knowlton 2004, Petraitis et al. 2009). In these examples, either corals (or mussels) or algae, whichever arrive first after disturbance, modify the local environment to create different sets of niches for late-arriving species to colonize. Similar phenomena of priority effects via niche modification have been suggested in freshwater systems, where two alternative stable states appear to exist, one dominated by submerged plants and one by floating plants (Scheffer et al. 2003).

3.3. Contrasting Niche Preemption and Niche Modification

One distinction between the two types of mechanisms is that niche preemption affects species within niches, whereas niche modification does so primarily across niches (**Figure 2**). More specifically, provided that species can be grouped into similar types, often called guilds (Simberloff & Dayan 1991) or functional groups (Hillebrand & Matthiessen 2009), priority effects via niche preemption affect the identity of species within, but not across, guilds or functional groups. In contrast, priority effects via niche modification affect the identity of species primarily across, and not necessarily within, guilds or functional groups.

There is no single, inherently correct way to assign species to functional groups (Hillebrand & Matthiessen 2009). Functional groups can be defined trophically (e.g., producers, herbivores, carnivores, or decomposers), or they can be defined more narrowly (e.g., plant functional types or animal-feeding guilds) or more broadly (e.g., autotrophs and heterotrophs). What makes the most sense depends on the function of communities of primary interest: Functional groups should be defined so that they correspond to the role that species play in driving the function of the communities that we are interested in understanding. Therefore, depending

on how functional groups or guilds are defined, a mechanism of priority effects can be categorized as either niche preemption or niche modification. In this sense, the distinction is artificial.

Nevertheless, classifying mechanisms into niche preemption and niche modification is still useful for understanding the significance of priority effects for communities because these mechanisms can have different consequences for community assembly. Specifically, niche preemption affects mostly the structure, and not the function, of the resulting community, because community structure at the functional level is not affected by priority effects in this case (Fukami et al. 2005). In contrast, niche modification can affect both community structure and function because priority effects create alternative communities that consist of functionally different species. In fact, it is possible for priority effects to influence community function more greatly than community structure (Dickie et al. 2012).

In **Figure 2**, niches are delineated on the basis of the requirement component. Under this framework, the extent to which niche modification, as depicted in **Figure 2b**, influences community function depends on how tightly the requirement niche and the impact niche are correlated. If there is a tight correlation, species that differ from one another in the requirement niche would also differ in the impact niche. In this case, niche modification would affect both the structure and function of the local communities. In contrast, if the requirement niche and the impact niche are not tightly correlated, niche modification might affect only community structure and not function.

4. CONDITIONS: WHEN IS HISTORICAL CONTINGENCY EXPECTED?

Numerous hypotheses regarding the conditions that promote historical contingency have been proposed, both for preemption- and modification-driven priority effects, particularly over the past decade. Although these hypotheses may seem diverse, they can be categorized into two groups, which together define the conditions for realization of priority effects (**Figure 4**). One of the two concerns the rate of local population dynamics relative to that of species immigration (**Figure 4b**). The other concerns the properties of the regional species pool in terms of species richness, species traits, and the decoupling of the species pool from local population dynamics (**Figure 4c**).

This categorization is similar to Chase's (2003), which classifies factors into local and regional ones. Here, however, I seek to refine and expand Chase's approach in three ways. First, Chase focused on priority effects on community structure. Since then, evidence has been accumulating for priority effects on community function as well as structure (Dickie et al. 2012, Fukami et al. 2010, Körner et al. 2008, Zhang & Zhang 2007). I will consider both function and structure by taking both niche preemption and modification into account. Second, Chase discussed community assembly as an ecological process. Since then, inclusion of evolution into community assembly theory has been a rapidly advancing topic, prompted by increased appreciation of eco-evolutionary dynamics over the past decade (Fussmann et al. 2007). I will consider community assembly not only as an ecological phenomenon but also an eco-evolutionary one, in which local adaptation and diversification interact with ecological processes such as competition and predation to affect historical contingency (Knope et al. 2012). Third, Chase focused on alternative stable states, reflecting the general trend in community ecology at the time. However, as I discuss above, alternative stable states are only one of the three types of long-term consequences of priority effects. The other two types, alternative transient states (Fukami & Nakajima 2011) and compositional cycles (Steiner & Leibold 2004), are increasingly recognized as important in understanding the conditions for historical contingency in community assembly. I will try to be inclusive in this respect as well.

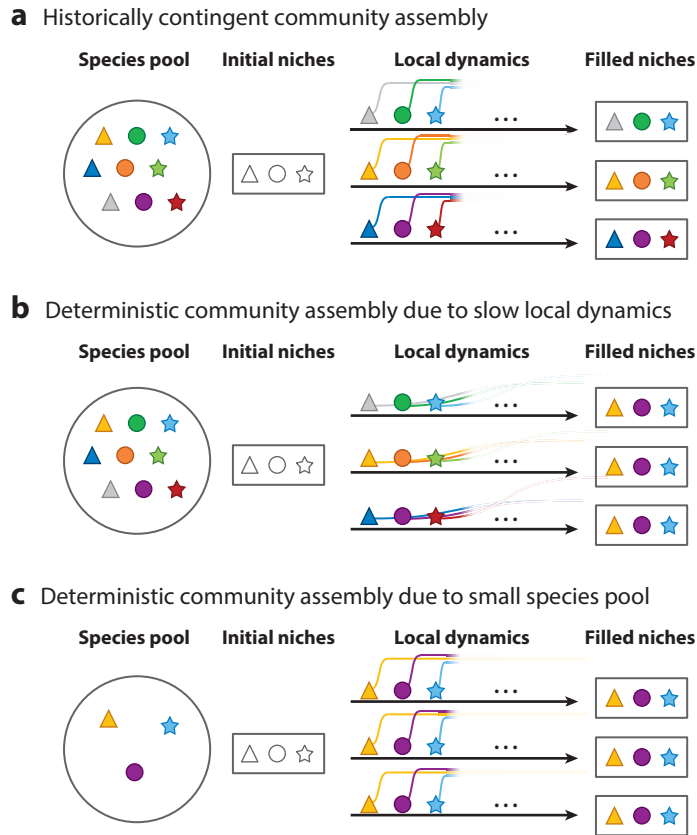


Figure 4

Schematic representation of the conditions for historical contingency in community assembly. Historical contingency, depicted in panel *a*, does not happen if local population dynamics are too slow for early-arriving species to substantially preempt or modify niches before other species arrive, as shown in panel *b*, or if the species pool does not have a set of species that cause priority effects, as shown in panel *c*. Symbols are as in **Figure 2**. Colored curves represent population growth after each species arrives.

4.1. Local Population Dynamics

For priority effects to occur, early-arriving species must grow rapidly in biomass or population size to preempt or modify niches substantially before the arrival of late-arriving species (**Figure 4b**). Otherwise, communities would converge to a deterministic set of species, each of which is most suited to its respective niche. Consequently, no alternative stable state would be possible. Further, without rapid population dynamics, communities driven by niche preemption would tend to follow similar successional trajectories, with each niche temporarily occupied by multiple species whose arrival timings do not substantially differ, until all but one species per niche eventually become extinct through competitive exclusion. Little variation in species composition would therefore be expected among communities before they reach a stable state; thus, there would be limited scope for alternative transient states or compositional cycles.

Some of the factors that have been hypothesized to promote strong priority effects, such as small habitat patch size (Fukami 2004a, Orrock & Fletcher 2005), high productivity (Chase 2010, Kardol et al. 2013), low environmental variability (Tucker & Fukami 2014), and low predation

pressure (Chase et al. 2009, Morin 1984), are conceptually similar in that they all promote fast local population dynamics. For example, studies have indicated that priority effects can be stronger in smaller habitat patches than in larger ones (Fukami 2004a, Orrock & Fletcher 2005) because populations reach carrying capacity more quickly in smaller patches than in larger ones given the same number of immigrants. High productivity (high rate of supply of energy and nutrients) can also increase the importance of priority effects, presumably because higher productivity generally leads to a higher rate of population growth (Chase 2010, Kardol et al. 2013, Vannette & Fukami 2014). Likewise, temporal variability in environmental conditions can cause reduction in the population growth rate, resulting in weaker priority effects (Tucker & Fukami 2014). In addition to abiotic local conditions, biotic conditions of the local environment could also affect population growth rate. For example, priority effects can be stronger in a prey community when predators are absent than when they are present because predators reduce growth rates of prey populations (Chase et al. 2009, Morin 1984).

All of the above factors focus on the local conditions under which community assembly proceeds. These factors modify population growth rate within communities. However, the rate of local population dynamics is relevant only when considered relative to the rate of immigration. Any factor that affects the immigration rate can thus cause changes in the relative rate of local dynamics, ultimately affecting the strength of priority effects. For example, given the same set of potential colonizers, the immigration rate will be a function of how well connected local habitat patches are to the source of immigrants. The less connected the patches are, the lower the immigration rate and therefore the faster the local dynamics will be relative to the immigration rate, leading to stronger priority effects (Chase 2003, Fukami 2005).

Although the traditional focus has been the rate of ecological population dynamics, the rate of evolutionary dynamics has recently been considered in community assembly research. For example, theoretical work has suggested that local adaptation strengthens preemption-driven priority effects (Loeuille & Leibold 2008, Urban & De Meester 2009). Because local adaptation can occur more rapidly when fueled by standing allelic variation than solely by *de novo* mutation, priority effects may occur more quickly with standing variation than with mutation (Urban & De Meester 2009). Therefore, the initial amount of genetic variation at the time of species arrival may influence the strength of priority effects by affecting the rate of evolutionary dynamics.

4.2. Regional Species Pools

Even if local conditions allow for rapid population growth, priority effects would not occur if the regional species pool did not contain a set of potential colonists that would engage in the local interactions that yield priority effects. Thus, the second category of the conditions for priority effects is concerned with the regional species pool that supplies immigrants to the local communities (**Figure 4c**). Many properties of species pools have been discussed in relation to priority effects, but they can be organized into three general groups: (*a*) species richness, (*b*) species traits, and (*c*) the decoupling of the species pool from local communities.

4.2.1. Species richness. Theoretical work has indicated that historical contingency is, on average, more likely when more species are in the species pool (Fukami 2004b, Morton & Law 1997, Steiner & Leibold 2004). There are multiple reasons for this. For example, if the species pool contains more species that can fill the same niche, niche preemption will be more likely, on average. Similarly, niche modification may also be more likely under a larger species pool, which, on average, is more likely to contain, for example, more predators and more prey species that cause compositional cycles (Morton & Law 1997).

If species richness does matter, then the obvious question is where variation in species richness in the regional pool can come from. Variation can arise both across and within regions. Different regions may vary in the size of the species pool, reflecting differences in biogeographical evolutionary history of regions and/or environmental heterogeneity at the regional scale (Lessard et al. 2012). Within regions, local habitat patches may vary in their effective species pool, or the local pool (*sensu* Pärtel et al. 1996), due to differences in the local filters that affect which species can potentially colonize each patch. For example, productivity and disturbance have been indicated to act as such local filters (Chase 2003). Thus, these factors can change the extent of historical contingency in two ways: by influencing the speed of local population dynamics, as discussed above, and by influencing the size of the effective species pool.

4.2.2. Species traits. Although species richness is informative, its effect can be discussed only as a statistical property. Biological explanations of priority effects require consideration of the ecological traits of species relative to one another and these traits' influences on species interactions in local habitats. Surprisingly, however, direct use of species traits to predict the strength of priority effects has not been widely attempted. In one attempt, it was argued that trait-based predictions could be improved by decomposing species traits into three niche components: niche overlap, impact niche, and requirement niche (Vannette & Fukami 2014). The authors hypothesized that these components have interrelated but distinct roles in determining the strength of priority effects (**Figure 5**): “[P]riority effects should be strong when (1) species display a high degree of similarity in resource use (high overlap), (2) early-arriving species strongly affect the environment (high impact), and (3) the growth rate of late-arriving species is highly dependent on the environment (high requirement)” (Vannette & Fukami 2014, p. 116). If these hypotheses are true, as shown for microbial species that inhabit floral nectar (Vannette & Fukami 2014), then species pools containing species that meet these criteria should be more likely to cause historical contingency in local communities.

One limitation of this work is that the hypotheses are focused on pairwise species interactions. It remains unclear how well niche components explain historical contingency at the whole community level involving many species. Another study provides a hint as to what may happen in species-rich communities (Fukami & Nakajima 2013). This computer simulation study indicated that high variation in impact niche and requirement niche among species [e.g., as observed among plant species interacting via plant–soil feedbacks (van de Voorde et al. 2011)] could

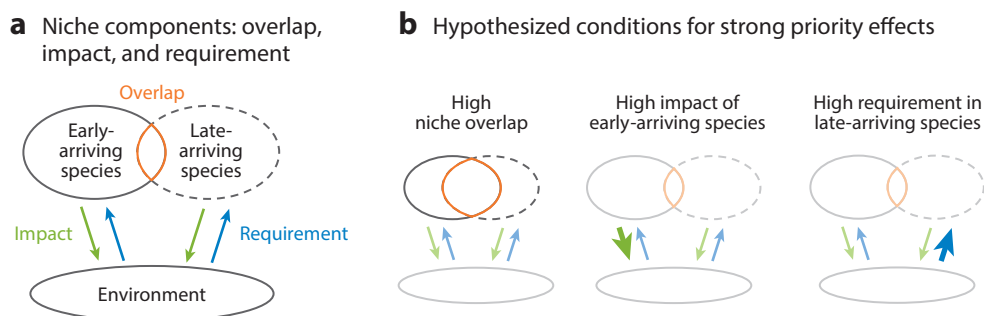


Figure 5

Schematic representation of (a) niche components, including overlap, impact, and requirement, and (b) how they are hypothesized to influence the strength of priority effects. Figure modified from Vannette & Fukami (2014) with permission.

promote alternative transient states by driving communities onto different trajectories, even if communities eventually converge in species composition. Therefore, the diversity of niche components among species in the species pool may promote historical contingency.

Aside from the niche components, another species trait that is clearly relevant to community assembly is dispersal ability, or how quickly species disperse to local habitats. For priority effects to contribute to variation in local species composition, immigration history needs to be variable among local communities in the first place. Thus, dispersal ability has to be similar among species. Otherwise, communities would likely be assembled with a deterministic sequence of species arrival, from good to poor dispersers, providing little scope for historical contingency. Another possibility is that, when the likelihood of dispersal is affected by the local community itself, this dependence of dispersal likelihood on local species composition strengthens priority effects. For example, when the decision to oviposit is influenced by the identity of species already present in the local community, as observed in frogs (Resetarits 2005) and mosquitoes (Munga et al. 2006) in freshwater habitats, this plastic decision can make immigration history sensitive to the resident species composition, enhancing historical contingency. Another consideration regarding dispersal ability is which of the species in the species pool are likely to arrive together. When priority effects occur via niche preemption, if species requiring the same niche tend to arrive together, history may be less important than if species requiring different niches were to arrive together.

Species traits are often assumed to be static, but evolution of traits can influence the strength and likelihood of priority effects. For example, as discussed above, species with great potential for local adaptation (i.e., those that can quickly adapt to local conditions after arrival) can enhance the importance of niche preemption, as predicted by the community monopolization hypothesis (Loeuille & Leibold 2008, Urban & De Meester 2009).

Furthermore, on a longer timescale in which in situ diversification contributes to community assembly (Gillespie 2004, Seehausen 2007), species poorly adapted to the local conditions that they experience upon arrival may cause greater historical contingency than do species that are well adapted (Knape et al. 2012). This hypothesis is based on the following logic. Well-adapted species cannot diversify because they competitively suppress the growth of mutants that would lead to diversification. Because they are well adapted, however, they always dominate local communities regardless of their arrival timing relative to other species. Conversely, poorly adapted species have the potential to diversify if given an opportunity, but they have to arrive early to exploit resources and increase in number sufficiently to result in diversification. If they arrive later than another potential species, the opportunity would have already been used by early-arriving species. As a result, historical contingency is expected when community assembly involves poorly adapted species. Derived from a microbial experiment (Knape et al. 2012), this hypothesis might explain some of the variation in the extent of diversification observed in, for example, African cichlids (Seehausen 2007).

Most of these trait-based mechanisms have been either suggested merely as a theoretically plausible hypothesis or supported by only one or a few empirical tests. Clearly, more work is needed to gain a better understanding of species traits relevant to historical contingency.

4.2.3. Decoupling of the species pool from local dynamics. Finally, theory suggests that priority effects may be more likely when the regional species pool is stable and not influenced by local community dynamics (Fukami 2005, 2010). To explain this theoretical prediction, it helps to consider two contrasting models of community assembly. One is the classic mainland-island model (MacArthur & Wilson 1967), in which the species pool is a large stable reservoir of species unaffected by the dynamics of local communities (**Figure 6a**). The other model is the metacommunity model (Leibold et al. 2004, Wilson 1992), in which there is no external species

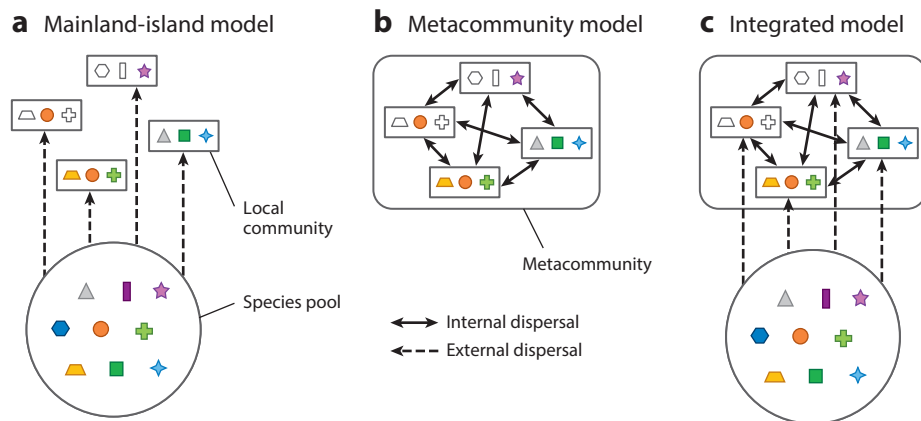


Figure 6

(a) Mainland-island, (b) metacommunity, and (c) integrated models of community assembly. Symbols are as in **Figure 2**. Figure modified from Fukami (2005) with permission.

pool that supplies immigrants from outside the metacommunity. Instead, the local communities within the metacommunity collectively make up the species pool (**Figure 6b**). In both models, disturbance events occasionally set local communities back to the initial stage of community assembly, creating a mosaic of communities that are at different successional stages, as depicted by the patch dynamics model (Levin & Paine 1974).

With sufficient variation in immigration history among local communities, historical contingency is possible in both mainland-island and metacommunity models. However, in the metacommunity model, the regional coexistence of alternative stable states via priority effects may be more difficult than in the mainland-island model. The reason for this difficulty is as follows: When one stable state happens to be more common or more likely to be realized, that particular state is likely eventually to dominate across the metacommunity via a positive feedback at the local community level (Shurin et al. 2004). Therefore, with everything else assumed the same, a greater degree of decoupling of the species pool from local dynamics should prevent this positive feedback and consequently facilitate the maintenance of alternative stable states in the metacommunity. In other words, an external supply of species from outside the metacommunity, as assumed by the mainland-island model, may ensure that alternative stable states, each of which can be developed only with certain sequences of species arrival, can be realized.

Theory suggests, however, that there are cases where historical contingency readily happens even in a metacommunity characterized by a completely internal species pool. For example, the long-term maintenance of alternative stable states in a closed metacommunity may be possible given the right spatial scale at which environmental conditions vary within the metacommunity. When environmental heterogeneity occurs on a large scale (i.e., primarily across, rather than within, local communities), different local patches having different local conditions can each serve as a spatial refuge for a subset of species, from which they disperse to patches of intermediate conditions where priority effects can then occur (Shurin et al. 2004). For this reason, the spatial scale at which environmental heterogeneity is observed relative to the scale of local habitat patches where community assembly proceeds is a potential factor affecting the extent of historical contingency.

Currently, virtually all of these ideas about the decoupling of species pools from local communities are no more than untested theoretical hypotheses. As I elaborate more in the next section, this area of research is particularly in need of more work in the future.

5. FUTURE: HOW CAN THE UNDERSTANDING OF HISTORICAL CONTINGENCY BE IMPROVED?

Having surveyed the current understanding of the mechanisms and conditions for historical contingency, we can now examine where major knowledge gaps lie. On one hand, factors affecting the rate of local dynamics seem relatively straightforward and well understood, at least conceptually. Any factor that accelerates local dynamics relative to the rate of species immigration should promote historical contingency, with everything else assumed the same. On the other hand, there is much room for improvement in our understanding of the ways in which properties of regional species pools affect historical contingency, particularly for community assembly involving many species that interact with one another both directly and indirectly and both ecologically and evolutionarily.

A more fundamental challenge is to understand the conditions that facilitate the generation and maintenance, in the regional species pool, of a set of species that yields priority effects. The majority of community assembly studies have so far assumed that the species pool is a static external reservoir that supplies immigrants to local communities, as in the mainland-island model (**Figure 6a**). This conceptual simplification has been instrumental to the theoretical development of community ecology (Drake 1990, MacArthur & Wilson 1967, Morton & Law 1997). In reality, however, species pools rarely exist externally. In many cases, local communities contribute to shaping the regional species pool, so there is feedback between local communities and the species pool (Mittelbach & Schemske 2015, Shurin et al. 2004), making the pool internal, as in the metacommunity model (**Figure 6b**).

Can a species pool that yields priority effects be maintained when there is such feedback? This question is largely left unanswered. As discussed above for alternative stable states, one theoretical study suggested that historical contingency might be difficult to maintain under an entirely internal species pool (Shurin et al. 2004). However, the only empirical test of this theory that I am aware of yielded contradictory results (Pu & Jiang 2015). In a laboratory experiment with freshwater protists, Pu & Jiang (2015) found that alternative community states were maintained for many generations in a closed metacommunity, even with high dispersal among local communities. It is unclear what underlies the discrepancy between these results and Shurin et al.'s (2004) predictions, but one key difference may be the number of interacting species considered. Pu & Jiang (2015) found evidence for complex priority effects by niche modification involving several species (with the strengths of species interactions dependent on assembly history), whereas Shurin et al.'s (2004) model included only two species. It may be important to consider historically contingent interactions among many species, not just a few species, to understand the conditions under which alternative stable states persist with an internal species pool. It is also possible that Pu & Jiang's (2015) communities were in long-lasting transient states, whereas Shurin et al. (2004) focused on stable states. These possibilities require further exploration. Even less is known about how difficult it may be to maintain a species pool that enables compositional cycles.

Although not entirely external, most species pools are not entirely internal, either. For example, for a given habitat type, species that are highly specialized in using that habitat type are likely to have an internal species pool. But some other species that participate in community assembly in the same habitat type may have a wide range of other habitats where they can also survive and reproduce. These species may then have an external reservoir of immigrants that are not affected

by local community dynamics. In this case, the collective species pool for the focal habitat type is partially internal and partially external (**Figure 6c**). For example, consider the case of yeast communities that develop in floral nectar via among-flower dispersal aided by pollinators (Peay et al. 2012, Vannette & Fukami 2014). Some yeast species are found almost exclusively in nectar, with flowers functioning as local habitat patches and collectively forming an internal species pool. But other species are found in various other habitats in addition to floral nectar (Brysch-Herzberg 2004); thus for these species, flowers are surrounded by an external species pool. What degree of decoupling of the species pool from local dynamics is needed for historical contingency in these cases? This is another unanswered question. The relationship between the degree of decoupling and the degree of historical contingency may be nonlinear (Fukami 2005). In addition, the answer may depend on how the traits of species differ between species that are mostly contained in the metacommunity and those that have a reservoir of immigrants outside the metacommunity.

The issues discussed above concern the regional maintenance of species over ecological time. Ultimately, we also need to understand how species pools are generated over macroevolutionary time at large, geographical spatial scales in order to know why pools have the set of species they do. For example, estimating how species have come together by diversification occurring at these large scales may help to explain when to expect many competitively equivalent species in the same species pool (McPeck & Brown 2000, Mittelbach & Schemske 2015), which would increase the chance of priority effects by niche preemption at the local scale. It is difficult to ask questions about the species pool without a practical definition of it, but some promising advances have been made recently for species pool delineation (Carstensen et al. 2013, Cornell & Harrison 2014).

It should be clear by now that a full understanding of community assembly can be expected only from consideration of both the origin and maintenance of regional species pools that promote or restrict historical contingency. The origin of these pools is mainly a biogeographical and macroevolutionary question (Lee et al. 2012, Mergeay et al. 2011, Seehausen 2007), whereas their maintenance is primarily an ecological and eco-evolutionary question (Shurin et al. 2004), necessitating multidisciplinary approaches. Fortunately, research on priority effects has a good tradition of taking advantage of multiple methods, including mathematical modeling, numerical simulation, laboratory and field experiments, phylogenetic comparison (Peay et al. 2012, Tan et al. 2012), and analysis of long-term historical records over both ecological (Duncan & Forsyth 2006) and evolutionary time (Emerson & Gillespie 2008, Lee et al. 2012, Mergeay et al. 2011) at multiple spatial scales. The outstanding questions on historical contingency would be addressed most effectively if multiple methods were used in combination to take advantage of their complementary strengths.

6. SIGNIFICANCE: WHY STUDY HISTORICAL CONTINGENCY?

Although community assembly research has been driven primarily by intellectual curiosity, advancing the understanding of historical contingency has direct relevance to a variety of societal issues that involve management of ecological systems. In this section, I briefly highlight some of these issues relating to conservation, agriculture, and medicine.

In conservation, when priority effects influence community assembly, restoring and maintaining native biodiversity in degraded sites may require specific sequences of exotic species removal and/or native species introduction (Lockwood & Samuels 2004, Suding et al. 2004, Wilsey et al. 2015, Young et al. 2005, 2015). Furthermore, non-native species can disrupt the role of priority effects in enhancing native species diversity, suggesting that consideration of historical contingency may be needed to identify why and when maintaining native diversity is made difficult by non-native species invasion (Fukami et al. 2013). Recent work also suggests that pathogen spillover

from introduced plants to native plants can be influenced by priority effects (Mordecai 2013). In addition, as climate change induces more and more phenological shifts, biodiversity conservation will require explicit consideration of how the seasonal order of species arrival and interactions will be altered by climate change (Yang & Rudolf 2010) and how this alteration in phenology will in turn change the role of priority effects in community structuring and functioning (Grman & Suding 2010, Rasmussen et al. 2014).

In agriculture, consideration of priority effects may be needed for successful biological control, particularly when the biological control agent interacts not only with the target species but also with nontarget species, whether as competitors, predators, or mutualistic partners, because these additional, indirect species interactions can make priority effects more likely to happen (Hougen-Eitzman & Karban 1995). Similarly, the successful inoculation of agricultural soils with beneficial fungi may depend on inoculation timing relative to establishment of plants or other soil microbes due to priority effects (Verbruggen et al. 2013).

In medicine, the ecology of the human microbiome is a burgeoning field of research. For example, the gut microbial communities of obese, undernourished, and healthy people have been hypothesized to represent alternative stable states (Fierer et al. 2012). Recent experimental evidence shows that the transmission and within-host abundance of microbial pathogens, such as strains of *Borrelia burgdorferi* that cause Lyme disease (Devevey et al. 2015) and strains of *Salmonella enterica* that cause diarrhea and typhoid fever (Lam & Monack 2014), can be strongly influenced by priority effects within hosts. The relevance of historical contingency in community assembly to curing human diseases affected by gut microbes is becoming increasingly clear (Costello et al. 2012).

7. CONCLUSION

In summary, I have proposed that the mechanisms of priority effects fall into two categories, niche preemption and niche modification, and that the conditions for historical contingency can be organized into two groups, those regarding the population dynamics in the local community and those regarding the properties of the regional species pool. Specifically, for community assembly to be historically contingent, two requirements need to be satisfied. First, local population dynamics must occur rapidly enough for early-arriving species to preempt or modify niches before other species arrive. Second, the regional species pool must contain species that can together yield priority effects. On the basis of this organization of current knowledge, I have identified the generation and maintenance of regional species pools that yield priority effects as an area of investigation that will be especially important in future research.

At the turn of the century, Lawton made a provocative claim that community ecology is “a mess” because it is inherently devoid of general laws (Lawton 1999). This claim has been countered numerous times, and many of the counterarguments are one of two kinds. One counterargument asserts that the claim is irrelevant because community ecology should rather focus on idiosyncratic particulars of each system to be of use to conservation and other environmental issues (Simberloff 2004). Basically, this is to say that community ecology should stay a historical science (Sober 2000). In contrast, the other counterargument maintains that community ecology does have general laws if approached at the right organizational level [e.g., emphasizing functional traits rather than species identities (McGill et al. 2006)] or if defined merely as a general statement of basic processes affecting community structure (Vellend 2010). In other words, community ecology can be, and should be, a predictive science (Sober 2000).

Studies reviewed in this article suggest a third possibility that emerges from a synthesis of the above two views. Namely, fundamental progress can be made in community ecology by making it

simultaneously a historical and predictive science. Through a combined use of theory, experiments, and observations, we should embrace, rather than ignore, historical influences affecting community structure and function because idiosyncratic contingencies of priority effects can indeed be great. Community ecology can nevertheless be made predictive through the study of when communities will be more sensitive to historical contingency and, conversely, when they will be more robust to it. Even though the organizing framework presented here is too simplistic to explain a specific instance of community assembly, I hope that it will serve as a conceptual basis on which a systematic understanding of the factors affecting the extent of historical contingency can be improved.

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