

Divergent perspectives on community convergence

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Community structure develops through myriad interactions among species in space and time, operating against a background of environmental variability and chance events. Making matters even more complex is the possible influence of higher-order processes such as self-organization and emergence. The relative importance of each of these components is fundamental to understanding the nature of the community and ultimately lies at the root of questions of biological diversity, evolution and extinction. Until recently, ecological thinking was dominated by a deterministic, equilibrium, almost balance-of-nature flavor (see Pimm¹). From this viewpoint, convergence to a stable deterministic endpoint is ultimately a matter of time, with nature eventually sorting itself out and arriving at some 'optimal' solution. In this deterministic framework, communities that develop 'in parallel' under the same conditions would converge to a common structure. Indeed, a good deal of evidence exists for convergence at many levels of scale. For example, communities developing on different continents but under similar environmental conditions exhibit many interesting parallels in species composition and morphology^{2,3}. Such global scale comparisons are conceived on the premise that similar environments lead to similar communities because: (1) in the short term, the environment delimits possible community configurations, and (2) in the long term, environmental similarity leads to some degree of evolutionary convergence among constituent species.

But how similar is similar? With challenges to the equilibrium, balance-of-nature paradigm, the role of history has reentered the picture as a formidable factor generating variation in community structure^{4,5}. Accordingly, the scope of the convergence–divergence question has converged as it were. Rather than examining community similarity across continents, ecologists have begun to ask, even under the same conditions, will similar communities develop? This narrowing of focus is manifest in a shift from studying 'similar' communities across continents to studying 'replicate' communities, which are highly similar in species pool and environment, under controlled or natural conditions.

Here, we review recent evidence for convergence and divergence at similar sites, taking into consideration the complex issues involved in searching for regularity and pattern in community structure. The studies included address a broad range of perspectives on community convergence and divergence. At first glance, Wiens' broad-scale comparison of morphological traits between birds and grasses across continents³ may appear incomparably different from Rodríguez's experiments tracking trajectories of periphyton communities on the scale of only a few centimeters⁶. Whatever the scale

Recent experimental and theoretical studies of community development, as well as more general studies of complex systems, indicate that historical differences and intrinsic indeterminism can lead to long-term community divergence. This observation has sparked a series of new investigations of community structure in systems that developed under controlled or natural conditions.

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or system type, working backwards to implicate causes of observed variation can be equally as difficult as predicting outcomes of assembly sequences (Table 1). Variation among all these developed communities has been derived from a range of sources, yet historical events which contributed to observed variation are, by definition, hidden in the invisible past. Mechanisms whose outcomes are predictable in theory or in a highly controlled experimental situation are often richly variable when acting in concert with the suite of mechanisms and processes operating in nature.

Convergence, divergence and concepts of community

Perceptions of community convergence or divergence depend directly on how a community is defined and thought to function. Studying convergence and divergence across a variety of types of systems requires attention to the varied concepts of community at three levels: community membership and boundaries, measures of community structure, and community dynamics. Before we can begin to synthesize information about convergence and divergence it is important to establish a framework for understanding communities at each of these levels.

Community definitions and membership

Where does a community begin and end? Are community boundaries a feature of the localized web of species linked by interactions such as competition and predation^{7–9}? Is a community boundary formed by limitations to the practical extent of energy flow^{4,10,11}? Or is the community a localized set of interacting species which exhibit limits to membership¹²? Perhaps all three provide useful elements to a community conceptualization. However conceived, we must be mindful that these are not simply semantic arguments.

Many purported community studies, indeed the majority of those in this survey, actually examine only portions of a community – generally, a guild. Unfortunately, such pieces do not possess all the properties of the level of organization being examined. Restricting a study to part of a community can obscure higher-level patterns and dynamics that may be important for understanding lower-level phenomena. For example, comparing two grasslands only on the basis of plant species composition may not reveal that a herbivore played a central role in shaping their similarity or difference.

The resolution at which community membership is defined can also be critical in comparing communities. Yodzis¹³ illustrates this point graphically by showing two drastically different food webs describing the northwest Atlantic. One contains three items: seals, cod, and everything else. The other is a dizzying maze of species and connections. Each

Table 1. Some sources of community variability and their relationship with prediction/explanation of community structure

Source of variation	Examples	Condition for prediction
Environmental gradients	Nitrogen levels, precipitation, altitude	Predictable, but depends critically on identifying relevant environmental factor(s)
Sequence effects	Community composition depends on order of species arrivals	Requires information about history
Chaotic dynamics	Sensitive dependence on initial conditions	Predictable <i>in principle</i> , but unlikely in the field
Indeterministic trajectories	Alternate endpoints, even under identical conditions	Unpredictable, even with precise information about environment and history
'Random' noise	Variation due to individual traits or environmental stochasticity	Unpredictable, even in the most controlled of systems
Any combination of the above	(a) Interacting; disturbance (b) Superimposed; chaos tempered by an environmental gradient	Prediction entails dissecting out the role of each type of process

community attributes, all communities appeared to have converged. Only at the level of taxonomic and functional groups did meaningful patterns suggesting an attractor related to succession become evident. Similarly, Rodríguez⁶ observing recovery following disturbance in periphyton communities found that total density, a community measure, converged to the state of an undisturbed control community early during the recovery period, whereas the relative taxonomic abundance never converged. Certainly, pattern is a matter of scale^{32,33}.

arguably represents the system, but we agree with Yodzis that 'we need to assume guilt until proven innocent, both theoretically and empirically' when it comes to excluding elements or connections from consideration in a system. When comparing community structures, the scope of inference is restricted to the least common denominator of community information.

Community structure

Even with defined boundaries and membership, community structure and pattern is ultimately in the eye of the beholder (Fig. 1). A given prairie can be described as a list of all species of plants, rodents, bugs, etc. and abundance of each. Alternatively, the same community is more coarsely defined in terms of ratios of grasses to composites to legumes, or simply as a system dominated by big bluestem. This is not even to mention the various species-independent community descriptors, such as properties and complexity of food webs^{7,9} or functional metrics¹⁸.

Different components of structure change at different rates. For this reason, ecologists are recognizing that meaningful comparison of structure and pattern requires community measures at a range of levels^{30,31}. We recently collaborated with Carmen Rojo to examine algal communities in fifteen aquatic field microcosms after eight years of assembly using four measures of community structure (unpublished). At the finest scale the communities appeared nearly random in composition, whereas for coarse-scale

Community dynamics

Further difficulty in the search for generality is evident in the varied concepts of the dynamic nature of the community. Do communities tend toward a single or multiple states? Are these true equilibrium 'endpoints', or are they nonequilibrium cycles, attractors or an unrelated series of states? These questions emulate the old and well-known climax community debate in the literature of plant succession. Clearly, this historical debate continues³⁴ while equilibrium, deterministic dynamics remain a formidable part of ecological thinking. Drake *et al.*²⁴, in a set of laboratory microcosm experiments, observed that differences in invasion success and persistence led to the development of alternative community states, but Grover and Lawton³⁵ argued that these patterns were related to inadequate time allowed to reach equilibrium. Differing views of community dynamics lead to varied concepts of community stability and regularity (Box 1).

What and how much information is needed to assess convergence depends critically on the nature of the community dynamics. A true stable, equilibrium community can be defined by its state at a single point in time, whereas the series of states in a nonequilibrium system requires a time series. Viewing a nonequilibrium system, either cycling or apparently random, from a single point in time can be misleading since a set of such systems may appear very similar at one time yet very dissimilar at another (Box 1c,d). In this way, systems may appear to have diverged when they have actually converged to a cycle, but are temporally out of sync.

Divergence in empirical evidence, and the 'burden of proof'

Is it remarkable that communities developing at similar sites are anything but random associations of species? Or is each minor variation analytically intriguing, a nuance resulting in a particular deviation from the environmentally determined norm? Given the variety of community concepts, it is not surprising that approaches to the convergence-divergence question are equally diverse. Table 2 summarizes the community type, methods and conclusions of recent studies of convergence and divergence including natural systems^{3,14-17,19-22,28}, field experiments^{6,25,26}, and microcosms^{23,24,27}.

Conclusions about convergence are often commensurate with the authors' concepts of community and the assembly trajectory. For example, McCune and Allen²⁸ studied tree composition in 11 adjacent canyons with the same

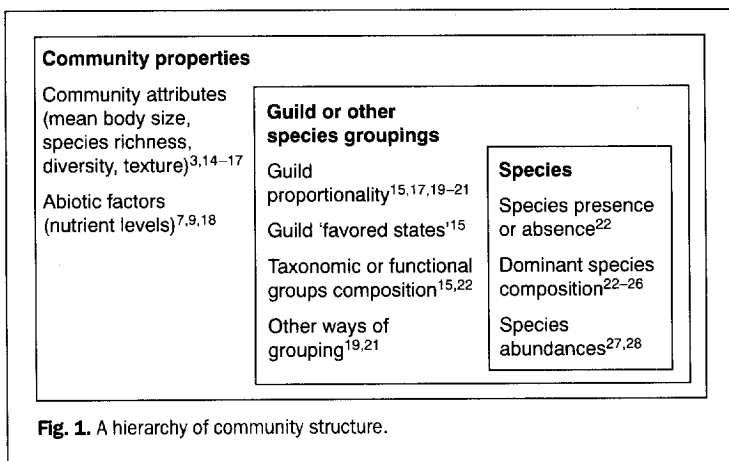


Fig. 1. A hierarchy of community structure.

geological history and general climate by examining the relationship between community variation and a suite of environmental factors. The variation in environment explained only 10 percent of the variation among communities. The remaining unexplained variability was attributed to a strong effect of chance events and history. Clearly, by assuming that variation is related to a small number of environmental factors and that the correct factors have been chosen and measured, this type of approach places the burden of proof on the side of convergence. At the opposite end of the spectrum Sommer²³ experimented with aquatic microcosms inoculated with species combinations from different lakes, comparing which species eventually came to dominate. In his experiment, convergence and 'time to convergence' were built-in criteria; the experiment was set to end *when* convergence occurred, making it difficult to imagine how nonconvergence or divergence would have been dealt with.

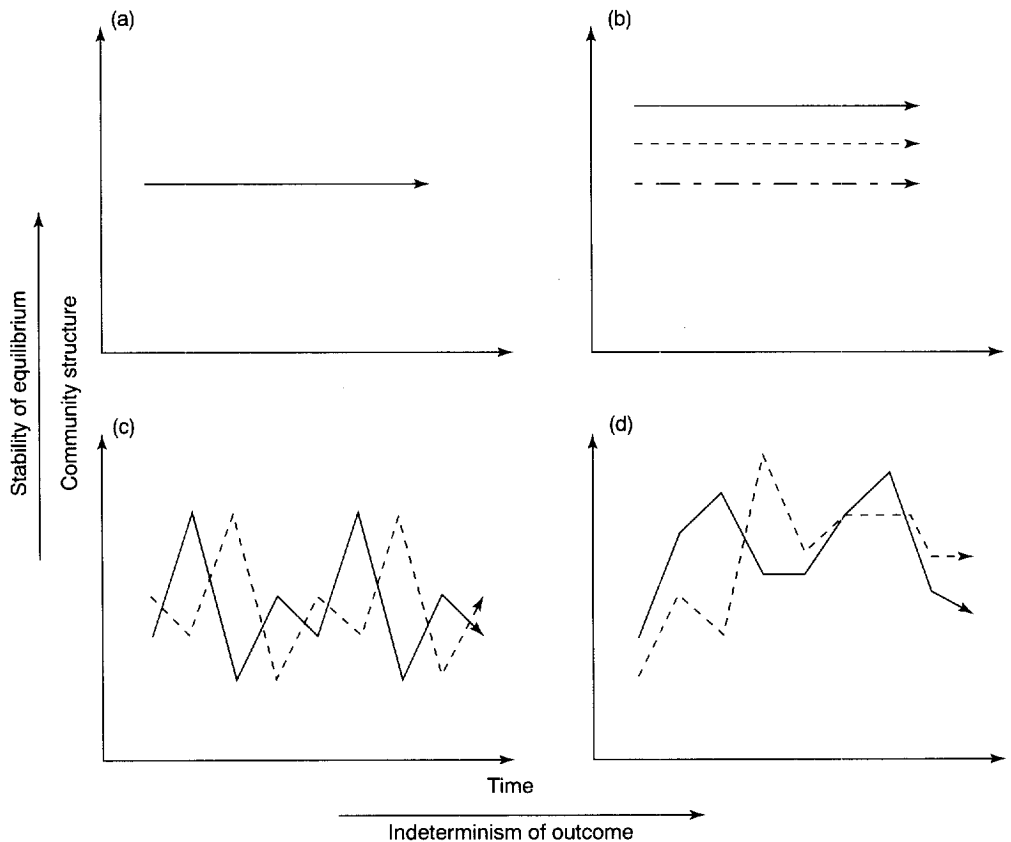
The meaning of convergence and divergence in evolutionary and ecological time

Allied with the varied expectations of community outcomes are different interpretations of the meaning of convergence and divergence. Schluter's²⁹ ANOVA method of testing community convergence centers around increasing similarity over that of their 'ancestral communities', emphasizing that similarity alone does not necessarily entail convergence. Medel¹⁶ used this method to compare community attributes of 42 harvester ant assemblages on three continents. He found an overall lack of convergence which could not be explained by precipitation differences that were considered to be the primary environmental difference. In fact, communities within the same precipitation interval exhibited more variation than those in different intervals. This failure of variability among locations to account for lack of convergence is the criterion, in Schluter's method, for implicating historical differences. Notably, this ANOVA approach is done using a measure of community structure at only a single point in time, so this method assumes an equilibrium or stable endpoint.

An alternative way of evaluating convergence or divergence involves tracking a trajectory of community development over time. From this point of view, convergence and divergence can imply either becoming more similar or reach-

Box 1. Concepts of community dynamics and convergence or divergence of community structure

- (a) **Single stable point:** Given sufficient time, communities under the same conditions will converge to a common, persistent, environmentally determined state.
- (b) **Multiple stable states:** Communities converge to one of a number of alternative stable states. While community structures vary, the type and magnitude of difference persist through time.
- (c) **Attractor or cycle:** Communities move through a repeating (or at least finite) series of states. Communities may converge in terms of this series, yet be offset in time. In the case of such temporal stagger, convergence can only be measured in a time series. At any one point in time, the communities may appear very similar or very different, but this relationship can change quickly and frequently.
- (d) **Random, chance-driven or chaotic trajectories:** Communities move through a series of apparently unrelated states, and each community is driven by its own history. A time series is necessary to compare communities and distinguish such systems from attractor or cyclic communities.



ing a specific state or set of states. How long a community must be observed in order to discern such dynamics, however, is unclear. Inouye and Tilman^{25,26} observed old-field succession in experimental plots subjected to different nitrogen treatments, following the changes in dominance. After four years of assembly, a trend toward convergence was found within nitrogen treatments. By the eleventh year, however, this apparent convergence had disappeared. Even 'long-term' studies such as this may not be sufficient to foresee the even longer-term trends. However, their findings may contribute to general concepts of convergence or divergence tendencies for particular types of system.

Convergence minus divergence = assembly rules?

Convergence and divergence is a question of finding the roots of variation among communities developing in similar settings. Chance and historical effects are unique in their nature and effects on each system^{36,37}, yet there may be 'rules' or patterns in the mechanics of community development which provide a framework for understanding the origins of variation. A variety of studies have sought general

Table 2. Summary of selected studies of community convergence and divergence

Community	Membership	Measure of structure	Site difference	Measure of convergence	Hypotheses tested	Degree of convergence
Lakeshore and mountainside ¹⁴	Plants	Community metrics	Productivity gradient	Statistical regression	Variation explained by productivity gradient	High
Aquatic laboratory microcosms ²³	Plankton	Dominant species	Initial conditions	Similarity; trajectories	Variation in convergence due to zooplankton	High
Desert ¹⁵	Rodents	Species, community metrics	History <i>via</i> location	Variance; null model	Guild proportions fit 'favored states' model	High
Saltmarsh ¹⁹	Plants	Guild proportionality (<i>a priori</i> and intrinsic)	Location along transects	Null model; significance	Convergence	High
Lake ⁶	Periphyton on artificial substrata	Dominant species	Disturbance regime	Similarity	Convergence	High
Rainforest ²⁰	Plants	Guild proportions (<i>a priori</i>)	Altitude gradient	Similarity to null model	Convergence	High
Shrubland ³	Plants and birds	Community	History <i>via</i> location	Similarity	Convergence	Medium
Freshwater laboratory microcosms ²⁴	Plankton	Dominant species	History	Similarity; trajectories	Convergence or divergence	Medium (convergence to alternative states)
Lawn ²¹	Plants	'Intrinsic guild' proportions	Untreated versus perturbed	Variance; null model	Convergence	Varying with guild scheme
Grassland (experimental) ^{25,26}	Plants	Dominant species	Initial conditions; nitrogen	Similarity; trajectories	Convergence or divergence among nitrogen treatments	Varying
Bracken ²²	Insects	Species; taxonomic representation; community measures	History <i>via</i> location	Various, depending on scale and community measure	Variation explained by ecological or evolutionary mechanisms	Varying with scale (continental, regional, local) and measure
Freshwater field microcosms (Rojo <i>et al.</i> , unpublished)	Plankton	Species; taxonomic groups; functional groups; community measures	History	Similarity; cluster analysis; correspondence analysis	Convergence	Varying with community measure
Carr (wooded fen) ¹⁷	Plants	Community 'texture' (morphology)	History <i>via</i> location	Null model; significance test	Convergence, divergence and significance	Low: only when abundant species are more heavily weighted
Freshwater laboratory microcosms ²⁷	Protists	Species abundance	Species; invasion timing	ANOVA on structure and invasibility	Assembly rules	Low, but explained by sequence effect
Forest ²⁸	Plants	Tree species	History; site factors	Similarity	Variation explained by site factors	Low
Desert ¹⁶	Ants	Community measures	History; precipitation	ANOVA (following Schluter ²⁹)	Convergence	Low

phenomenological responses from mechanisms which operate during the process of community development. Often, the specific mechanisms behind these responses are undetectable in the community that results; thus observing the details of community development is necessary to implicate mechanisms that are generating a specific structure. In this realm, the line between convergence and divergence is contingent upon information.

For example, in the controlled microcosm experiments of Drake *et al.*²⁴ and Lawler²⁷, the simplicity of the communities and short generation times make it possible to follow the complete history of a community. These studies have elucidated specific mechanisms (see *sequence effects*, below) that lead to alternative community states, offering a first-hand view of divergence in community structure. Lawler takes pains to point out that the contribution of these rules to divergence in natural systems remains to be fully explored. Under the microscopic scrutiny of a laboratory setting, mechanisms that may generate divergence in nature take on the rule-driven appearance of convergent, predict-

able behavior. When the entire history of a system is known, the difference between convergence and divergence is an assembly rule. Two types of assembly rules are potentially important for explaining trends in community structure among communities developing at similar sites, sequence effects and guild proportionality.

Assembly rules of species order and history

Events related to the timing and order of species introductions can, at least in theoretical and laboratory settings, lead to divergence in community structure^{4,38}. Figure 2 illustrates three such types of mechanisms that might be envisaged in the assembly of communities. First, *sequence effects* occur when community structures develop differently depending on the timing and order of species arrival. What species dominate the community can be a direct product of events early in the history of the system. If sequence effects occur, a regional species list would not translate to a single community structure. Second, communities may develop along trajectories which are deterministic or indeterministic. By definition,

systems developing along indeterministic trajectories are unpredictable – even with complete information about history. Last, it may not be possible to reconstruct a whole community using only the parts of the final state. Interactions in the past, the history of the relationship between species that are no longer there may be the invisible keys to understanding extant community structure. Convergence and divergence studies may provide much-needed critical evidence of the role these mechanisms play in structuring communities in nature.

Pattern in guild and community structures

A second approach to uncovering regularities in community development focuses on pattern derived from coarse-scale species attributes at the level of guilds or functional groups. Fox³⁹ first proposed a guild-level assembly rule by which community development proceeds while maintaining nearly equal representation of functional groups, termed 'favored states'¹⁵. While Fox's statistical methods and null model have recently been shown to be flawed^{40,41}, this approach has generated further investigation and insight into guild level assembly mechanics^{19–21}. Wilson and coworkers have evaluated a variety of systems for assembly rules based on both 'a priori' guilds (functional or taxonomic groups defined externally to the community being studied), and 'intrinsic guilds' (statistically determined from the community data.) Wilson and Roxburgh²¹ took the pattern-seeking approach to an interesting extreme by trying to fit different intrinsic guild patterns to their data until all communities were found to converge. While this method succeeds at finding a mathematically correct description of the guild proportionality, to advance predictability of community structure without having to study each community individually requires that patterns apply *generally*, at least to sets or groups of systems.

In systems governed by guild- or functional group-level assembly rules, while the precise species composition would still be unpredictable, the rule narrows down the number of possible outcomes from a given species pool. Such guild-level patterns would not be detectable from other measures, such as species diversity or richness, yet they certainly contribute dimensions of a general framework for assembly rules.

Convergence plus divergence = embedded dynamics

Nature would be intolerably regular if all communities converged to a single solution or attractor. If this were the case any differences among communities would simply reflect their relative position *en route* to an inevitable solution. In this case alternative states could be observed because disturbance can act to reset the system some distance away from the global attractor. Clearly the frequency and magnitude of disturbance interplay with the inertia of the assembly trajectory to determine the suite of observable states. Conversely, if each assembly trajectory diverged, communities would appear entirely idiosyncratic and fully structured by chance.

Studies of convergence and divergence implicate a variety of mechanisms and processes spanning a variety of levels of scale. Many of the studies reporting convergence found convergence at rather coarse structural levels (e.g. guild representation), while those reporting divergence observed divergence at finer levels of scale like species composition. Comparative investigations based on such distinctly different levels of organization must be cognizant of the dangers inherent in equating systems which represent such distinct levels of integration. It is easy to conceive of a situation

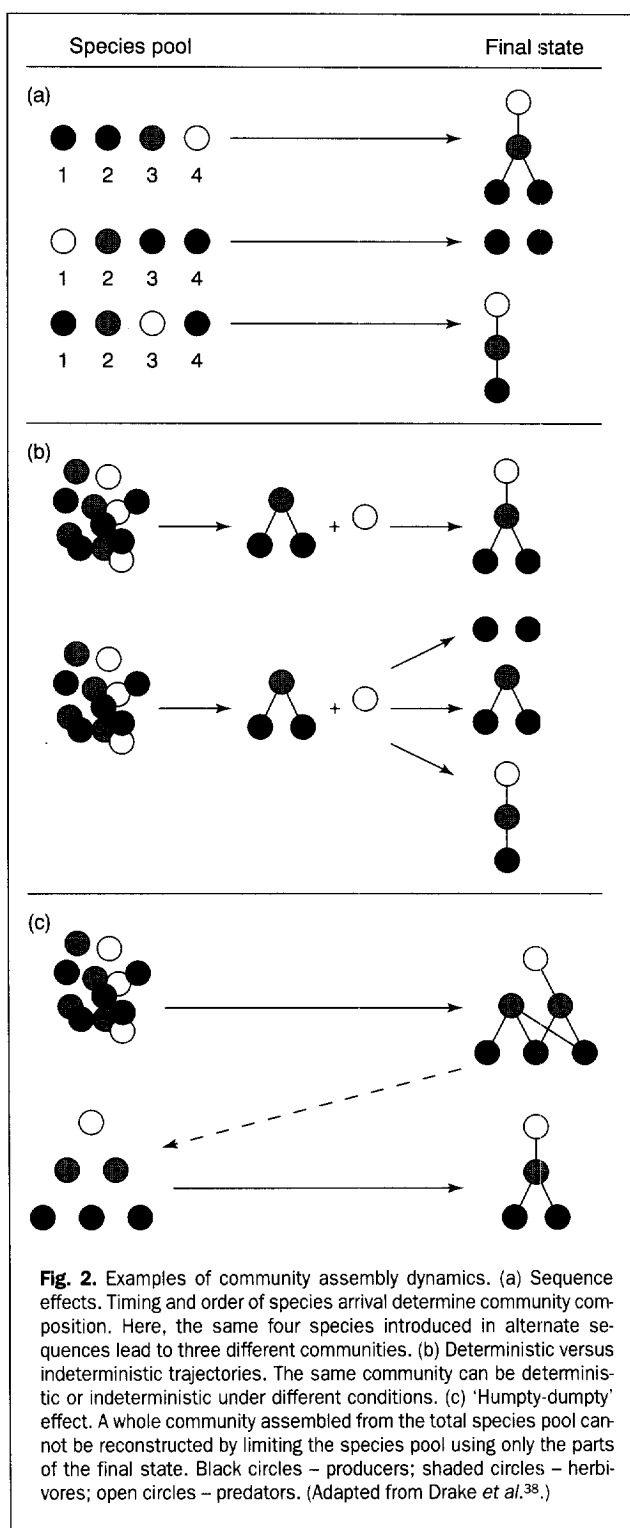


Fig. 2. Examples of community assembly dynamics. (a) Sequence effects. Timing and order of species arrival determine community composition. Here, the same four species introduced in alternate sequences lead to three different communities. (b) Deterministic versus indeterministic trajectories. The same community can be deterministic or indeterministic under different conditions. (c) 'Humpty-dumpty' effect. A whole community assembled from the total species pool cannot be reconstructed by limiting the species pool using only the parts of the final state. Black circles – producers; shaded circles – herbivores; open circles – predators. (Adapted from Drake *et al.*³⁸.)

where a single community, measured at two different levels of scale, would lead one to believe that the system converged on the one hand and diverged on the other.

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