Evolutionary Repeatability of Emergent Properties of Ecological Communities

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Abstract

Most species belong to ecological communities where their interactions give rise to emergent community-level properties, such as diversity and productivity. Understanding and predicting how these properties change over time has been a major goal in ecology, with important practical implications for sustainability and human health. Less attention has been paid to the fact that community-level properties can also change because member species evolve. Yet, our ability to predict long-term eco-evolutionary dynamics hinges on how repeatably community-level properties change as a result of species evolution. Here, we review studies of evolution of both natural and experimental communities and make the case that community-level properties at least sometimes evolve repeatably. We discuss challenges faced in investigations of evolutionary repeatability. In particular, only a handful of studies enable us to quantify repeatability. We argue that quantifying repeatability at the community level is critical for approaching what we see as three major open questions in the field: (1) Is the observed degree of repeatability surprising? (2) How is evolutionary repeatability at the community level related to repeatability at the level of traits of member species? (3) What factors affect repeatability? We outline some theoretical and empirical approaches to addressing these questions. Advances in these directions will not only enrich our basic understanding of evolution and ecology but will also help us predict eco-evolutionary dynamics.

1 Introduction

Stephen J. Gould captured the imagination of many with his now famous thought experiment where he proposed to replay “life’s tape” and observe “if the repetition looks at all like the original” [1]. Although evolutionary biologists have been interested in the repeatability of evolution for decades before Gould [2,3], his vivid metaphor set the stage for much of the modern agenda in the field [4–8]. Numerous documented cases of parallelism and convergence from natural and experimental systems support the idea that a biological system facing the same environment would evolve, with a non-negligible probability, towards outcomes that share some essential similarities [4,5,7–13]. As a result, many evolutionary biologists today believe that Gould’s thought experiment would reveal at least some degree of repeatability. A new goal, highlighted in the present journal issue, is to *predict* how populations will evolve [6,14–16].

While genuine prediction is the ultimate goal, the notion of evolutionary repeatability (i.e., replicates evolving along similar paths and/or towards similar outcomes) remains fundamentally important. Since evolution is driven by random processes, such as mutation, recombination, and genetic drift, evolutionary predictions are in general formulated in statistical terms, e.g., “substitution at site x will occur with probability p” or “population will on average evolve phenotype y”. However, knowing the statistics of an ensemble is often not enough if we want to predict the future behavior of a specific population (e.g., whether a pathogen population within an infected patient will develop drug resistance). Accurate predictions for individual populations are possible only when the uncertainty around one or a few typical evolutionary outcomes is low [6,15], i.e., when evolution is repeatable. Compare, for example, a situation when 100 different evolutionary outcomes can occur with probability 1% each (low predictability) versus a situation when one of them occurs with probability 99% (high predictability). In other words, repeatability of evolution affects our power to predict its course.

The multitude of cases of parallelism and convergence identified in the field and in the lab in recent decades have refined our understanding of evolutionary repeatability. For example, it is now appreciated that repeatability is not a binary category, i.e., evolution is not either repeatable or not repeatable [8]. Rather, repeatability is a matter of degree, which can be quantified (see Box 1 and Refs. [8,10,15]). Another important realization is that different characters evolve with different degrees of repeatability. In particular, the degree of evolutionary repeatability varies across levels of biological organization, with lowest repeatability generally found at the genetic level (with some important exceptions [17–21]) and highest repeatability at the level of fitness [5,11,22–26].

Much of the literature so far has been concerned with the repeatability of evolution of properties of individuals: genotype (reviewed in [14,27–29]), phenotypes (e.g., [5,8,18,28,30–33]) and fitness (e.g., [34–36]). However, most species belong to ecological communities where they interact with one another by competing for resources, parasitizing, cooperating, etc. These interactions endow communities with emergent properties, such as diversity, productivity, function, etc., that depend on but cannot be reduced to individual-level properties [37–43]. Such community-level properties are part of the environment in which community-member species evolve and to which they adapt. As they adapt, community properties can also change and thereby affect the subsequent course of species evolution. Due to such eco-evolutionary feedbacks [44–47], evolution at the level of individuals is inextricably linked to the evolution of the surrounding community. It is thus meaningful to ask how repeatable evolution is at the community level. Asking this question is important because it can help us identify the level of description of biological systems where evolution is most repeatable and therefore most predictable [39].

It is unclear *a priori* how repeatable we should expect evolution at the community level to be. On the one hand, interactions between species may multiply historical contingencies [7] and thereby make evolutionary outcomes at the community level non-repeatable. On the other hand, communities may self-organize into certain ecological states [48–50], which could make evolution of community-level properties highly repeatable. We return to this discussion in Section 4.3.

The question of whether similar environments repeatably select for similar ecological communities has a long history. Early studies documented similarities and differences between geographically distant communities, but did not establish how ecological and evolutionary processes generated the observed outcomes (e.g., [37,51–54]). More recently, this problem has been addressed primarily from an ecological perspective [38]. The role of evolutionary processes (i.e., those that cause heritable changes in the genetic and phenotypic composition of populations of community-member species) in causing repeatable outcomes at the community level has received less attention. Although, as we demonstrate below, the studies of adaptive radiations and species coevolution in nature and in the lab bear greatly on this question, their emphasis has been on the patterns and processes of phenotypic evolution rather than on the community-level properties. The goal of this review is to synthesize our current understanding of community-level repeatability from an evolutionary perspective and outline potentially interesting avenues for future research.

2 Defining community evolution and its repeatability

We understand an ecological community as a collection of individuals that belong to two or more ecologically distinct types, share space and time, and ecologically interact with each other. By “ecologically distinct types” we generally mean species, but two or more eco-types of the same species would qualify as a community if they are sufficiently distinct ecologically (e.g., [55,56]). The condition of shared space and time is meant to constrain the spatial scale and the temporal timeframe of ecological interactions under consideration. Without it, we may have to consider species that influence each other across vast geographic distances (e.g., phytoplankton affect the physiological processes of most of life on Earth by producing oxygen) or across exceedingly long stretches of time (e.g., fossil fuels). However, even with this restriction, one may not be able to observe all members of a community and may be forced to focus on certain subsets of community members [37].

Ecological communities possess *emergent community-level properties*, i.e., properties that depend on but cannot be reduced to the properties of individual members of the community [37–41]. For example, whereas beak morphology is a trait of an individual finch, the *distribution* of beak morphologies in a community of finches on an island is a property of the community. Other community-level properties include species composition and diversity, function, productivity, etc. The distribution of ecological interactions can also be considered a community-level property [12]. We do not endow the word “emergent” with any meaning beyond the fact that these properties do not exist at lower levels of biological organization, although it is implicit that community properties likely depend on the ecological interactions between community members. For example, different finch species on Galapagos islands have different beak morphologies as a result of competition [57].

To make the language clearer, we will refer to individual-level properties as *traits* (unless we specifically talk about genotype) but we will always say community-level *properties*. We will use the word *characters* to refer to community properties, individual traits or genotypes. Characters can be discrete or continuous, one- or multi-dimensional, and we refer to values that a given character can take as *character states*, as in “replicates have different character states”.

Community properties change over time for many reasons, but we can distinguish between three major classes of processes that cause communities to change. First, a community can change because of events external to it, i.e., those that occur regardless of the state of the community, such as yearly seasonality or an influx of migrants. Second, a community may change as a result of ecological processes within the community itself, such as births and deaths, production of certain compounds by member species, competition for resources, etc. The third class of processes that alters communities are heritable changes in the traits of community-member populations, i.e., evolution. As community members evolve, interactions between them may change, which in turn may alter the ecology of the community and precipitate further evolution of its members. In other words, community properties can change due to a complex entanglement between evolutionary and ecological processes, termed eco-evolutionary feedbacks [44–47,58].

While all these processes clearly operate in most if not all ecological communities, understanding how they all work together is difficult, due to differences in timescales on which they operate, differences in study methodologies, etc. To make investigations tractable, community ecologists tend to focus on the first two types of processes [38]. In this article, we focus on the community dynamics that are driven by the second and third processes, i.e., those internal to the community. As the fields of community ecology and evolutionary biology advance and converge, it will be important to integrate our understanding of all three types of processes [58].

Keeping this scope limitation in mind, what would be an ideal setup for investigating the repeatability of eco-evolutionary dynamics that are driven only by internal processes? We would ideally consider a collection of initially identical (replicate) ecological communities that are given the freedom to change and evolve over time in identical environmental conditions. One could then determine the degree of evolutionary repeatability by characterizing the similarity between these evolutionary “replays”. While such an idealized scenario never occurs in nature, investigating it is valuable for two reasons. First, it deepens our understanding of eco-evolutionary dynamics that are fundamental to any biological system. And second, because unpredictable external perturbations can only exacerbate divergence between replicates, an understanding of this idealized scenario could provide us with an upper bound on the repeatability of evolution in more complex situations.

The notion of evolutionary repeatability is related to those of evolutionary parallelism and convergence. However, repeatability presupposes that the initial character states are identical, whereas convergence implies that they are distinct (and become more similar during evolution). Parallel evolution occurs when the character states become neither more nor less similar over time, whether or not they were initially identical [8]. Thus, the notion of repeatability is more closely related to the idea of parallel evolution when the initial states are identical, but there are some distinctions. For example, parallel evolution implies a change in the character state. In contrast, a consistent absence of change across replicates (e.g., due to stabilizing selection) is a valid instance of repeatability. Another distinction is that parallelism is an attribute of a pair of populations/communities. In contrast, we envision repeatability as a property of an infinitely large ensemble of replicates (Figure 1B,C). For example, one way to quantify parallelism is by calculating the angle between the evolutionary vectors of two replicates [8]. The corresponding aspect of repeatability would then be characterized by the distribution of such angles (Figures 1B,C insets). In other words, repeatability is an abstract feature of a system that gives rise to observable instances of parallelism and convergence. And conversely, we can use these instances to infer the degree of evolutionary repeatability.

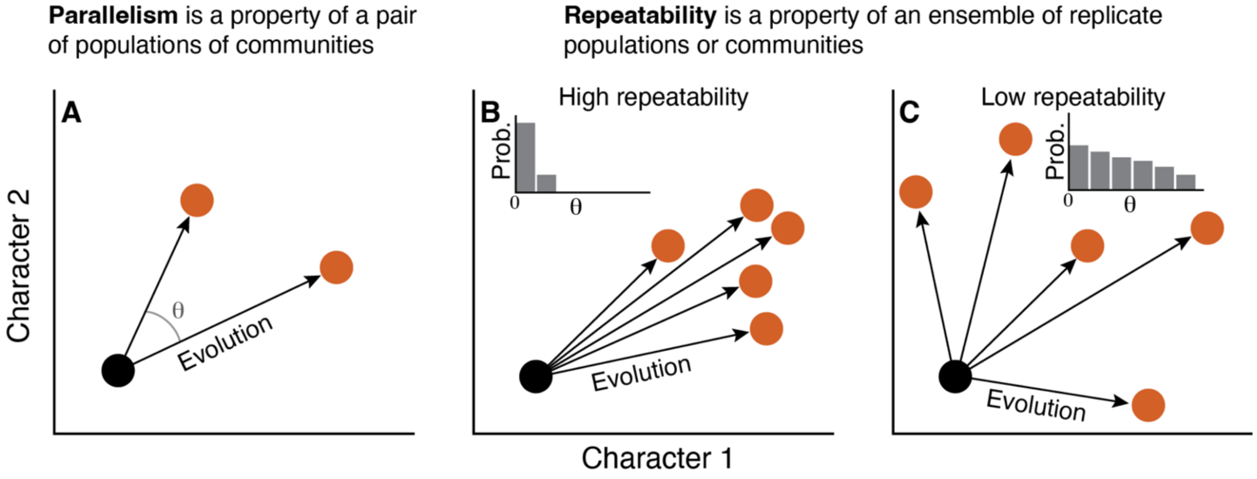


Figure 1. Distinction between evolutionary parallelism and evolutionary repeatability. A. Parallelism is a property of a pair of populations or communities (which may or may not be initially identical). The degree of parallel evolution can be quantified, for example, by the angle θ between the respective evolutionary vectors in the character state space [8]. $\theta \approx 0$ corresponds to high parallelism; $\theta \gg 0$ corresponds to low parallelism. **B, C.** Repeatability is a property of an ensemble of initially identical populations or communities. It can be quantified, for example, by the distribution of angles between pairs of replicates. A distribution of angles θ concentrated around zero corresponds to high repeatability (panel B inset); a wide distribution corresponds to low repeatability (panel C inset). Note that θ captures only one aspect of repeatability—whether replicates evolve in similar directions in the character state space—but ignores whether they evolve at similar rates (also see discussion in Box 1).

3 Evidence that evolution is repeatable at the community level

As mentioned above, to evaluate the repeatability of community evolution, we would ideally like to observe many initially identical replicate communities that independently evolve in the same environment. Although implementing such an ideal setup is impossible in natural systems, several well-described communities come close [7]. In addition, setups closely approximating the ideal are achievable in the lab [7]. While many studies of both natural and laboratory systems have investigated the repeatability of evolution of species traits in the context of ecological communities, fewer have specifically focused on the repeatability of community-level properties. We highlight these studies below and summarize the broad patterns that we identified in this literature.

3.1 Community evolution in nature

Our empirical understanding of the repeatability of evolution in nature comes from observations of parallelism and convergence. In most cases, these are reported at the genetic and trait levels (reviewed in [4,5,8,10,28,59]), but many of the traits evolving in parallel are directly involved in between-species interactions, e.g., dermal bones that are important for feeding in stickleback fish [60], host-plant preference in stick insects [61], or the ability to synthesize specialized metabolites used for attracting pollinators or defending against predators in plants [62]. Thus, it is likely that at least some aspects of the ecological community to which these species belong have also evolved in parallel. However, most instances of trait parallelism and convergence allow us to draw only indirect conclusions about the repeatability of evolution of community-level properties. More direct evidence for such repeatability comes from studies of adaptive radiations and from studies of co-evolving species pairs.

Adaptive radiations. A canonical case of adaptive radiation involves a single founder species that colonizes multiple neighboring islands or lakes [63]. These quasi-replicate founder populations subsequently diversify into communities of interacting (usually competing) species. The fact that the communities are initially identical (consisting of a single founder species) and the fact that they evolve on neighboring but largely isolated habitats with similar environments is important because it allows researchers to witness how quasi-replicate ecological communities are assembled by adaptive evolution and diversification. In many well-characterized cases, quasi-replicate communities evolve to similarly partition the morphological and ecological trait space, a community-level property. More precisely, these communities undergo parallel diversification into several “ecomorphs” each of which has stereotypical morphological, dietary and behavioral traits and occupies a distinct ecological niche. Examples of parallel ecomorph evolution include the evolution of large- and small-beaked Darwin’s finches on Galapagos islands [64–66], morphological and dietary parallelism in cichlids in Africa’s great lakes [67–70], benthic and limnetic stickleback fish in Canadian glacial lakes [71,72], pelagic and benthic feeding behaviors in damselfish in coral reefs [73], crown-giant, trunk-crown, trunk and trunk-ground ecomorphs in lizards on Caribbean islands [30,74], and matte white, dark and gold ecomorphs for *Tetragnatha* spiders on Hawaiian islands [75,76] (see Supplementary Table S1 for more details).

Although most communities that arose in replicated adaptive radiations reveal a degree of community-level parallelism, its underlying causes are often unclear (see Section 4.2). In particular, trait and hence community-level similarities can evolve by genetic drift or by natural selection driven by various ecological factors, and distinguishing between causal mechanisms is not straightforward, particularly when only biased subsets of species from replicate communities are examined in detail [77,78]. Mahler et al overcame this challenge by studying entire adaptive radiations of lizards of the genus *Anolis* in the Caribbean islands [78]. They used a recently developed mathematical model of trait evolution along a phylogeny [79] to show that the distributions of morphological characters on different islands were best described by a model where species convergently evolved towards a small set of adaptive peaks corresponding to ecomorph classes. This study provides a plausible mechanism for how evolving ecological communities independently arrive at a similar partitioning of the morphospace.

Co-evolving species pairs. Studies of co-evolution of ecologically interacting species also provide evidence that evolution at the community level can be highly repeatable. In these studies, researchers typically focus on multiple quasi-replicate pairs of co-evolving species. Species pairs can be both antagonistic, such as insects evolving to overcome plant chemical defenses [80], microbes evolving virulence to overcome host immunity [81,82] or animals evolving resistance to predator toxins [83,84]; or mutualistic, such as fig trees and wasps [85–90], plants and mycorrhizal fungi [91,92] and others [12,92–95]. In these cases, the community-level properties that evolve in parallel are the interactions between the community members [12,86,96–98]. In extreme cases, the interaction between partners in each pair can evolve to be highly specialized, so that partners interact almost exclusively with each other but not with other members of the clade. For example, many tree species of the genus *Ficus* form mutualistic host-pollinator associations with wasps of the family *Agaonidae*. The fig trees and the wasps have co-diversified and evolved pairs of species with highly specific host-pollinator interactions where one wasp species typically pollinates one fig tree species and vice versa [85–89]. Further analysis by Segar et al found that entire fig wasp communities in Africa, Australia and America form five ecological guilds that have independently evolved towards similar relative abundances [90].

Challenges. Cases of parallelism and convergence reviewed above strongly suggest that at least some community-level properties can evolve repeatedly even under natural conditions that may be far from the ideal setup. However, deviations from this ideal pose several important challenges. One challenge, specific to community-level repeatability, is to rule out the possibility that some community members evolved elsewhere and then repeatably assembled into communities that were later observed (rather than having repeatably evolved *in situ*). In other words, it may be difficult to establish that the observed community-level repeatability resulted only from internal eco-evolutionary processes rather than from migration-driven community assembly.

Other challenges that we see arise both at the level of communities and at lower levels of biological organization, and we discuss them in this broader context. Ascertainment biases pose several challenges to our ability to quantify repeatability. One bias, known as the “denominator problem", arises because not all populations or communities that would qualify as replicates are observed or analyzed [99], e.g., because researchers intentionally focus on quasi-replicates that evolved in parallel rather than those that diverged. Such focus is well intentioned because quasi-replicates that diverged are more likely to have experienced different environments and would not have qualified as true replicates. However, should they have qualified but diverged due to the intrinsic randomness of evolution, excluding them inflates the perceived degree of repeatability. Another source of the denominator problem are extinctions. Some replicates cannot be observed because they went extinct, and extinction may be biased with respect to the character whose parallelism is investigated. Regardless of the reasons, if not all replicates are observed, the true degree of repeatability cannot be accurately inferred. Another bias arises from the very requirement for replication, which, as mentioned above, can be satisfied by species and communities that live on islands or in lakes. However, ecological communities in these habitats are often less complex than elsewhere. Thus, if ecological complexity affects evolutionary repeatability, our perceptions of the degree and prevalence of repeatability may be skewed.

Another challenge is that populations or communities where parallel evolution is observed are not true replicates. Quasi-replicates vary at least somewhat in the environment they experience and in their initial state (community structure, genetic composition of member species, population sizes, etc.). On the one hand, the fact that parallelism is observed despite these "extrinsic" differences between quasi-replicates suggests that evolution would have been even more repeatable among true replicates. On the other hand, extrinsic variation compromises our ability to interpret any quantitative measure of repeatability. Specifically, if some quasi-replicates did not evolve in parallel, it is unclear whether the lack of parallelism should be attributed to the intrinsic randomness and contingency of evolution or to the extrinsic variation between quasi-replicates. Imagine that 50 out 100 quasi-replicates evolved character state *A* and the other 50 evolved character state *B*. Clearly, evolution is somewhat but not perfectly repeatable. This lack of perfect repeatability could be a genuine feature of evolution, e.g., just by chance, 50 quasi-replicates acquired mutations that confer character state *A* and the other 50 acquired mutations that confer character state *B*. But it is also possible that each quasi-replicate experienced one of two environments, either one that selects for *A* or one that selects for *B*, and evolution is in fact perfectly repeatable in each environment.

These challenges can be mitigated by more complete and less biased sampling in natural systems. Nevertheless, fully overcoming them may only be possible in experimental systems, which we discuss next.

3.2 Community evolution in the lab

Evolution experiments allow researchers to observe how the (almost) exact replicates of a population or a community evolve in (almost) identical conditions [7,99]. Such a setup is ideal for studying the repeatability of evolution driven by intrinsic factors, although controlled disturbances or migration can also be added [100,101]. Furthermore, the fact that all replicates are observed by the experimentalist—rather than a possibly biased subset of them—avoids the denominator problem and makes it possible to quantify the repeatability of evolution.

Laboratory evolution studies have been carried out in various antagonistic (usually, bacteria-phage [18,20,102–134]), mutualistic and commensal [135–150] systems with two- or more [151–160] species and in adaptive diversifications [55,100,101,161–167]. While most of these studies do not focus on evolutionary repeatability per se, the data they collect show that various community-level properties, such as absolute and relative abundances of community members [105,139,140,168], species interactions [18,169,170], community growth rate [136,138,168] and productivity [135,136,151], change over the course of evolution with some degree of repeatability (see Supplementary Table S1 for details).

Another important observation is that the repeatability of community evolution is variable between systems. For example, *Pseudomonas fluorescens* diversifies in a static spatially heterogeneous liquid medium into three ecotypes with perfect repeatability [55], whereas phage evolves the ability to infect *Escherichia coli* through a new receptor in only about 25% of replicates [18]. Identifying features of the community or the environment that predict the repeatability of community evolution is an emerging area of research (see Section 4.2 below). In particular, two recent studies tested an intriguing hypothesis that species interactions influence the repeatability of community evolution [152,171]. Researchers compared communities formed by coevolved species with those formed by the same species evolved alone in otherwise identical abiotic conditions. Celiker and Gore found that communities formed by six soil bacteria were more diverse in terms of their structure (i.e. the relative abundances of all species) after the member species evolved all together compared to them having evolved alone [152]. In contrast, Venkataram et al found that the interaction between yeast *Saccharomyces cerevisiae* and alga *Chlamydomonas reinhardtii* shifted more repeatably towards stronger mutualism when yeast evolved in the presence of the alga than alone [171]. Thus, species interactions appear to affect repeatability, but further studies will be needed to understand this effect.

In another recent study, Meroz et al assembled 87 two- and three-species bacterial communities and evolved them for about 400 generations [158]. They found that the community-structure similarity between replicates of the same community declined over time, but replicates of the same community remained more similar to each other than to other communities. Interestingly, the structure of evolved three-species communities could be to some extent predicted based on the structures of evolved two-species sub-communities. In Box 3, we use this study to illustrate how quantitative experimental approaches can help us answer interesting questions about the repeatability of community evolution, e.g., whether and how repeatability depends on community complexity.

Challenges. Experimental studies confirm that evolution can be repeatable at the community level. They also allow researchers to move beyond merely documenting the cases of parallelism and begin quantifying repeatability and dissecting its underlying mechanisms. However, the experimental approach to the problem of repeatability faces a major challenge. What can the results obtained in the lab tell us about the repeatability of community evolution in nature?

Most laboratory evolution studies use model microbes, owing mainly to practical matters such as their small size, short generation times, and the ability to survive cryopreservation. These features allow researchers to maintain many replicates, observe interesting evolutionary changes over tractable time scales of only weeks or months, and directly compare evolved and ancestral types as well as dissect the molecular mechanisms of evolution. But these important benefits also impose major limitations. Microbes are unicellular and interact with each other largely (although not exclusively) by exchanging metabolites. Experimental microbial communities have low complexity and have one or at most two trophic levels. The selective environment is usually constant or subject to regular periodic fluctuations, and laboratory evolution is usually observed over short periods of time, corresponding to only hundreds of generations. It is thus unclear whether the results obtained in experimental microbial communities can be generalized to more complex, multitrophic communities, communities of multicellular organisms, and to longer time scales. Results from evolution experiments may generalize most easily to other microbial communities, such as the gut microbiome, but also with some caveats, e.g., the environment in the gut is spatially structured, temporally variable and subject to feedback control by the host.

Overall, probing and extending the limits of generalizability of experimental results will require researchers to observe evolution over long (~10^4 generations [172]) and ultra-long (~10^5 generations [99]) timescales that are still accessible in some experimental systems (see Methods) and in more diverse experimental and semi-natural communities with non-model species. For example, it is now possible to study microbiome evolution in the mouse gut [173] or observe how microbes adapt to their host plants [174]. Community evolution studies are also being conducted in simple metazoa such as insects [175,176] and *Daphnia* [110,153]. It will be important to identify similarities and differences in how such communities evolve compared to their microbial counterparts.

3.3 Summary

Studies of ecological communities in nature established the foundational fact that the evolution of community-level properties can be to some extent repeatable, even under non-ideal conditions. However, quantifying the repeatability in natural systems and attributing it to exclusively internal processes is problematic. Community-level repeatability is also readily observed in the lab where it can be quantified and where the factors that influence repeatability can be probed. However, the generalizability of results obtained in the lab is an important challenge.

4 Open questions in the study of evolutionary repeatability

Previous research has established that evolutionary repeatability is worth studying at the community level, but the inquiry is still at its early stages. The next phase will center on addressing more exciting but difficult questions [12]. We discuss three questions that we think are the most interesting and important:

1. Is the observed degree of repeatability surprising or consistent with our expectations?
2. How is the repeatability of evolution at the community level related to that at other levels of biological organization?

3. Which features of the community predict the repeatability of its evolution?

Addressing these questions will require researchers to quantify the degree of evolutionary repeatability. In Box 1, we discuss three general notions of repeatability, which apply at any level of biological organization. State repeatability tells us how similar replicates are at a given snapshot in time. Trajectory repeatability tells us whether replicates evolve along similar paths in the character state space and do so at similar rates. Path repeatability tells us whether replicates traverse geometrically similar paths, regardless of the speed. Since replicates can take different trajectories towards the same state, state repeatability can change over time (Figure 2) and a high degree of state repeatability at one or multiple time points does not necessarily imply a high degree of path or trajectory repeatability. Similarly, high path repeatability does not imply high state or trajectory repeatability because replicates may traverse similar paths at different rates. On the contrary, a high degree of trajectory repeatability implies high degrees of both path repeatability and state repeatability at all times. Thus, trajectory repeatability is the strongest notion of the three.

4.1 Is the repeatability of evolution surprising?

Once the degree of evolutionary repeatability is quantified, it is natural to ask whether this degree is surprisingly high (or low). Since this question is relevant both in the context of community properties and individual traits, we discuss it here in this broader context, noting the differences where appropriate.

Surprise implies an underlying model of eco-evolutionary dynamics against which the observations are compared. Fundamentally, the degree of repeatability depends on how initially identical replicate populations or communities diverge over time, which is governed by the four evolutionary processes of mutation, recombination, genetic drift and natural selection, and by the ecological interactions between community members. Thus, the degree of repeatability we expect (at any level of biological organization) depends on which processes we include into our model and how we model them. In Box 2, we suggest four types of models that researchers can consider for explaining the patterns of evolutionary repeatability observed in their systems.

Because natural selection and ecological interactions can explain almost any observed pattern and because evolution even in the absence of selection or ecological interactions can be to some extent repeatable [77], Occam's razor dictates that we should first ask whether the observed degree of repeatability is consistent with *neutral null models*. It is relatively straightforward to construct and parameterize neutral null models for sequence evolution, which include only mutation and genetic drift [26,177–180]. At the community level, if one is interested in understanding whether absolute species abundances (or other properties that depend only on species abundances) evolve repeatably, a null model must include demographic fluctuations. Parameterizing neutral models for the evolution of other traits and community-level properties is considerably harder because it requires measuring how mutations and recombination affect these characters [77,181]. Essentially, such null models must specify the genetic and developmental constraints under which community members evolve (see Box 2). Regardless of the details however, the salient feature of neutral models is the absence of attractors. As a result, replicates are expected to diffuse in the character state space and diverge from each other (Figure 2A,B). Then, the state repeatability has to monotonically decline over time, eventually approaching a (possibly non-zero) equilibrium value (Figure 2C). However, a monotonic decline does not imply neutral evolution; it could be consistent with neutral or non-neutral evolution.

If the observed patterns of repeatability are inconsistent with neutral models (e.g., if state repeatability is a non-monotonic function of time), one can ask whether they are consistent with models with a single point attractor in the character state space (see Box 2). Since such models generally permit multiple distinct paths towards the attractor [182,183], replicates are expected to take diverse paths and initially diverge. However, if all paths lead to the same attractor, a fitness optimum in the trait space or to the eco-evolutionary attractor in the community-property

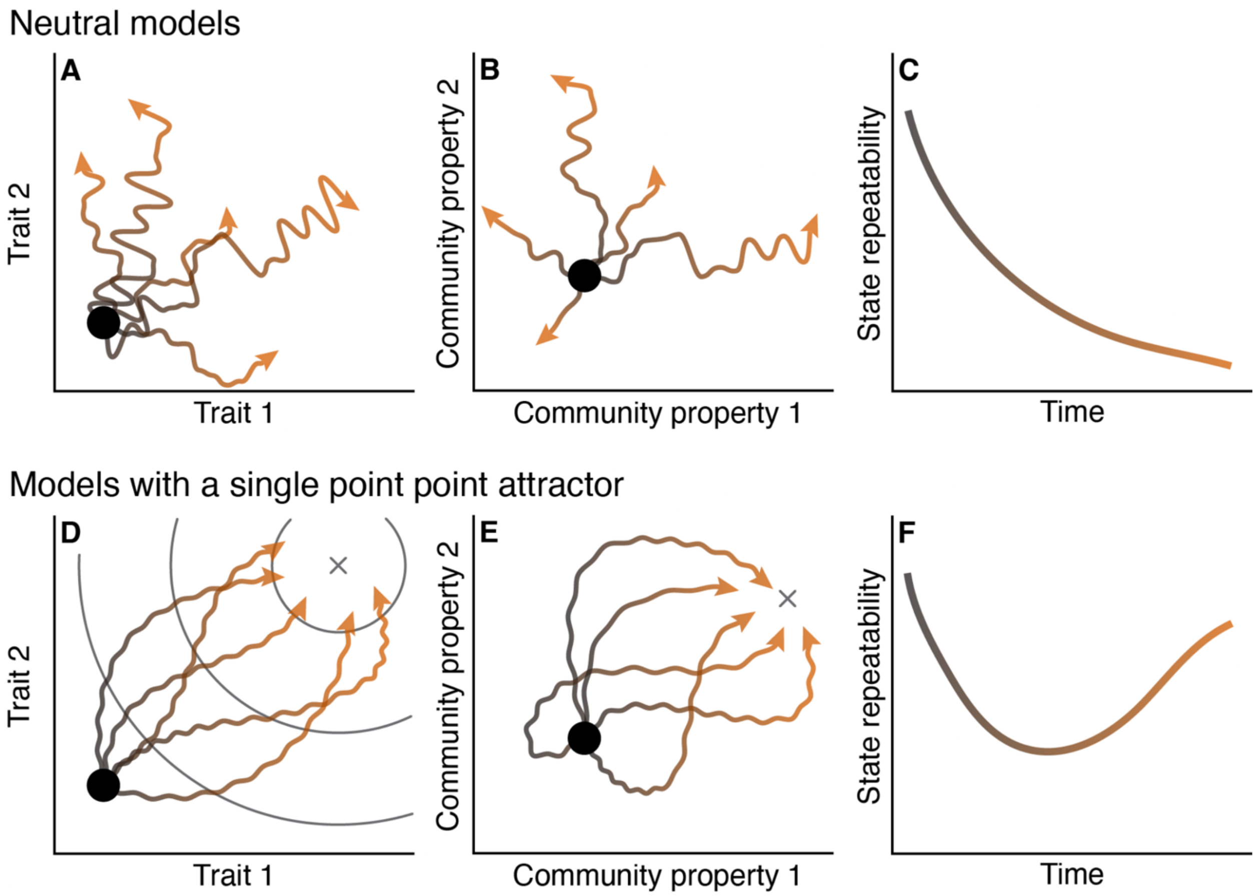


Figure 2. Expectations for evolutionary repeatability under simple models. A–C. In neutral models, replicates are expected to gradually diverge in the trait space (A) as well as in the space of community properties (B). As a result, state repeatability is expected to monotonically decline over time (C). **D–F.** In models with a single adaptive peak, replicate populations are expected to initially diverge and later converge in the trait space (D). Similarly, in models with a single eco-evolutionary point attractor, replicate communities are expected to initially diverge and later converge in the space of community properties (E). As a result, state repeatability is in general expected to be a U-shaped function of time (F). However, the time point where the repeatability begins to increase and the magnitude of the increase will depend on the details of the system (see text). Note that trajectories may intersect because different mutations can fix in different replicates. In all panels: black point indicates the initial state, color represents time (darker = earlier, lighter = later). In panels D and E, “x” marks the evolutionary attractor. In panel D, gray curves represent fitness isoclines.

space, replicates are expected to eventually converge towards it (Figures 2D,E). The timescale when convergence begins and its rate are determined by multiple factors, including species population sizes, the strength of selection. If the populations are sufficiently large, we expect the state repeatability to be a U-shaped function of time (Figure 2F). Thus, an increase in state repeatability suggests the presence of a single attractor (or possibly multiple neighboring attractors). However, genetic drift in smaller populations may erode this trend inversion, and repeatability may never increase.

If the observed patterns of repeatability are inconsistent with either neutral evolution or evolution towards a single attractor, more complex models can be considered, such as models with multiple and dynamic attractors or eco-evolutionary models, all of which can be sufficiently flexible to fit almost any observed pattern (Box 2). We illustrate what can be learned from comparing data to predictions of some simple models in Box 3, using the data obtained by Meroz et al [158].

Overall, developing better models of evolution of community-member traits and community-level properties and testing them against data are important goals for future research. Work in this direction will improve our understanding of how genetic constraints, various selection pressures and ecological interactions between community members work together to make eco-evolutionary dynamics more or less repeatable.

4.2 How is the repeatability of evolution at the community level related to that at other levels of biological organization?

The second question that we see as fundamental is how the repeatability of evolution at the community level relates to that at the level of the underlying traits of community members. This question can be broken down into two more basic problems. How do species traits map onto community-level properties [40,42]? And how does evolution explore the trait space?

The first problem, which can be termed “structural”, is the ecological analog of the problem of the genotype to phenotype to fitness map in evolutionary biology [184]. At one extreme, community-level properties could be insensitive with respect to the variation in the underlying traits that typically arises by mutations and recombination (Figure 3A), i.e., the trait-to-community map could be “robust”, analogous to a “smooth” fitness landscape [15]. An indication that trait-to-community maps are to some extent robust comes, for example, from studies showing that microbial species that diverged millions of years ago form communities that are apparently functionally equivalent [48,50,185]. If trait-to-community maps are generally robust, many distinct evolutionary trajectories and outcomes at the trait level (and hence low repeatability) would usually translate to similar trajectories and outcomes at the level of community properties (and hence high repeatability).

The opposite extreme is also conceivable: different trait variants that typically arise by mutations and recombination could shift communities into qualitatively different ecological states (Figure 3B), i.e., the trait-to-community map could be “sensitive”, analogous to a “rugged” fitness landscape [15]. A study of an experimental mutualism between *Salmonella enterica* and *Escherichia coli* suggests that some trait-to-community maps may in fact be sensitive [138].

Douglas et al found that different mutations in *S. enterica* that have apparently similar effects on protein function produced a wide range of effects on community growth. If the trait-to-community maps are typically sensitive, low diversity of evolutionary trajectories and outcomes at the trait level (and hence high repeatability) would often result in high diversity of trajectories and outcomes at the community level (and hence low repeatability). It is possible that both extremely robust and extremely sensitive as well as intermediate trait-to-community maps are realized in different systems or even in the same system, e.g., robust with respect to some traits but sensitive to others, or some community properties may be robust while others sensitive. It seems important to empirically characterize the sensitivity of various community-level properties with respect to various ecologically relevant traits of constituent members and to develop theory for understanding these dependencies.

The degree of evolutionary repeatability depends not only on the structure of the map from traits to community-level properties but also on the dynamics of evolution. Selection pressures exerted on a species by the surrounding community could force it to evolve along a narrow path in its trait space. Then, evolution at both trait and community levels would be highly repeatable, even if the trait-to-community map is sensitive. As mentioned above, there is some evidence

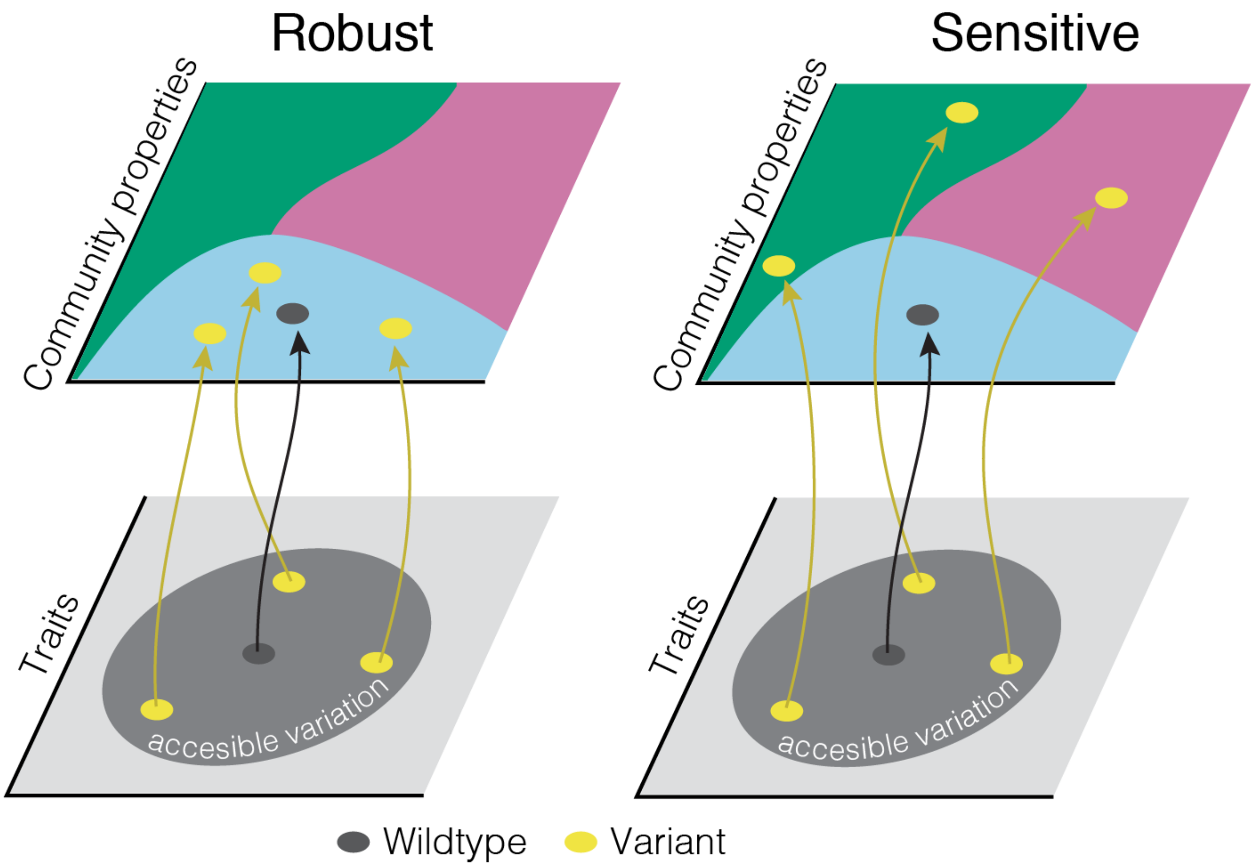


Figure 3. Robust and sensitive trait-to-community maps. Community-member species can access a limited region of the trait space by mutations and recombination (large gray ovals around the wildtype). Arrows show the fact that species traits determine community-level properties. A robust trait-to-community map (left) is one where communities formed by accessible variants have similar properties (colored regions). A sensitive map (right) is one where communities formed by different accessible variants have distinct properties.

that the diversity of evolutionary outcomes depends on whether community members evolve in each other's presence or alone [152], which suggests that selection pressures exerted by the community change the way evolution explores the trait space.

It may be interesting to focus some future work on disentangling the effects of structure and dynamics on the repeatability of community evolution. To explore the local structure of the trait-to-community map, one could generate variation that is maximally unbiased by selection (e.g., by random mutagenesis), and measure the effects of these random variants on community properties. One could also measure which of these variants pass the selection filter, which would give one a glimpse at how selection biases the exploration of the trait space and, consequently, the space of community-level properties.

4.3 Which features of the community predict the repeatability of its evolution?

The third worthwhile goal is to identify which system properties most reliably predict the repeatability of its evolution [6,39]. For example, is evolution under selection imposed by ecological interactions more or less repeatable than evolution under abiotic selection pressures? Do communities with certain types of ecological interactions evolve generally more repeatably than others (e.g., mutualistic versus antagonistic communities)? Is evolution at the community level more or less repeatable for more complex communities, for communities with more trophic levels, or those that evolve in more nutrient rich environments? These questions are probably easier to approach experimentally and theoretically than in natural systems because they require measuring community-level repeatability across communities that vary only by a single factor, e.g., complexity. In Box 3, we use the study by Meroz et al [158] to illustrate the potential for community evolution experiments to address some of these questions. While research in these directions is at its earliest stages, the initial results are encouraging [152,158,171]. One important potential outcome of this work would be to identify general rules for predicting a system's evolutionary repeatability based on its features.

5 Summary and conclusions

Our ability to predict evolution hinges on evolution being to some extent repeatable, at least under identical environmental conditions. How repeatable evolution is depends on the level of biological organization at which it is observed. We focused in this article on the repeatability of evolution of community-level properties. Our review of the relevant literature showed that there is substantial evidence that evolution at the community level is to some extent repeatable, but the more difficult and profound questions remain largely unresolved. We identified and discussed three of them. (1) Is the degree of repeatability surprising? (2) How does repeatability at the community level relate to that at lower levels of biological organization? (3) Which features of the community predict its evolutionary repeatability? Addressing these questions will require new data and the development of new theory and methods. We outlined some approaches that could be fruitful.

Box 1. Quantifying the repeatability of evolution

Evolutionary repeatability is a matter of degree. Quantifying it enables us to test models against data as well as compare the degree of repeatability, e.g., across systems (see Box 3 for an illustration).

Suppose we are interested in the repeatability of evolution of character X, which can be a genetic sequence, a trait or a community-level property. X can be discrete or continuous with one or multiple dimensions. As each replicate i evolves, its character will trace a stochastic trajectory $X_i(t)$ in the character state space. There are three ways to describe this ensemble of evolving replicates [186]. The *probability distribution of states* describes how likely a replicate is to have a particular character state x at time t. The *probability distribution of trajectories* describes how likely a replicate is to have a particular trajectory $x(t)$ in the character trait space [186–188]. Importantly, $x(t)$ is considered explicitly as a function of time. Finally, it is also possible to view the trajectory $X_i(t)$ of replicate i as a geometric curve in the character state space, ignoring the times when the replicate passes through each state. We refer to such a curve as a “path”. Then, the ensemble of replicates is described by the *probability distribution of paths*; it tells us how likely a replicate is to trace any given geometric path.

These three descriptions lead to three corresponding notions of repeatability which emphasize different aspects of this idea [186]. *Path repeatability* tells us whether replicates evolve along similar curves in the state space, regardless of speed. *Trajectory repeatability* tells us whether replicates evolve along similar curves and do so at similar speeds. Finally, *state repeatability* tells us how similar the character states of different replicates are at any given moment. Szendro et al also used the notion of *endpoint repeatability* which is a special case of state repeatability at $t = \infty$ [186]. In practice, measuring or inferring full trajectories or paths may be extremely difficult. Instead, one might be able to measure some of their features, e.g., the angles of divergence between replicate paths (Figure 1). The distributions of different features will then capture different aspects of repeatability.

Our intuitive notion of repeatability corresponds to the narrowness of a probability distribution and, as such, it can be quantified with various measures of distribution narrowness, such as entropy, variance or Hill’s diversity [189]. Simpson’s diversity index, a special case of Hill’s diversity [189], is a particularly convenient measure because it has a simple interpretation as the probability that two random replicates have the same character state [190] or evolve along the same path or trajectory. All these measures of distribution narrowness are well defined for discrete characters, e.g., genetic sequences. However, some of the more convenient measures, such as entropy, Hill’s and Simpson’s diversity, do not have natural convenient extensions for continuous characters. The repeatability of evolution of continuous characters can be quantified by discretizing them, by using measures of distribution narrowness that are applicable to continuous characters (e.g., variance along the direction of maximum variation) or by defining a similarity metric and calculating, for example, the expected similarity between pairs of replicates. However, these approaches have caveats; for example, entropy may depend on a particular discretization scheme, and a similarity metric may not capture all the relevant aspects of similarity between states, trajectories or paths.

The above considerations are general and apply to all types of characters, from genotypes to community-level properties. However, the best choice of particular type of repeatability (state, path, trajectory) and its measure (entropy, Simpson’s diversity, expected similarity, etc.) will depend on the characters whose repeatability is investigated and on the research question. For example, one can evaluate the similarity of any pair of evolved character states using the angle between the respective evolutionary vectors (see Figure 1 and Ref. [8]) and then quantify state repeatability using the average angle among pairs. This measure clearly captures one aspect of repeatability—whether replicates evolve in the same direction in the character state space—but neglects another potentially important aspect: whether the replicates evolve at similar rates along different paths.

In general, to calculate any measure of repeatability one needs to know the underlying distribution of states, trajectories or paths. Thus, the first step towards quantifying repeatability is to estimate one or more of these distributions. In Box 3, we use the data by Meroz et al [158] to illustrate this approach.

Box 2. Modeling the repeatability of evolution

We suggest four types of models against which the observed patterns of evolutionary repeatability (at any level of biological organization) can be compared.

Neutral models. The main component of a neutral model is the variation that can be generated by mutation and recombination as well as demographic stochasticity. If the genetic mutation rates and mutational biases are known, standard population genetic models can be used to obtain the neutral null expectation for the distribution of replicates in the genotype space (and, hence, the null for the degree of repeatability) [26,177–180]. At the community level, a demographic noise null model can be easily constructed for absolute and relative species abundances as well as any other properties that depend on them (see Box 3 for an example). To obtain the null expectation for trait and other higher-level characters, one has to specify how the organism's genetic and developmental architecture constrains the variation at the relevant level that is produced by mutations and recombination [5,191,192]. These constraints can be modeled with **G** and **M** matrices [193,194], which can be estimated from mutagenesis and breeding experiments [195,196]. Constraints can change over time as populations evolve [197], but they likely change slowly [194,196]. Thus, it is reasonable to start with a neutral model of evolution under constant constraints.

Models with selection and a single attractor. The simplest models of selection are the adaptive landscape model [194,198] and the related Fisher's geometric model [199,200], both of which assume that the organism evolves on a fitness landscape (over a trait space) with one optimum. In this model, the location and the shape of the fitness peak are free parameters in addition to those present in neutral models. One can extend this type of model to an ecological community by assuming that each community member evolves on its own adaptive landscape [79]. Such communities will evolve towards a single attractor in the community-property space. Ecological interactions are not explicitly incorporated in this type of model.

Complex models with selection. More complex forms of natural selection can be captured by adaptive landscape models with multiple optima [79,201] or a moving optimum [202]. These models can have an arbitrary number of free parameters and therefore can generate any patterns of repeatability. One should therefore attempt to fit these models to data only if simpler models fail to provide a reasonable fit.

Eco-evolutionary models. In models discussed so far, selection is imposed on organisms externally, as if the environment that exerts selection is not affected by the evolving population. An example would be adaptation to higher altitude [203]. However, in ecological communities, selection on individual community members is at least in part exerted by the ecological interactions themselves [146,151]. Such selection can be captured by eco-evolutionary models where the rates of reproduction and death of each eco-type depend on the traits and abundances of other eco-types [41,204]. These models require some knowledge of ecological interactions in the community, but this knowledge pays off because ecology then specifies the direction and strength of selection on each community member. Thus, such models can be both more realistic and more parsimonious than the complex models with selection.

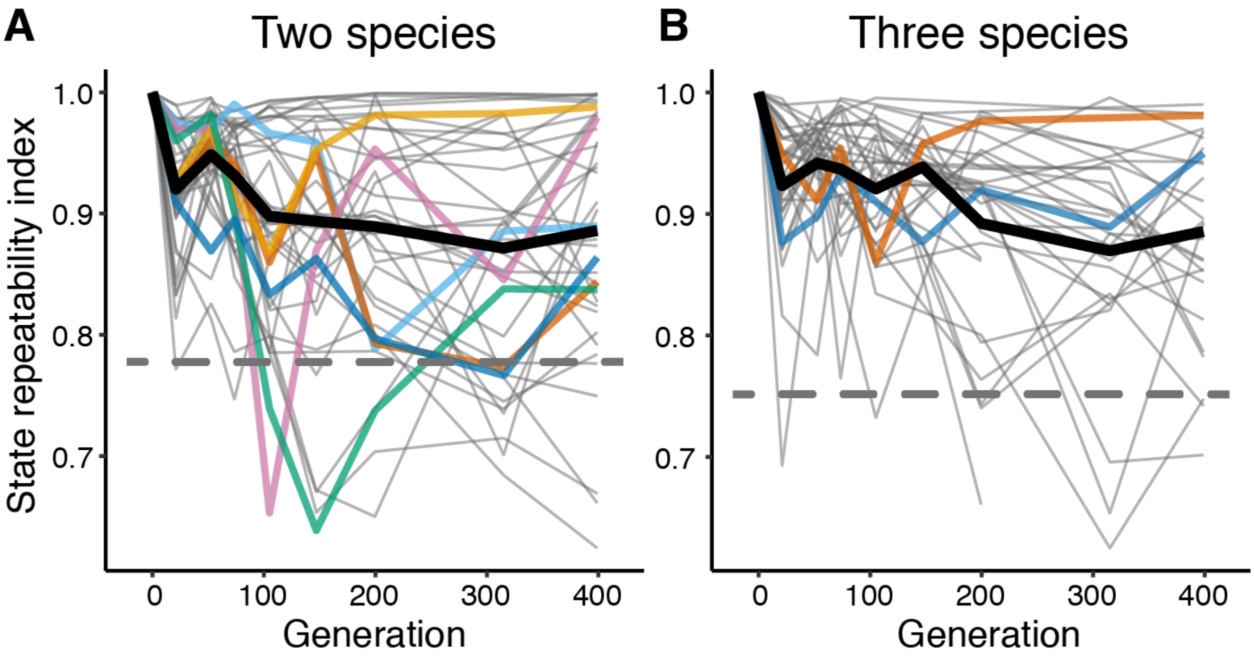
Box 3. A case study in quantifying the repeatability of community evolution

Here, we use the study by Meroz et al to illustrate how quantitative experiments can advance our understanding of the repeatability of community evolution. Meroz et al assembled 87 two- and three-species bacterial communities by drawing members from a panel of 16 species that had no prior history of association [158]. They evolved 3 to 18 replicates of each community for about 400 generations in batch culture and measured how the community structure (i.e. the relative abundances of all species) changed over time. Here, we reformulate some of their findings in terms of measures of repeatability and make some new observations after reanalyzing their data.

We first quantified the state repeatability (see Box 1) of the eco-evolutionary dynamics using a euclidean distance-based measure (Methods) and found that it declined on average (see Figure; $P = 0.025$ for two-species communities and $P = 0.006$ for three-species communities, repeated-measures ANOVA, excluding the first 70 generations; see Methods for details), consistent with the authors' conclusions. Interestingly, the rates of decline varied between communities. In 6 out of 40 (15%) two-species communities and in 9 out of 29 (31%) of three-species communities, the repeatability declined less than expected under demographic fluctuations ($P < 0.05$, t-test after Benjamini-Hochberg correction), suggesting that ecological interactions between species stabilize their abundances. In contrast, in 14 (35%) two-species communities and in 12 (41%) of three-species communities, the repeatability declined more than expected under demographic fluctuations ($P < 0.05$, t-test after Benjamini-Hochberg correction), suggesting that different replicates evolved distinct changes in ecological interactions. In the remaining communities, repeatability was either consistent with the neutral expectation or deviated in the opposite directions at different time points.

Furthermore, we identified six two-species communities and two three-species communities where the repeatability changed non-monotonically over time, such that their replicates evolved towards surprisingly similar compositions by the end of the experiment despite significant differences at intermediate timepoints (see colored lines in the Figure). These observations suggest that in these communities replicates evolved towards the same or similar eco-evolutionary attractors.

Finally, we found that the repeatability of community evolution did not differ significantly between two- and three-species communities ($P = 0.94$; ANOVA $F = 0.006$, $DF_n = 1$, $DF_d = 462$; compare panels A and B in Figure). This suggests that higher-order species interactions may have only minor effects on the eco-evolutionary dynamics, consistent with the authors' finding that the structure of three-species communities can be predicted based on the composition of two-species communities.



Community-level repeatability changes over time in experimental microbial communities. Data from Ref. [158]. **A.** Two-species communities. **B.** Three-species communities. Each line represents a unique community. Communities with significantly non-monotonic state repeatability are colored (see Methods). Thick black lines show the average state repeatability. Dashed lines show the expected repeatability for communities with random relative abundances.

6 Methods

6.1 Duration of evolution experiments

We estimate the duration of the longest realistic evolution experiments based on the fact that the shortest known generation times are around 10 minutes [205,206]. If such a rapid growth rate can be sustained, an evolution experiment would proceed at a rate of 144 generations per day. A 30 year-long experiment (approximately a duration of one research career) at this rate would then yield about 1.5 million generations. In practice, the number of generations per day rarely exceeds 10 [172,207] and in most existing model communities the number is even lower [136,140,152,158,171]. At this rate, ~10^4 generations can be achieved within about 3 years, i.e., within the span of a typical funding cycle. The longest (i.e., career-long) experiments at this rate are unlikely to substantially exceed ~10^5 generations. The longest running microbial evolution experiment to date is the LTEE started in 1988 by Richard Lenski, which is now at between 70 and 80 thousands of generations [208].

6.2 Analysis of Meroz et al data

Data source and preprocessing. We downloaded from the github repository the scripts and the data on species abundances for two- and three-species microbial communities collected by Meroz et al [158]. The iPython Notebook provided with the data was used to preprocess the data and generate a table of relative species abundances for each replicate community at each sampled time point.

Quantifying the repeatability of evolution. Replicate community i can be represented at time t by a vector $\boldsymbol{x}_i(t)$ of relative abundances of community members, such that the sum of components of each vector $\boldsymbol{x}_i(t)$ at each time t equals 1. We calculate the similarity metric $s_{ij}(t)$ between any pair of replicate communities i and j at time t as $s_{ij}(t) = 1 - d_{ij}(t)/\sqrt{2}$ where $d_{ij}(t)$ is the euclidean distance between vectors $\boldsymbol{x}_i(t)$ and $\boldsymbol{x}_j(t)$. $s_{ij}(t)$ takes values between zero (when the replicate communities have maximally dissimilar relative abundance vectors, e.g., (1,0,0) versus (0,1,0)) and one (when the replicate communities have identical relative abundance vectors). We then use the mean similarity $\langle s(t) \rangle$ over all pairs of replicate communities as an index of state repeatability at time t. To generate a null expectation for $\langle s(t) \rangle$, we sampled 3 random communities with relative abundances drawn from a uniform distribution and normalized to 1. This sampling procedure was carried out 10,000 times each for two-species and three-species communities.

For interpreting the values of $\langle s \rangle$ it is important to note that in the limit of infinitely many replicates $\langle s \rangle$ is bounded from below by $1/n$ where n is the number of species in the community. To demonstrate this, consider an ensemble of maximally dissimilar replicate communities. Such an ensemble contains only replicate communities with a single species, and every species is represented equally among all replicates. In other words, fraction $1/n$ of replicates have only species 1, fraction $1/n$ have only species 2, etc. Thus, two randomly sampled replicate communities are maximally distinct ($s_{ij} = 0$) with probability $1-1/n$ and they are maximally similar ($s_{ij} = 1$) with probability $1/n$, which implies that $\langle s \rangle = 1/n$.

Community repeatability under demographic noise. Community evolution under demographic noise alone, without selection or ecological interactions, is equivalent to the neutral Wright-Fisher model. We instantiated each replicate of each community with frequencies observed at generation 70, the time point by which the communities reached their ecological equilibria, with a total size $N = 10^5$. Communities were propagated across generations using multinomial sampling. 1000 such simulations were conducted for each replicate of each community for 330 generations. For each simulation of each replicate, we estimated the relative species abundances at the respective sampling time points from samples of 100 random individuals. For each community composition, we then calculated $\langle s(t) \rangle$ as described above and thereby obtained the null distribution of this statistic. We then calculated an empirical two-tailed *P*-value for the observed $\langle s(t) \rangle$ for each community at each sampling time point after generation 70. We found that every community composition had at least one time point where the observed $\langle s(t) \rangle$ had an empirical *P*-value < 0.05 after Benjamini-Hochberg correction (across all communities and time points), indicating that no community evolved in a manner consistent with demographic noise alone.

Statistical analysis. We conducted repeated-measures ANOVA analysis to test for significant changes in the repeatability of community evolution over time and between communities. This analysis was conducted using the `anova_test` function using the rstatix package in R. For this analysis, the within-subjects variable was defined to be each unique pair of replicate cultures for which we estimated $s_{ij}(t)$. Time effects other than for trios as generation 0-400 are reported after Greenhouse–Geisser sphericity correction. The results of this analysis are shown in Table 1.

Communities with significant increases in repeatability were identified as follows. For each community, we first found a time point where the minimum of $\langle s(t) \rangle$ was achieved, excluding the final time point. We then conducted pairwise t-tests between this time point of the minimum and the final time point. Communities with *P* < 0.05 after the Benjamini-Hochberg correction were considered to have a significant systematic change in their repeatability, and then communities where the minimum of $\langle s(t) \rangle$ was achieved at the final time point were excluded.

# Species	Generations	Time effect	Composition effect
2	0–400	$F = 5.4$, $DF = 2216$ $P = 7\times10^{-11}$	$F = 5.79$, $DF_n = 36$, $DF_d = 410$ $P = 3\times10^{-20}$
2	70–400	$F = 4.3$, $DF = 1928$ $P = 0.025$	$F = 5.57$, $DF_n = 37$, $DF_d = 447$ $P = 6\times10^{-20}$
3	0–400	$F = 0.87$, $DF_n = 8$, $DF_d = 120$ $P = 0.545$	$F = 2.4$, $DF_n = 1$, $DF_d = 15$ $P = 0.143$
3	70–400	$F = 2.97$, $DF = 53.46$ $P = 0.006$	$F = 0.43$, $DF_n = 1$, $DF_d = 18$ $P = 0.521$

Table 1. Results of the repeated-measures ANOVA for the repeatability of community evolution in Meroz et al data.

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Supplementary tables

Supplementary Table S1. Details of studies describing the evidence for the repeatability of evolution at the community level.

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