



REVIEW

The legacy of the past: effects of historical processes on microbial metacommunities

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ABSTRACT: Distinguishing the importance of different community assembly mechanisms is an emerging topic in microbial ecology and much focus has been placed in recent years on investigating how contemporary environmental conditions, dispersal and stochastic processes influence the spatial turnover of communities. However, historical events, such as past environmental conditions or dispersal events, can be important as well. We provide a short summary of the processes that can lead to so-called legacy effects, where past biotic or abiotic factors influence the composition of present-day communities. Priority effects, which arise if early colonizers gain advantage over later-arriving species, can lead to persistent legacy effects. In contrast, time-lags in environmental selection can lead to transient legacy effects. Dispersal rates as well as factors that influence the adaptability of species to changing environmental conditions should be important factors that determine the relative importance of contemporary selection versus historical processes and whether legacy effects are likely to be permanent or temporary. Working with microbial communities offers the advantage of feasible time series studies and multi-generation experiments, and can therefore make important contributions to a novel systematic framework on how historical processes shape complex metacommunities in nature.

KEY WORDS: Historical factors · Metacommunities · Assembly mechanisms · Microorganisms · Legacy effects · Priority effects

INTRODUCTION

During the last decades, microbial biogeography has been widely studied (e.g. Foissner 2006, Martiny et al. 2006, Ramette & Tiedje 2007, Lindström & Langenheder 2012, Duarte et al. 2016) and the consensus of this work is that microorganisms, in spite of their high passive dispersal ability, show clear differences in species distribution patterns at various spatial scales. In a metacommunity context, where local communities are connected to each other through dispersal, spatial differences in community composition can be due to a combination of different processes, including selection by local environmental conditions (spe-

cies sorting), dispersal, and stochastic (drift) events (Leibold et al. 2004, Vellend 2010). Dispersal can be either limiting, therefore leading to differences in community composition in habitats with similar environmental conditions, or on the contrary, homogenising in cases where dispersal rates are very high, leading to so-called mass effects (Leibold et al. 2004, Vellend 2010). Many studies have shown that microbial communities are often assembled by species sorting processes (see, for example, reviews by Martiny et al. 2006, Hanson et al. 2012, Lindström & Langenheder 2012). However, there is also evidence that other processes are important as well (e.g. Sloan et al. 2006, Fontaneto & Hortal 2012, Stegen et al. 2013).

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One major challenge is to link spatial patterns in community composition to different assembly processes. Typically, samples from various locations within and/or across ecosystems are taken, and differences in the presence or absence of species or their abundances are related to differences in environmental conditions measured at the same time. Various statistical approaches, including distance approaches (e.g. Martiny et al. 2006, Warton et al. 2012) and variation partitioning (e.g. Borcard et al. 1992, Ramette 2007) that account for effects of spatial autocorrelation of environmental factors can then be used to determine whether differences in community composition between locations are due to pure spatial effects (indicative of dispersal limitation or mass effects) or pure environmental effects (indicative of species sorting processes). In parallel, the increasing availability of sequencing data and bioinformatics tools have facilitated a rapid expansion of studies that use phylogenetic data and methods to explore ecological and evolutionary factors that determine the assembly of communities (e.g. Cavender-Bares et al. 2009). The basic premise is that phylogenetic data can provide a historical framework with which to quantify evolutionary and ecological patterns/processes, as reviewed by Emerson & Gillespie (2008). Phylogenetic data have been used in bacterial communities to quantify the relative importance of different assembly processes (e.g. Wang et al. 2013), including species sorting, drift, dispersal limitation and mass effects (Stegen et al. 2013).

The majority of studies are based on snapshots in time, which has the major drawback that they do not allow one to clearly disentangle the effect of events that occurred in the past. Therefore, the impacts of past environmental conditions or dispersal events remain hidden in the spatial component of the statistical framework described above, even though they can leave their imprint on present-day communities. For example, the absence of a given species from a location could be the result of unsuitable contemporary environmental conditions, but may also reflect historical processes (i.e. processes that relate to events that happened in the past, e.g. species sorting by past environmental conditions and priority effects) (Hanson et al. 2012, Fukami 2015) that influence community assembly (see below). Moreover, species can be present in a locality even if habitat conditions are not optimal for them at a certain time point as the result of historical processes (Fontaneto & Hortal 2012). Generally, historical processes can lead to historical contingencies or legacy effects, which can be defined as constraints on compositional changes

in response to contemporary conditions created by past biotic or abiotic conditions. Hence, legacy effects can influence present-day communities when effects of past environmental conditions and/or dispersal events persist through time and leave their imprint on the affected contemporary communities even if the environment changes (Hawkes & Keitt 2015, Fukami 2015).

The aim of this review is to provide a short overview about how such legacy effects can arise, how they influence the spatial structure of present-day microbial communities, how we can detect them, and under which circumstances we can expect them to be important. We specifically developed a general conceptual framework to explain by which mechanisms past environmental conditions influence contemporary beta-diversity. We discuss the importance of legacy effects in aquatic microbial communities and provide some suggestions for how aquatic microbial ecologists can contribute to this emerging research area.

MECHANISMS THAT CAN CAUSE LEGACY EFFECTS

One possible mechanism that can cause legacy effects are the time-lags in species sorting that can occur if microbial populations are adapted to environmental conditions at some point in the past (Blanquart & Gandon 2013, Fox & Harder 2015). As a consequence, compositional and environmental turnover do not match up and community composition is not able to track environmental changes to the extent shown in Fig. 1A, but instead the 'environmental tracking' is delayed (Fig. 1B). Such time-lags in species sorting can occur because there is always at least a certain degree of dispersal limitation for some time—simply because it takes time for dispersing taxa to arrive, grow and establish themselves in local communities (Hanson et al. 2012). The same applies to dormant resident taxa, which also need time to re-suscitate and grow in order to establish themselves as active members of the local communities. Thus, community composition lags behind contemporary conditions, resulting in stronger effects of species sorting by past, compared to present, environmental conditions (Fig. 1B). Importantly, however, the effect of past environmental conditions will be transient (Fig. 1B).

Secondly, the assembly history of communities (the sequence and timing in which species or their propagules reach an ecological community) can profoundly affect community composition through so-called priority effects (Fukami et al. 2007, Fukami

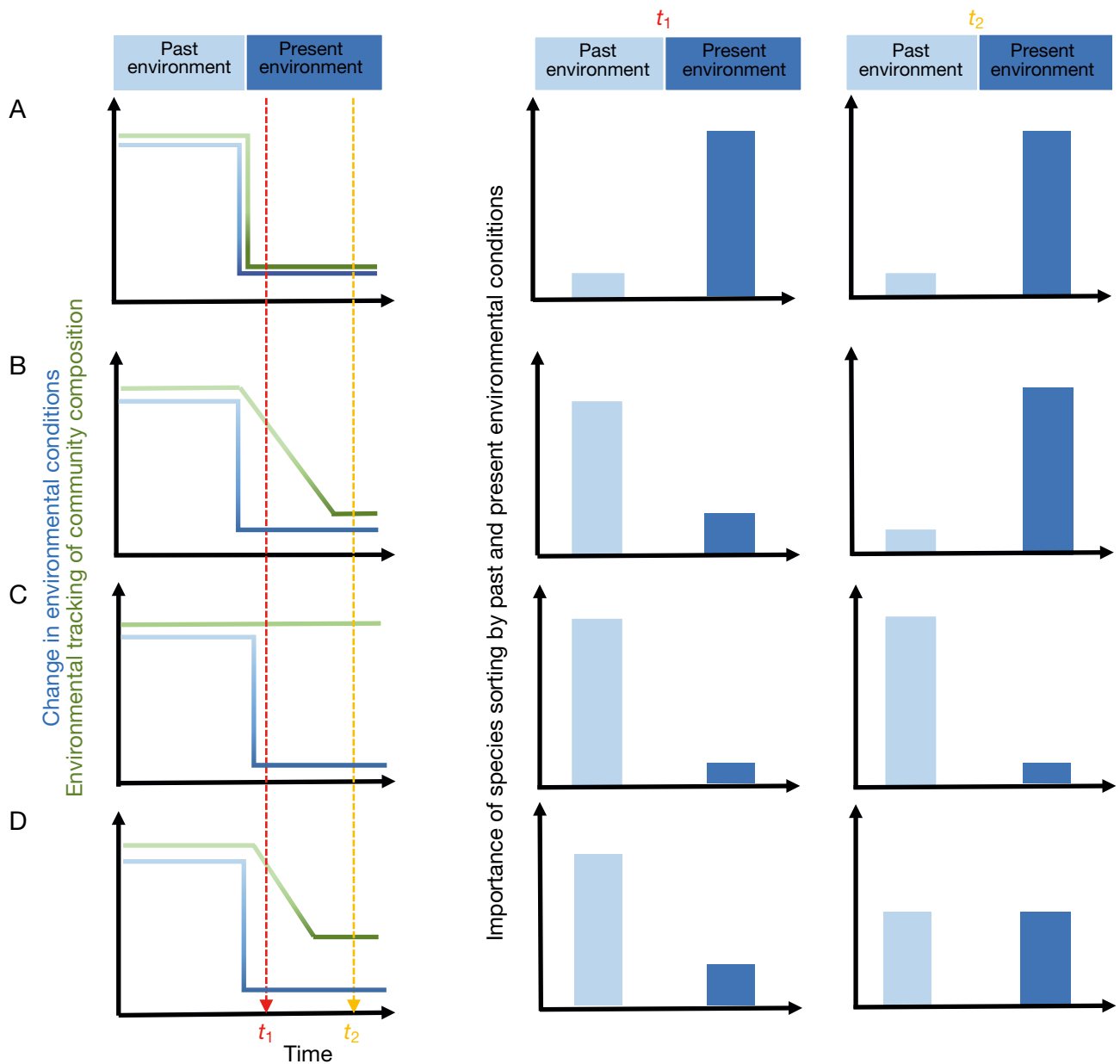


Fig. 1. Different species sorting scenarios that include selection by both contemporary and past environmental conditions. The column on the left shows the extent to which communities track changes in environmental conditions; the 2 columns on the right show to which extent variation in community composition is due to species sorting by past and present environmental conditions at 2 hypothetical time points (t_1 and t_2). (A) No legacy effects: community composition closely tracks changes in environmental conditions so that species sorting by contemporary environmental conditions is stronger than that by past environmental conditions at both time points. (B) Transient legacy effects: changes in species composition lag behind changes in environmental conditions, either due to time-lags in species sorting or temporary priority effects (see 'Mechanisms that can cause legacy effects' for details). In this case, species sorting by past environmental conditions can be stronger than that by contemporary conditions at a time point close to the environmental change event when communities are still in a transitional stage (t_1). However, effects of past environmental conditions are transient, and communities will eventually be replaced by dispersed species or species resuscitated from local seed banks selected by the contemporary conditions (t_2). (C) Persistent legacy effects: priority effects completely prevent environmental tracking. This can lead to persistent effects of past environmental conditions if species initially selected by these conditions monopolize communities through adaptation after the environmental change event. Consequently, the effects of contemporary conditions will be weak at both time points. (D) Mixed scenario: part of the community shows persistent priority effects and other parts time-lags in species sorting. Hence, at time point t_2 taxa that are selected by contemporary and past environmental conditions co-exist and explain a similar amount of variation in community composition

2015), and can thereby cause historical contingencies. In general, priority effects presume that early colonization offers an advantage for a species in its interactions with future colonists (Shulman et al. 1983), so that it attains high relative abundances in a local community simply because it has arrived first (Lockwood et al. 1997). This effect can arise because early-arriving species either consume available resources leading to niche preemption, or change the types of available niches in a location (niche modification) (Fukami 2015). Furthermore, if niche preemption-driven priority effects are enforced by evolutionary processes (i.e. adaptation of early colonizers), this can lead to so-called monopolization effects (Urban & De Meester 2009, De Meester et al. 2016). Monopolization effects can also explain effects of past environmental conditions if the early colonizers that have initially been selected by environmental conditions have the ability to rapidly adapt to any environmental change or disturbance, and thus continue to persist and dominate the local community even if environmental conditions change. Such a scenario can either lead to transient (temporary) effects of past environmental conditions if monopolizers are eventually replaced by pre-adapted later-arriving species (Fig. 1B), or alternatively, persistent effects of past environmental conditions on community composition if that is not the case (Fig. 1C). Finally, it is also possible that the processes related to selection by present and past environmental conditions overlap, so that some taxa are selected by the present and others by past conditions (Fig. 1D).

FACTORS THAT DETERMINE THE IMPORTANCE OF LEGACY EFFECTS

Fukami (2015) provided a review detailing the circumstances under which priority effects are likely to occur, and therefore a description of all the intrinsic and extrinsic factors underlying priority effects is beyond the scope of this paper. Most importantly, legacy effects will primarily be influenced by the adaptive potential and growth rates of local communities in relation to the time it takes for better adapted external taxa and/or dormant resident taxa to arrive or resuscitate and grow to become abundant community members. This will then ultimately determine the relative importance of contemporary species sorting processes compared to historical processes (Urban & De Meester 2009, Mergeay et al. 2011, Fukami 2015, Vanoverbeke et al. 2015, Grainger & Gilbert 2016). If dispersal rates are high and dis-

persed taxa that are selected by the new environmental conditions grow rapidly, the time window for which the legacy of past environmental conditions can be detected should be short (Fig. 1A). In contrast, if dispersal and/or colonisation rates are very low, the time window will be longer (Fig. 1B–D) due to dispersal limitation. Moreover, the likelihood of priority effects increases due to the lower number of potential colonizers/competitors arriving via dispersal (e.g. Fukami 2015, Vanoverbeke et al. 2015, Grainger & Gilbert 2016). How dispersal rates affect the occurrence of priority effects has rarely been tested, with the exception of one recent study that did not provide support for the theoretical prediction that higher dispersal should weaken the importance of priority effects because the likelihood for the arrival of better-adapted dispersing species increases (Pu & Jiang 2015). This could be because monopolization effects (where early arrivers or local resident species rapidly adapt to new environmental conditions) are expected to be high in microbial communities (De Meester et al. 2016). However, this study was based on a simple model community consisting of only a few bacterial strains; more studies are therefore needed to test these ideas.

Other factors, such as environmental fluctuations (the strength and frequencies of environmental change and disturbances that disrupt communities), productivity, grazing and the ecological traits of the community members that influence their growth and dispersal abilities might also influence legacy effects by changing the above-mentioned balance between growth of resident versus dispersing taxa (Fukami 2015). The frequency of environmental fluctuations, for example, may determine whether or not there is sufficient time for dispersing taxa to establish in local communities, or emerge out of the local 'seed-bank' in response to new environmental conditions. Strong environmental fluctuations may also promote priority effects by species that are 'generalists' and that can rapidly track changes in the environment, thus reducing the importance of species sorting processes (Loeuille & Leibold 2008). A recent study, using simple protist communities in laboratory microcosms, found evidence that assembly history influenced the identity of the dominant species through priority effects, which was, however, modified by dispersal and disturbances (Ojima & Jiang 2016). Hence, it is the complex interaction between dispersal and environmental history that, together with the traits found in a community, will determine the importance and character of legacy effects that influence community composition at a given point in time.

EVIDENCE FOR THE IMPORTANCE OF LEGACY EFFECTS IN MICROBIAL COMMUNITIES

Hanson et al. (2012) conducted a literature survey including a broad range of aquatic and terrestrial systems and showed that most studies (92.6%) found that selection imposed by the contemporary environment shapes the spatial distribution of microorganisms; however, in 68% of all studies there were also significant spatial distance effects. Such spatial distance effects are often interpreted as support for dispersal limitation, but they may also encompass other historical processes, such as priority effects and species sorting by past environmental conditions. Direct evidence showing that priority effects are important in structuring microbial communities comes primarily from studies that have manipulated the assembly history in culture experiments based on isolates from various ecosystems (e.g. Fukami 2004, Fukami et al. 2007, Jiang & Patel 2008, van Gremberghe et al. 2009, Peay et al. 2012, Tucker & Fukami 2014, Hiscox et al. 2015, Seftom et al. 2015). Their general importance in more complex microbial communities, including those in aquatic ecosystems is still unclear. When it comes to species sorting, one study has shown that past environmental conditions can be better predictors of spatial differences in bacterioplankton communities than contemporary environmental conditions (Andersson et al. 2014). Specifically, differences in bacterioplankton composition between 16 rock pools were analysed and related to differences in environmental conditions between pools measured on the same day and 2, 4, 6 and 8 d prior to the sampling for bacterial composition. The study period covered a time interval during which a major rainfall event led to a decrease in the mean and variability of environmental variables in the pools. Using both distance-based approaches and variation partitioning, the authors showed that differences in environmental conditions (in particular, salinity) prior to the rainfall event explained more of the variation in bacterial community composition than the difference measured at time points after the rainfall event and those measured on the same day on which the communities were sampled. This is, to our knowledge, still the only study that has clearly shown that abiotic historical contingencies constrain changes in bacterial community composition at the metacommunity scale, even though it is not known for how long back in time these constraints exist. Time-lags of several days between environmental conditions and community responses have been observed in bacterio- and phytoplankton communities (Berga et al. 2012, Recknagel et al. 2013), suggesting that changes

in community composition lag behind changes in the environment. Based on this, one could presume that legacy effects should be transient; but this needs to be investigated further. To summarise, there is evidence that shows that legacy effects are important during the assembly of microbial communities, including those in aquatic ecosystems, but more work is needed to determine whether and to what extent and under which circumstances these mechanisms are important.

HOW TO MEASURE AND STUDY LEGACY EFFECTS

Above, we concluded that it is important to study legacy effects, which brings up the question how this can be done. In general, it is a major challenge to detect and quantify the importance of legacy effects. A huge limitation is that the often-applied statistical approaches mentioned above cannot efficiently and completely separate the relative importance of past dispersal events or past environmental conditions, which therefore remain hidden in spatial effects or are simply overlooked (Hanson et al. 2012, Lindström & Langenheder 2012). There are, however, new statistical tools that can help to decipher the importance of contemporary versus historical processes. For example, Leibold et al. (2010) developed and tested a quantitative framework on freshwater zooplankton, which should be applicable to microbial communities as well, that disentangles whether the phylogenetic structure of metacommunities is due to historical events (e.g. dispersal barriers, colonisation history, past environmental conditions) or more contemporary species sorting processes. Other methods, such as extended local similarity analysis (eLSA) (Xia et al. 2011, 2013) and similar network approaches (e.g. Faust et al. 2015) can identify time-delayed associations between occurrences of taxa and environmental variables. They might yield important insights into time-lags in species sorting processes structuring metacommunities if they can be expanded to include a spatial dimension as well. One way to investigate whether priority effects structure natural microbial communities is to include effects of past environmental conditions (Andersson et al. 2014), which, if found to persistently structure communities through time, provides indirect evidence that they are strong. For such field-based analyses to become possible, more temporal monitoring programmes of microbial communities at both local and particularly metacommunity scales (e.g. lake and stream networks) are needed, where environmental variables and dispersal rates

are measured at frequent sampling intervals. Finally, experimental approaches that actively manipulate historical processes such as dispersal events and past environmental conditions are inevitable as future tools to study legacy effects. Experiments could, for example, be designed to test how far back in time we can detect legacy effects independent of dispersal rates, environmental fluctuations and past disturbance events, and be used to investigate how factors influencing legacy effects differ among various groups of microorganisms in relation to traits that influence their dispersal ability and growth rates, ability to form resting stages, as well as their niche breadth, plasticity and adaptability.

SUMMARY AND PERSPECTIVES

It has previously been argued that snapshot ecosystem metrics are good proxies to explain regional variation in extant diversity, but can be misleading when analysing the drivers of biodiversity (e.g. Armitage 2015) because they overlook the importance of historical legacies. There is increasing evidence to suggest that legacy effects related to dispersal history and past environmental conditions are important in structuring microbial communities; however, their importance in complex natural communities is still unresolved. Here, working with microbial communities offers a major advantage because microorganisms have shorter generation times, which make field surveys and experiments that address legacy effects feasible. In particular, microbial communities from surface waters can be suitable targets for long-term monitoring programmes and tools for 'whole community experiments' because they are relatively easy to sample at regular frequencies and are commonly used in various experimental setups, such as micro- and mesocosm experiments or continuous cultures in a metacommunity setting (Logue et al. 2011). In conclusion, we believe that investigating the complex issue of legacy effects will provide important and useful insights into the regulation of the biodiversity of microorganisms. Legacy effects might further play an important role in predicting how microbial assemblages respond to different types of changes in the environment, such as anthropogenic climate change and/or pollution. We strongly believe that collectively investigating legacy compared to contemporary effects can result in a systematic framework on how ecological history shapes (meta)communities, to which aquatic microbial ecologists can make important contributions.

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