

The interplay between microevolution and community structure in microbial populations

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The structure of microbial communities is key to their functionality. However, this structure is likely to be influenced by adaptive genetic change in members of the community, which can occur over a matter of days. Changes in community structure can in turn influence the evolutionary trajectories of species within the community, further altering community structure. Microbial communities provide evidence for this interplay between rapid evolution and community structure. To date, studies are primarily limited to simple *in vitro* systems, but we suggest similar processes are inevitably operating in both natural and derived communities, which are important for biotechnology.

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Introduction

Microbial communities are key to a range of natural processes, ranging from health of their eukaryotic hosts [1] to global nutrient cycling [2]. This functionality has been exploited by industry for the production of food, biofuels and waste treatment [3]. Recent years has seen a growing interest in both understanding the functionality of these communities and ultimately designing communities with optimal functionality [3,4*,5,6]. Surprisingly, there has been little attention on the importance of rapid evolution in determining community structure and function in these applied contexts.

There is now unequivocal evidence that microbes undergo rapid evolutionary change such that evolutionary and ecological (*i.e.* changes in species composition within communities) time scales are often blurred [7]. As a result, rapid evolution (or microevolution) can potentially play a major role in the structure and function of microbial communities [8,9]. Community context can affect the

rate and trajectory of evolution of focal species within the community, which in turn is likely to be fed back into determining the community structure [8,9] (Figure 1). In this brief review, we discuss evidence for this interplay between microevolution and community structure in microbial communities. Although we are unaware of any work that explicitly addresses this interaction, evidence from experimental evolution studies in the lab provides a good foundation for considering how this potentially crucial issue is important in contexts directly relevant to biotechnology.

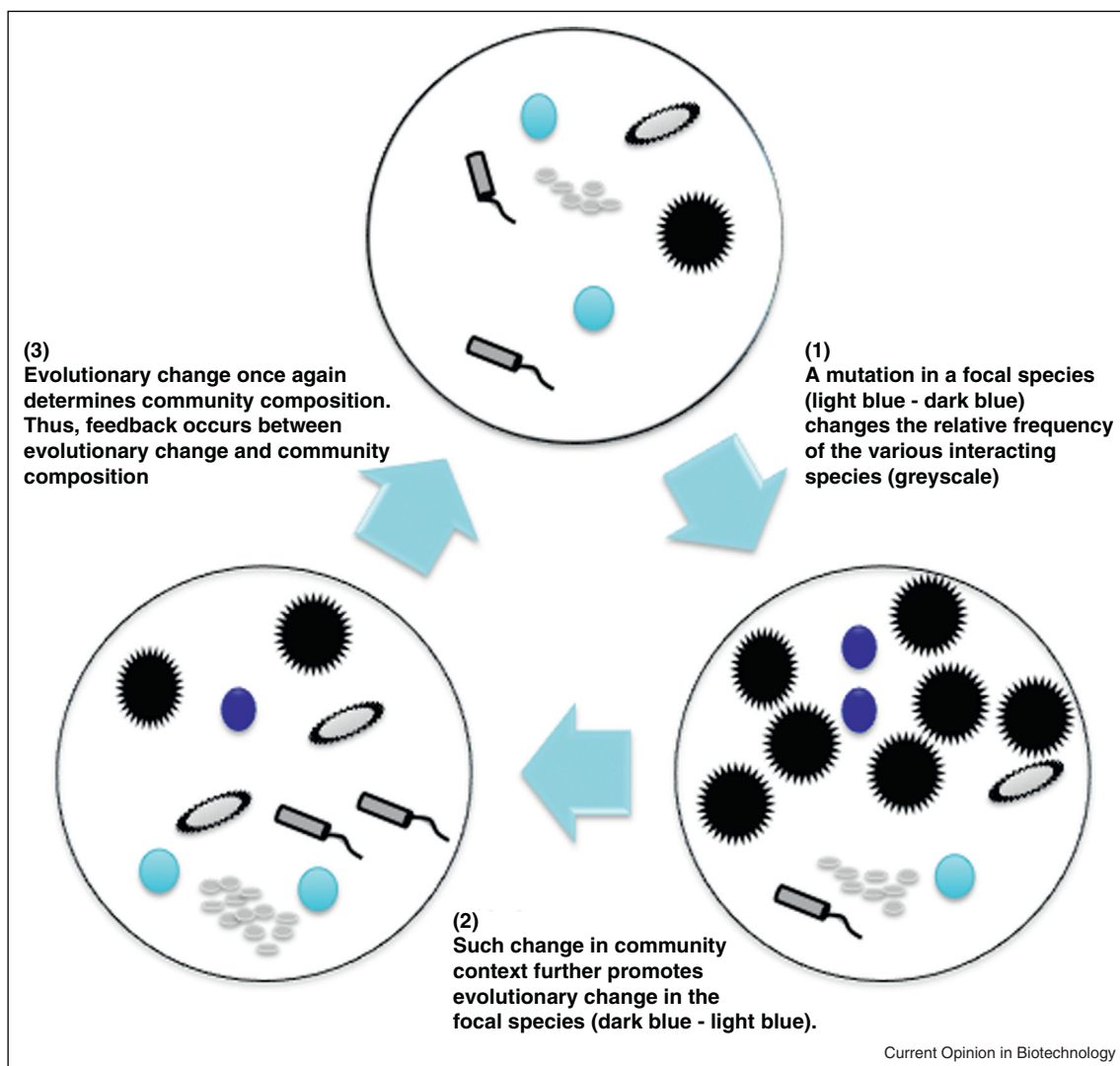
Rapid evolution on ecological timescales

Experimental evolution studies have shown real-time adaptive evolution in bacteria, viruses, fungi and algae [7,10–13]. Crucially, rapid evolution also occurs in more natural environments. For example, Köhler *et al.* [14] found that clonal infections of *Pseudomonas aeruginosa* rapidly evolved changes in their social behaviour in intensive care patients. Specifically, in a number of patients Quorum-Sensing (*lasR*) mutants arose from initially wildtype populations, and dominated infections over a matter of days. Another clinical study documented the evolution of rapid genetic diversity from initially clonal populations of *Escherichia coli* during relatively short-term infections [15]. Finally, a controlled evolution study in a more natural setting (soil, including the resident community) demonstrated that bacteria and viruses undergo reciprocal evolution of resistance and infectivity (antagonistic coevolution) over a matter of weeks; a similar time scale to that observed *in vitro* [16,17].

Community context affects evolutionary change

Species within a community are not distinct entities and interact in many different ways. Many of the clearest examples of interspecific interactions dramatically altering microevolution are where there are strong antagonistic interactions between species; one species has a very negative impact on the fitness of the other such as the effect of virulent parasites on their hosts. This is because highly damaging parasites impose strong selection for resistance, and if the parasite subsequently evolves to overcome this resistance (*i.e.* hosts and parasite coevolve), then parasite-imposed selection will be relatively continual [18]. For example, the bacterium *Pseudomonas fluorescens* and a ϕ 2 (a 40 kb ds DNA phage) have been shown to undergo continual cycles of resistance and infectivity [17], and this can dramatically alter the evolution of *P. fluorescens* traits not directly associated with

Figure 1



A mutation in focal species (light blue–dark blue) changes the frequency of the various interacting species. Such a change in the community context further promotes evolutionary change in the focal species, so that there is feedback between evolution and community context.

phage resistance, including ecological diversity [19], mutation rates [20] and intraspecific cooperative behaviours [21]. Other studies have shown that predators [22–24] and competitors [25,26,27] can also have a major impact on the short-term evolutionary trajectories of experimental bacterial populations.

Can we make any generalisations about the impact of community complexity on microevolution of focal species? A long-standing prediction is that interactions with other species should speed up evolutionary change, because other species create strong and continually changing selection pressures [28,29]. A number of studies support this prediction, including recent work using

P. fluorescens and phi2 that demonstrate more rapid (adaptive) molecular evolution in genes involved in phage attachment when coevolving with *P. fluorescens*, compared to when they evolved with a non-evolving host [30]. However, there is currently no empirical work to determine if this prediction holds in the context of interactions within whole communities as opposed to just one (or a few) enemy species. On the one hand, increasing the number of interacting species may result in even more rapid evolution, as selection acts on increasing numbers of traits. On the other hand, interactions with large numbers of species may instead constrain the rate of evolutionary change if adaptations to one species trade off with adaptations to other species.

While species interactions may (or may not) speed up evolution *per se*, perhaps a more relevant consideration for industrial processes such as waste treatment is how species interactions affect adaptation to the physical environment. The physical conditions within bioreactors change through time as a result of variation in the input of organic matter, and genetic adaptation to these changing conditions is likely to increase the rate at which substrates are broken down. Recent theory suggests that community complexity constrains genetic adaptation to the physical environment, because species sorting in response to environmental change (*i.e.* the most successful species increase in frequency) reduces the effectiveness of natural selection (*i.e.* sorting of genes within species) [31]. Experimental results are consistent with this general prediction, but not the specific mechanisms. For example, Lawrence *et al.* [26**] found that bacteria propagated within five-species communities evolved to feed on each other's excreted metabolites, but also grew less well in the absence of the rest of the community than did species evolved as monocultures. This suggests a trade-off between adaptation to biotic and abiotic components of the environment. A similar trade-off between biotic and abiotic adaptation has been demonstrated in viruses: adaptation to a thermally deteriorating environment was constrained when viruses antagonistically coevolved with their bacterial hosts compared to when hosts populations were held evolutionary constant [32]. In this example, reduced population size in the coevolving virus populations also contributed to poorer abiotic adaptation. It is however possible that community complexity may in fact enhance abiotic adaptation where horizontal gene transfer brings together beneficial mutations from different species into the same genome [33]. This is simple speculation, however, and demonstrates the need for research into how interactions among the natural microbial community may be altering the rate of evolution and consequently influencing the effectiveness of industrial processes that principally rely on microbial communities.

Microevolution affects community structure and function

Microevolutionary changes in individual species are likely to have little consequence for the functioning of entire communities, assuming the structure of the community remains relatively constant. However, it is well known from ecological studies of plants and animals that some species have disproportionately large effects on community structure as a whole, with their removal resulting in radical changes in community composition [34]. Moreover, not one, but all species are likely to be evolving within microbial communities. Rapid evolution is therefore likely to play a major role in structuring microbial communities. For example, rapid evolution in human gut microbiota might promote genetic diversity and alter mutualistic interactions between microbiota and host [35,36]. When bacterial diversity is high, there is

selection for the most competitive bacterial genotypes rather than the ones most beneficial to the host, destabilising the mutualism [35]. Furthermore, disturbances in microbiota diversity underlie diseases such as Crohn's disease, and research is now exploring the use of manipulation of gut microbial communities to treat these conditions, using probiotics and prebiotics [37,38].

Unfortunately, our understanding of the role of real-time evolution on community structure and function is very limited. *In vitro* experiments using simple predator–prey and host–parasite species convincingly show that rapid evolution can significantly alter population dynamics of the interacting species [39–41]. For example, by using a combination of mathematical models and experiments, the evolution of *E. coli* resistance to T4 phages was shown to be responsible for significant alterations in bacteria–virus population cycles and densities [39]. An even more obvious outcome of the evolution of host resistance to viruses is phage extinction [42]. The likely relevance of these *in vitro* studies has recently received support from a study of bacteria and virus dynamics in a wastewater treatment plant [43**]. Specifically, the relative abundance of operational taxonomic units (OTUs; based on 99% similarity of 16S rDNA) through time correlated with infective phage density such that increases in density of a bacterial group subsequently resulted in an increase in the density of phage infecting that particular group. Crucially, different host clones within a single OTU showed very different resistance profiles to phages isolated from different time points, which is consistent with rapid coevolution between bacterial resistance and phage infectivity altering population densities.

The importance of rapid evolution altering community structure is not only limited to interactions between trophic levels, but also operates within trophic levels. A recent study [44] showed how a two-species cross-feeding interaction between *Acinetobacter* sp. and *Pseudomonas putida* (*P. putida* fed on a waste product of the *Acinetobacter*) evolved to be more exploitative after a few days growth as biofilms. Evolved *P. putida* started to grow in closer proximity to the *Acinetobacter*, resulting in a negative impact on *Acinetobacter* growth, presumably as a result of increased competition for oxygen. Crucially, this evolved interaction, while having a negative impact on the *Acinetobacter*, increased total community biomass. Similarly, the mutualistic coevolution between a sulphate reducing bacterium, *Desulfovibrio vulgaris* and the methanogenic Archaeon, *Methanococcus maripaludis*, evolved to be 30% more productive (per mole of substrate) after a few hundred generations of co-culture [45**].

While demonstrating that rapid evolution can affect community structure, the above studies only demonstrate the impact of evolution on the interaction between two species within a community. We are aware of one *in vitro*

study [46^{*}] that shows that changes in two-species interactions (specifically bacteria and viruses, again) resulting from evolution can affect nutrient cycling. Surprisingly, studies that investigate the consequences of rapid evolution for 'real' communities are dominated by studies of large organisms. For example, a recent study has shown how past adaptive diversification of sticklebacks into distinct morphotypes can affect the structure and function of natural communities [47]. Specifically, distinct stickleback morphotypes (limnetic and benthic forms), that have repeatedly diversified in Canadian lakes around 10 000 years ago, were independently introduced into experimental mesocosms and the consequences for the density of prey species and a range of ecosystem traits were measured. While extremely elegant, this [47], and other related studies [9] do not demonstrate that evolution *in situ* can affect community structure on what are normally considered ecological timescales. Nonetheless, they provide a good justification for careful consideration of how rapid evolution may be disturbing microbial community structure, particularly in industrial processes where microbe community stability may be crucial.

Perspectives

The interplay between microevolution and community context is intricate, but imperative. Despite this, there have been no thorough studies investigating the interplay between real-time evolution and community structure in either natural or synthetic communities relevant to industry. Such studies are inevitably difficult, but much could be learnt from experiments and observations that compare real-time phenotypic and genomic evolution of a focal species and changes in community structure. Theoretical models could determine if generalisations about microevolution and community structure can be made, although the disadvantage is that they trade off generality for specificity. For example, is microevolution more important in changing the structure of relatively simple *versus* highly diverse communities? This question is crucial for determining the benefits of developing simplified synthetic communities to carry out defined functions, as opposed to using existing natural communities. The implications of rapid evolution in biotechnology are unclear, but could explain the change in function of industrial processes. While this review provides very few explicit answers as to the real importance of microevolution-community structure feedback, we hope it highlights its relevance to natural ecosystems, the importance of considering the issue in microbial biotechnology and finally, emphasises the need for novel approaches for further research in this area.

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