

# A concept highlighting the interplay between $\alpha$ -niche evolution and $\beta$ -niche evolution in bacteria

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When bacteria evolve new traits, this can be either to our benefit or harm. Trying to steer and control evolution in desirable directions is a major, but daunting aspiration of recent research. In natural systems and complex communities, however, it is repeatedly observed that trait evolution regularly deviates from predicted avenues suggested by *in vitro* experimentation on monocultures.

5 This pinpoints the effects of species interactions within microbial networks, which opens the door to use them to direct evolution. Unfortunately, this is not trivial; the impacts of ecological interactions between species within communities on evolutionary trajectories are not yet fully understood. Beside the introduced complexity caused by multiple species interactions, the nature of affected niches should also be important. When evolution of environmental  $\beta$ -niche traits (e.g.

10 pH adaptation or antibiotic treatment resistance) is of concern, biotic interactions may have little direct impact. However, evolution of resource-based  $\alpha$ -niche traits (e.g. broadened resource consumption) within competitive communities commonly is and could modify evolution of  $\beta$ -niches indirectly. Thus, co-evolving communities may display so far unprecedented opportunities to deflect trait evolution that cannot be achieved in other ways. Intelligent designed studies, building

15 on ecological and evolutionary principles, will be needed to move this field forward.

## Interactions between bacterial species impact evolution

Bacteria are one of the most diverse life forms on earth; evolving into an astonishing variety of ecological functions. In the environment they perform biochemical recycling which is vital to all food chains, linking higher trophic levels to the molecules required by primary producers (1). In host

20 microbiomes, they provide essential mechanisms to breakdown nutrients and form the first line of defence against pathogens (2). Besides these positive aspects of bacteria, there are malign traits that cause serious problems for health or food production (1). Issues arise when specific strains bloom and dominate communities (3). Current methods to fight bacterial pathogens mostly rely on externally

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<sup>1</sup> This work is building on a project called *EcoEvoComm* studying evolution in complex ecological communities with a first part published in Scheuerl et al. NatCom 2020. I conducted EcoEvoComm during my times at Silwood. From EcoEvoComm there are more works planned that will be indicated in this way to link them together.

25 applied antibiotics that either kill cells or stop growth. Unfortunately, such actions impose huge  
selection pressures on pathogens, and globally we observe rapid evolution of undesirable traits (4).  
Specifically, rapid evolution of resistance deprecates the power of our most important weapon to fight  
pathogens and we have few tools to prevent this (4). Directing, or even controlling, evolutionary  
trajectories to prevent evolution of unwanted traits, or to enhance desirable ones, is thus a major  
30 aspiration of current research.

With *in vitro* models we can follow the process of bacterial adaptation in real time and watch evolution  
in action (5, 6). To transfer our knowledge into natural settings, however, we still lack key  
understanding of principal processes (7). Unlike most *in vitro* experimental approaches, bacteria rarely  
evolve in isolation but co-evolve with many other organisms within in the same habitat (8). Even when  
35 bacterial communities are strongly disrupted by chemical addition, deterministic and stochastic  
processes combine to allow different species to survive. Along with newly arrived immigrants, species  
are then bound in a complex co-evolving ecological network during community re-assembly (3).

The role of the community on bacterial evolution is still of great debate and comes with many open  
questions (7). Species are known to exploit and fight each other using antimicrobial warfare, while  
40 supporting close alliances that provide benefits to them (9). This may affect the whole habitat or only  
congeners within close proximity (10). With constant conflict and species sorting, open or newly created  
niches, that are not filled by ecological release and new invasion, may rapidly be occupied by adaptive  
radiation if conditions are suitable (5). It is possible that in diverse communities, with many higher  
order interactions (i.e. those not involving the focal species), the surrounding biodiversity effect is  
45 diluted, allowing species to evolve with limited interference from other agents. But evidence  
accumulates that being embedded in a complex community leads to modifications of evolutionary  
trajectories and adaptive rates (8, 11, 12). There are studies that demonstrated evolutionary constraints  
with increasing biodiversity, e.g. by niche filling (8, 13). Other studies, however, suggested that co-  
occurring species facilitate evolution, e.g. by providing new niches via cross-feeding (12). While  
50 evidence accumulates that surrounding communities have an effect on evolutionary trajectories (8, 11–  
13), what this effect is, how important it is, and whether we can capitalize on it, are widely open  
questions (7).

### **When biotic interaction should have an impact on evolution, and when not**

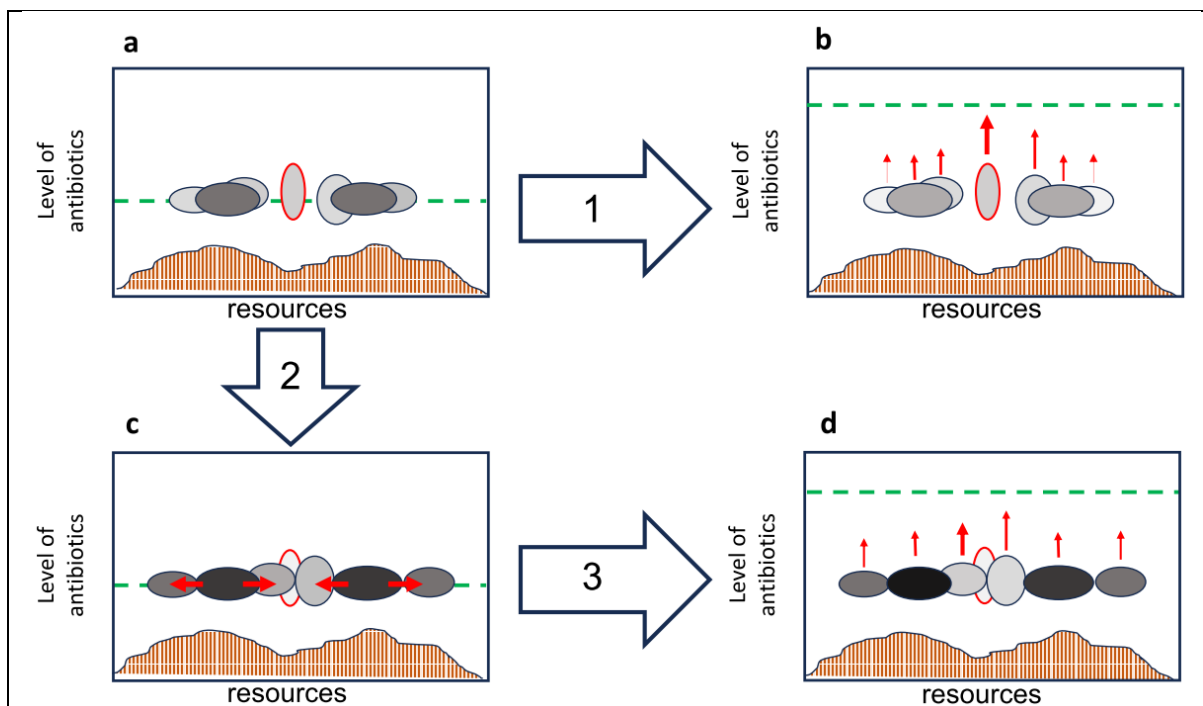
55 In principal, evolution increases with number of generations and its rate depends on the strength of  
selection and the presence of heritable additive genetic variance (14). Genetic variance is influenced by  
population size, mutation rate and mutation effect size, as well as recombination rate, whilst the strength  
of selection can be amended by ecological tolerance, phenotypic plasticity, the rate of environmental  
change and genetic covariances. Evolution proceeds at a faster rate when the selection gradient acting  
60 on phenotypes is steeper and the population harbours more additive genetic variance (15). The  
availability of suitable resources to grow and reproduce is a central theme during evolution, as changes  
can influence various aspects from population sizes and number of generations, experienced natural  
selection and expressed genetic variances including alterations of opportunities for adaptive radiations.  
Whilst we can measure evolutionary rates of single species when grown in manipulatable *in vitro*  
65 monoculture systems (16), this often fails for bacterial communities with hundreds of interacting species  
making individual measurements difficult.

Is there a biodiversity effect on evolution in general or do complex interactions cancel out? Important  
insight comes from studies exploring how heterotrophic bacterial communities evolve compared to  
species evolved in monocultures (9, 11, 13). One study shows how bacteria evolve facilitative  
70 interactions in simplified communities, using waste products from congeners to minimize resource  
competition, while mono-culture evolved species remain competitive (11). The study provided clear  
evidence that biotic interactions can indeed lead to different evolutionary outcomes. Another study

75 tracked evolution of focal species embedded in highly complex communities and found more adaptation in low-diverse communities, which suggests that niche filling constrains evolutionary potential (8). Another study, however, found that interactions facilitate adaptive evolution potentially via cross-feeding (12), so we have mixed results on this question. All studies so far, however, emphasise that biotic interactions between species have the capacity to alter evolutionary trajectories, but in different ways. For the alternative, that complex interactions are out-diluted, we have little evidence.

80 How then can we predict the impact of species interactions on the evolution of component species? To address this, we should conceptualize the niche space that a species inhabits with resources and environmental stressors. Species are e.g. located along a resource spectrum; this refers to the  $\alpha$ -niche (Fig. 1a). Differences in  $\alpha$ -niche traits permit coexistence between species, e.g. by partitioning resource use (14). When evolution drives trait changes around food, co-occurring species have a direct effect on each other by limiting or facilitating ecological opportunities in form of available resources.

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**Fig. 1. Conceptual illustration of two types of selection pressures.** Starting community of 7 species with their phenotype plotted on two niche axes; resources (shaded area on X-axis) and antibiotics level from externally supplied treatment (green line on Y-axis). The populations inherit variation in niche space (ellipses). (a) Species overlap in their niches but can potentially evolve to use new resources or resist increased levels of antibiotics. More abundant species are darker; a pathogen is indicated by the red circle. Antibiotics increase (b). All species experience selection (arrows) in the same direction ( $\beta$ -niches). Co-occurring species have little effect on antibiotic resistance evolution of the pathogen (red arrows), the pathogen harbours wide genetic variation and evolves substantially. Some species may have little evolutionary capacity (thin arrows) and go extinct. Niche space evolves (c). Species adaptively adjust their resource spectrum ( $\alpha$ -niches), which leads to direct interaction between the pathogen and the co-occurring species. E.g. the light grey species experience selection to shift to the centre because of competition with the darker species. Competition limits resistance evolution (d). When the level of antibiotics changes under niche overlap, competition may constrain resistance evolution. Now, population sizes are reduced, and interactions constrain ecological opportunities. Hence, diversity is predicted to have more direct effects on evolution when  $\alpha$ -niches are affected compared to  $\beta$ -niches. We stress that this is just a concept, and findings may reveal different or no effect.

Conversely,  $\beta$ -niche traits determine survival in a particular environment and tend to be experienced by co-occurring organisms in similar ways (14). Here, often abiotic environmental factors like the temperature or pH, or externally supplemented antibiotic treatment (which can be biotic when produced by other bacteria), come into play. Different species have different tolerances for such abiotic pressures, which limits or expands their habitat range. In such situations, a plausible prediction is that without niche-overlap adaptive trait changes are not amended (Fig. 1b); as long as a species is located in its own  $\alpha$ -niche (no or limited resource competition), and there is no direct interference (e.g. toxic secondary metabolites), there should be little effect of species interactions on how species evolve to  $\beta$ -niche changes. When, however, species compete for resources, initially vacant  $\alpha$ -niches can become filled by adaptive niche shifts or expansions (Fig. 1c). Here, the evolution to exploit vacant resources is impacted by biodiversity, caused by various changes in strength of selection and available genetic variances. Consequently, when competitors take ecological opportunity away in form of available resources, this should lead to an indirect reduction in evolutionary potential of  $\beta$ -niches, e.g. by reducing the population size (Fig. 1d). When competitors have opportunity to co-evolve and broaden their  $\alpha$ -niche, this should therefore impact  $\beta$ -niche evolution. Of course, alternative scenarios are possible; other species may excrete more waste products under abiotic pressure, thus extending resource availability and potentially enhancing resistance evolution. In complex co-evolved networks, however, these new opportunities are likely to be seized by many alternative competitor species.

### Worked example: Antimicrobial resistance

When we envision an elevation of abiotic stress, especially on microbiomes, a common place example is during the onset of antibiotic treatment. Here, a foreign chemical is introduced to the host at high concentration, either systemically or targeted, and sensitive bacteria must respond or perish (4). Depending on the antibiotic, an individual bacterium may evolve resistance (e.g. mutations in the topoisomerase/ DNA gyrase preventing fluoroquinolone binding, or mutations to increase efflux pump efficiency (17)) that renders the antibiotic ineffective in that individual. Resistance is usually associated with fitness costs (18). If, however, the individual can evolve to use more rewarding nutrients, within our framework, the costs will be more easily ameliorated. Thus, adaptation to consume resource niches, potentially made vacant by species susceptible to the antibiotic, is likely to promote evolution of resistances. Support of this comes from studies that found that selection of resistances is increased under resource fluctuation in mixed communities (19). Even when there is no option to escape the original  $\alpha$ -niche-space,  $\beta$ -niches may still evolve, but at a lower rate. As such, interactions between  $\alpha$ - &  $\beta$ -niche evolution are an important topic to be explored in the future.

In summary, we predict species' evolution of  $\beta$ -niches to be less impacted by community interactions when  $\alpha$ -niche competition is not involved (7, 14). With this concept in mind, approaches to seize evolutionary potential of communities to direct adaptation can be envisioned. Adding, or removing, specific species to direct evolution is a first avenue to attempt, but we consider approaches that allow the surrounding biodiversity to evolutionary shift into or away from niches of focal species as even more important as niche occupancy is fine-tuned by evolution. This could be enhanced by supplementation of specific resources.

Beside exploring the presented concept above, there are several more open questions as outlined below that are needed to be better understood.

### More detailed understanding of the effect of biodiversity on community evolution

So far, our knowledge about community evolution is still in its infancy and more data are needed. Not only is there a paucity of studies investigating evolution in a community context (7), we need more

studies that explore how interactions themselves evolve (9, 11). Interaction strengths and signs are ephemeral in different habitats and at different times, making their measurement difficult, and maybe even calls for new concepts. Two species may compete for resources in one environment but facilitate each other in a slightly modified environmental context (20), which raises the question how can  
140 transient interactions impact population dynamics. Moreover, how stable are they over evolutionary time scales? Laboratory based studies found evolution of neutral interactions starting from competitive situations; but then why are these competitive at all? Direct interactions, like excretion of toxic metabolites, are maybe easier to study as there are often quantifiable molecules that are used to kill competitors, but in low nutrient environments, as often found in nature, it is not clear how relevant this  
145 is (21). Finally, a clearer picture is needed how important population sizes are, if generalists or specialists are more evolvable, and how quantity and quality of resources impact evolutionary trajectories. Moreover, co-evolved networks may show greater stability against disruptive effects imposed by an invader. Directly interacting species in the co-evolved community may be potentially protected if better integrated into overall networks. The question about stability in co-evolved  
150 communities still needs to be much better explored, as evolution may either stabilize or destabilize communities (22), which implies the question if and when eco-evolutionary feedbacks are important in complex communities.

### **Characterizing “ecological opportunities” in greater detail**

155 With interactions based on resources, the difficulty is that environments hold thousands of different carbon molecules that may serve as food for heterotrophic bacteria. Regrettably only a tiny fraction of these molecules are described in detail and metabolic pathways characterized (23). Thus, large numbers of resources may potentially be available as niches that are currently completely unknown; without which however we are unable to accurately understand the  $\alpha$ -niche space in which these communities inhabit. Only if this vast number of resources can be described, and how they are metabolized by  
160 bacteria, will true understanding of ecological niches, and their role in microbial evolution be possible. Potentially recalcitrant resources may foster more collaborative interactions, but then key species are known that initiate breakdown of recalcitrant molecules resulting potentially in competition limiting diversity (24). Recent years have seen exciting new developments in describing the present resource  
165 molecules in environments; Ultra-high resolution mass spectrometry has unveiled molecular structures and thus has the power to elucidate how the vast number of potential resource niches could be used by bacteria (25). First results are very promising that these methods can give insight into microbial resource-niches in unprecedented detail (23). Ongoing works try to characterize this molecular diversity before and after bacterial activity and this will provide insight which resources are used, how they are  
170 partitioned and how they are metabolised. This knowledge will reveal how bacterial communities transform carbon in changing environments and elucidate mechanism as to how this affects ecosystem services in a world faced with global change.

### **The uneasy alliance of ecological and evolutionary research**

175 Blocking blooms of specific bacteria ecologically by adding bacterial communities is a straight forward idea (2) and developing pro-biotic food supplements building on this is an quickly expanding market. But a recent review concluded that probiotics are not yet effective enough (26). This is likely because ecological networks of interacting bacteria are fluid and newly assembled communities have not developed an interactive landscape robust enough to amend ecosystem process. First, resource-  
180 niche overlap may not necessarily be of the right extent. Second, species to fill particular niches may be missing. Third, niche-competitors may be present, but dampened within the community due to higher-order interactions, leaving a problematic species as the superior competitor. Recent research focus has concerned ecological mechanisms with a surprisingly low appreciation for the evolution of

185 species. As highlighted above, co-evolving bacterial communities can quickly adjust niche range (6, 11, 13); they evolutionarily occupy vacant niches and consume resources more broadly, therefore altering ecological dynamics. Applying the *ecology of communities* could thus be exploited to modify evolution of focal species by knowing how interactive networks permit broadest consumption of ecological opportunities. However, there are many additional unanswered questions for future research (Box 1).

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#### **Box 1. Future Research Directions**

There are a number of outstanding questions that need to be addressed to fully appreciate how these two ecological and evolutionary processes combine:

- In what conditions will species interactions amend evolutionary trajectories or not?
- Are higher-order biotic interactions important and what is the best way to measure them? Alternatively, are the main drivers pairwise, or widely simplified, interactions as envisioned previously?
- Do strong interactions have a pronounced effect compared to widespread weak or diffuse interactions among many species?
- Do facilitative interactions, where species rely on partners, increase or decrease the amount evolution in community contexts?
- Are negative (e.g. competition) or positive (e.g. mutualism) interactions on average more important?
- How does a mixture of interactions and higher-order interactions impact the process?
- What exactly are interactions and how can they be calculated so that experimental and theoretical works can better be combined?

When we think about resources as ecological opportunities:

- Which resources do different species use, and how do species within communities partition them?
- What can bacteria metabolize on their own and for what kind of resources are collaborative networks required?

#### **Concluding remarks**

195 We suggest that the concept of  $\alpha$ -niches and ecological opportunities in resource use are important for understanding  $\beta$ -niche evolution of species of interest. Community interactions provide vital information for the elucidation of evolution with a dynamic interactive landscape. Bridging the gap between ecological and evolutionary research will likely propel our ability to directly manipulate evolution in natural microbiomes.

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#### **205 Autor contribution**

TS conceived the idea of the work with input from DR, TB and TS developed the concept, TS wrote the first draft which was finalized by DR and TB.

#### **Declaration of interests**

210 No interests are declared

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