

Review

Evolutionary engineering of synthetic microbial consortia in bioproduction

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Microbial consortia offer significant advantages over monocultures in biotechnological applications, including access to a broader metabolic repertoire, functional redundancy and the capacity for division of labour. Adaptive laboratory evolution (ALE) has similarly proven to be a powerful tool in metabolic engineering, uncovering solutions inaccessible through rational design alone. Despite their individual potential, the intersection of ALE and synthetic microbial consortia in bioproduction contexts remains underexplored. This review examines recent advances at this intersection, with a focus on bottom-up synthetic consortia and co-cultures.

Artificial selection operates at organismal and supra-organismal levels in microbial communities, and this not only shapes their productive output, but it may also compromise the evolvability of costly production functions. This effect can be limited by engineering ecological interactions that stabilise community composition. ALE and synthetic consortia mutually expand each other's applicability through a variety of implementation logics. However, current approaches predominantly rely on growth-based selection, and we argue that implementing inter-community artificial selection strategies holds considerable untapped potential.

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Introduction

Biotechnology captures, isolates and modifies the metabolic activities of microbes and other organisms to integrate them in industrial processes. However, a key feature that is often missed in this process is the ecological and social context microbes operate in, which is an essential feature for their success as biochemical catalysts [1]. Microbes rarely operate in isolation. Instead, they form microbial communities that leverage an expanded catalogue of metabolic tools. Their functional redundancy makes them more resilient to exogenous fluctuations, and they can accommodate distributed pathway architectures that support division of labour and specialisation [2]. Although microbial communities have been part of many fundamental biotechnological processes, the field has only recently started to rationally implement consortia with defined, engineered activities [3–6].

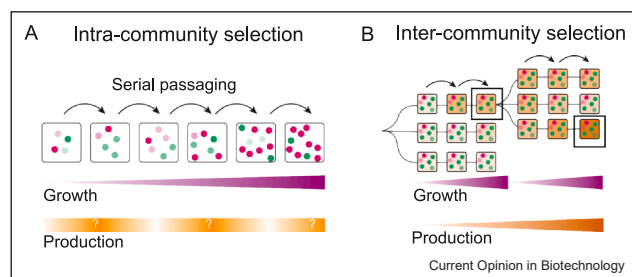
On the other hand, experimental evolution has driven essential progress in the field of metabolic engineering and bioproduction. It has unlocked engineering solutions that would not have been accessible from rational approaches with the available knowledge at the time [7–9]. More recently, experimental evolution has started to explore the solution space of microbial consortia in bioproduction applications [10,11]. Furthermore, synthetic microbial consortia have themselves been used as tools for designing tailored experimental evolution strategies in bioproduction contexts, expanding the range of possible targets [12–14].

In this article, we discuss recent advances at the intersection between experimental evolution and synthetic microbial consortia in a bioproduction context. This includes interventions aimed at improving the performance of production consortia, but also the use of consortia as a tool to design growth-coupled evolutionary interventions in a bioproduction context. We will focus on bottom-up synthetic consortia and co-cultures, rather than natural microbial communities or top-down consortia assembled from environmental isolates.

Artificial selection in microbial communities

Artificial selection strategies have been used for decades to engineer biological systems in situations where rational engineering becomes limiting [7,15]. Selection typically occurs at the gene and protein levels or at the cellular level, but it can also be applied to groups of

Figure 1



Two types of selection operate in microbial consortia. **(a)** Intra-community selection enriches a consortium in fast-growing clones, but this provides no guarantee of improved production. **(b)** Inter-community selection can be exerted if multiple communities are passaged in parallel, and the better-performing ones are propagated. This ensures direct selection of the desired production phenotype.

organisms, such as co-cultures or communities [16]. However, when groups of organisms are subject to artificial selection, we find that selective pressures operate at two levels. Individual cells are subject to intra-community selection: as communities are serially passaged, faster-growing clones take over the population [17,18]. This is the type of selection most frequently applied to bioproduction problems [19,20]. As communities are passaged in the desired conditions, their performance improves in terms of growth rate or saturation cell density (Figure 1a). However, growth improvements do not necessarily correlate with better production. In fact, intra-community selection may favour the emergence of “cheaters” that do not perform the production function but proliferate faster, or it may lead to the exclusion of a strain that is essential for bioproduction but it grows slowly. This is particularly relevant in the context of bioproduction, as functions are typically burdensome for the cell, making them more likely to be selected out [21,22].

A second layer of selection can be introduced to counter this effect. When several communities are subject to evolution in parallel, inter-community selection can be applied: communities are ranked in terms of how well they are performing the desired bioproduction function, and the better-performing lineages are further propagated (Figure 1b) [23]. This approach, however, is rarely applied in bottom-up synthetic consortia.

Bioproduction as a community function: implications for evolutionary engineering

The term ‘community function’ is used to describe an emergent process that is carried out collectively by a group of organisms, such as a bioproduction process that is catalysed by a microbial consortium [24]. This term highlights the intuitive idea that population composition

(i.e. the abundance of each species or strain in the community) impacts its productivity, and it can vary dynamically from inoculation to harvest. This phenomenon and its implications for bioproduction have often been discussed in the literature in terms of the impact of inoculation ratios in production co-cultures [25,26].

These changes in population composition result from ecological interactions within the community: they are trajectories in a community-function landscape where bioproduction activity is a function of population composition [27,28]. Ecological attractors shape these trajectories and, depending on their sign, they can lead to the competitive exclusion of community members or, conversely, can stabilise coexistence and minimise variations in population composition [29].

This has crucial implications for experimental evolution strategies: the bioproduction function that is being maximised varies not only as a result of inheritable changes (e.g. mutations), but it also responds to ecological trajectories in the population composition space, which may have limited inheritability. It has been argued that optimal adaptive evolution of microbial communities happens after a stable population composition has been achieved through serial passaging in the absence of selective pressure [18,27]. This plasticity in community population composition complicates the identification of mutations with a significant contribution to the target phenotype. In bottom-up consortia, the preferred approach involves isolating single clones from a bulk evolved population, characterising them and identifying inheritable changes [14,20]. However, this approach is inherently biased by selection and precludes a population-wide scan, potentially overlooking variants.

When working with synthetic microbial consortia for bioproduction, it is not unusual that one of the strains in the consortium carries a higher burden than the others, which can lead to its competitive exclusion after a sufficient number of generations [30,31]. Although this may not be apparent in a batch production process, it can become limiting when serially passaging a community in an ALE experiment. A frequent approach to limit the effects of population composition changes in ALE consists of introducing obligately mutualistic cross-feeding between strains [32–35]: each strain is auxotrophic for a metabolite that is provided by another strain, rendering them co-dependent and ensuring a stable coexistence of strains throughout the ALE course. Engineered auxotrophies also facilitate strain identification when isolating clones from the bulk evolved population, simplifying the assignment of mutations to their strain of origin.

This obligate cross-feeding strategy can also be used to expand the potential of ALE and explore a variety of

community- and strain-level traits beyond community-level growth. This has been leveraged for bioproduction applications by designing co-cultures with specific co-dependencies involving costly functions that would otherwise not be growth-coupled. Namely, production and secretion of a specific metabolite can be targeted for ALE by co-culturing the producing strain with an auxotroph for that metabolite [13,14].

What can evolution do?

In the last decade and a half, numerous theoretical works have described the effects of artificial selection on synthetic consortia and microbial co-cultures [32,35,36]. But how does this translate to bioproduction problems? In answering this question, new selection targets and intervention logics appear. We defined three types of interventions, based on the compositional context where evolution and bioproduction happen (Figure 2):

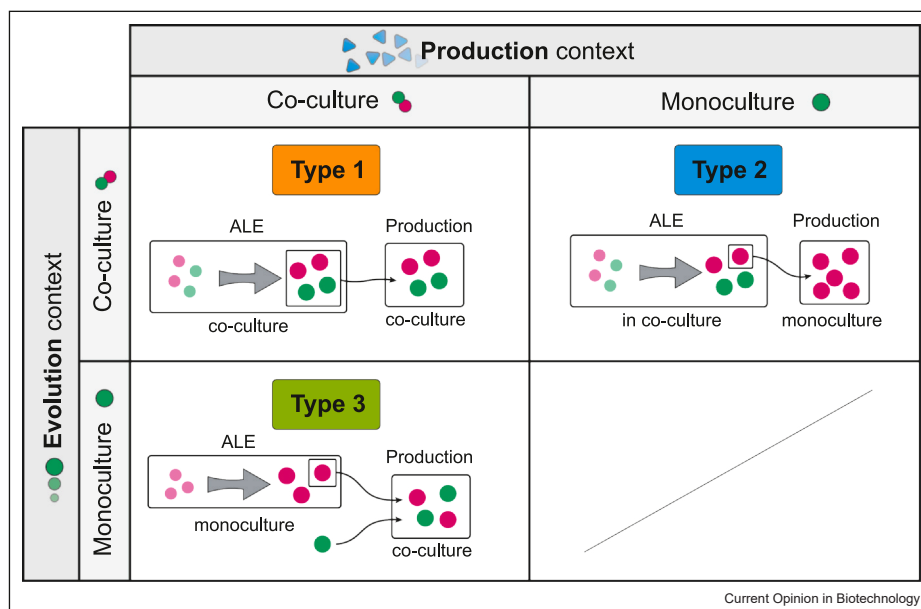
- *Type 1. Evolution and production in a consortium.* ALE is applied directly to a bioproduction consortium to improve its performance. In this case, both evolution and production happen in a consortium.
- *Type 2. Evolution in a consortium, production in a monoculture.* A synthetic co-culture is set up to apply selective pressure on a specific trait that is relevant for production, typically through an engineered mutualistic interaction. This evolved trait is later exploited for production in a monoculture.

- *Type 3. Evolution in a monoculture, production in a consortium.* ALE is applied to a monoculture of a specific strain to improve a trait that would later become relevant in the consortium setup used for production.

Examples of type 1 strategies are scarcer than others in recent literature. He et al. used serial passing to enhance assimilation and tolerance to non-protein nitrogen sources in a soil microbial consortium, to improve the performance of a valorisation bioprocess where agricultural residues were converted into high-protein feed [19]. In optimal conditions, the protein content of the final product increased from 2.7% to 10.4%. Similarly, Zou et al. evolved a *Ketogulonigenium vulgare* and *Bacillus cereus* co-culture by serial passing the co-culture to improve the production of 2-keto-gulonic acid, increasing yields from 77% to 93% [20]. In neither of these examples was there a selection strategy for the production phenotype (protein accumulation or 2-KGA production), but these traits evolved concomitantly with community-level growth (Figure 3). This approach based on intra-community selection was successful in both cases, as there was arguably a positive correlation between growth and the objective function, but it may be limiting in other scenarios.

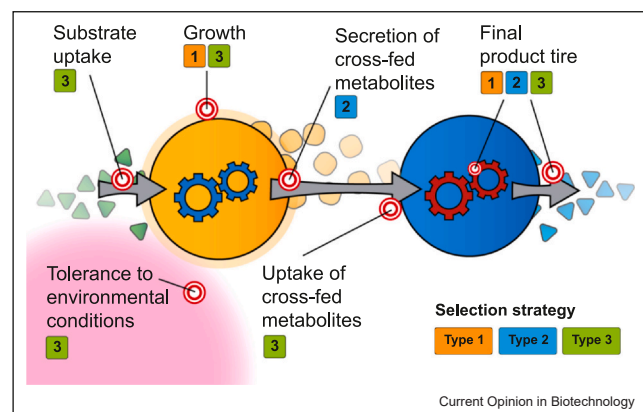
Recent examples of type 2 interventions include obligately cross-feeding co-cultures that were designed to

Figure 2



Three types of ALE interventions for bioproduction in consortia, depending on the compositional context of the evolution and production phases. Experimental evolution (ALE) can be deployed directly in the consortium (types 1 and 2) or in one of the strains in isolation (type 3). The evolved strains can be subsequently used in a bioproduction process either in a consortium (types 1 and 3) or in a monoculture (type 2).

Figure 3



Potential ALE targets in a 2-strain bioproduction co-culture. Current strategies target phenotypes that are specific to a co-culture, such as the uptake and efflux of exchanged metabolites, but also other general phenotypes that operate at a single-strain level (environmental tolerance, substrate uptake, growth, etc.). The most common selection strategies used in recent literature (type 1, 2 or 3) are indicated for each one of these targets.

improve the production or secretion of a specific metabolite (Figure 3). Zuchowski et al. built a 2-strain *Corynebacterium glutamicum* co-culture with reciprocal cross-feeding of arginine and leucine. Using ALE, they improved co-culture level growth rate by 23% and, upon closer study of the specific mutations supporting this, they identified non-obvious mutations that resulted in an increase of arginine production and export with potential interest for production applications. For this, they plated samples from the last ALE passage on arginine- or leucine-supplemented medium, and isolated six clones from each lineage [14]. Konstantinidis et al. followed a similar logic with an obligately mutualistic co-culture between *Saccharomyces cerevisiae* and *Lactobacillus plantarum* to identify clones with improved riboflavin production, some of them reaching a 14.4-fold increase over the parental strain [13]. Kawai et al. followed an analogous strategy for improved phenylalanine production and secretion in an *E. coli* co-culture [12].

In type 3 interventions, ALE is used in monoculture to improve traits later relevant to the performance of a production consortium (Figure 3). For example, Rafieenia et al. used ALE to improve citrate assimilation in one strain of a β -carotene-producing co-culture [39]. Similarly, Kawai et al. used ALE to improve mevalonate uptake in *E. coli*. This was later implemented in a split-pathway co-culture for isoprenol production, where mevalonate was an exchanged intermediate. The co-culture, including the evolved mevalonate consumer, achieved a 3.2-fold increase in isoprenol productivity in optimal conditions [37]. Xing et al. designed an ALE strategy to enhance the aroma of a

dairy beverage brewed with a co-culture of *Kluyveromyces marxianus* and lactic acid bacteria (LAB). To do this, they separately evolved a *K. marxianus* monoculture to improve its acid tolerance. This would later boost its growth and improve phenylethyl alcohol production by 28-fold under the acidic conditions generated by LAB [38]. Further examples of recent type 3 interventions were reported by Zhang et al. and Duan et al. [39,40].

Conclusions

Microbial communities, consortia and co-cultures are gaining traction as platforms for bioproduction [2], and promising applications are emerging in their intersection with evolutionary engineering. In parallel, a substantial body of work in microbial ecology and synthetic ecology has begun to explore artificial selection and directed evolution of microbial communities [41,42]. The convergence of these two trends suggests the field is primed for rapid progression.

Despite the availability of strong theoretical backgrounds to design artificial selection strategies in groups of organisms, current ALE approaches for bottom-up synthetic consortia mostly rely on serial passaging without artificial inter-community selection for production traits. Although this growth-based approach has proven useful for a range of problems [12–14], an adequate implementation of *ad hoc* artificial selection strategies has the potential to unlock radically new solutions.

ALE is being used to tackle bioproduction problems from a variety of angles, including decoupled approaches where evolved traits are transferred between co-culture and monoculture setups. This type of work highlights how ALE can expand the possibilities of consortia in bioproduction, but also how consortia can reciprocally broaden the applicability of ALE for metabolic engineering problems.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

We declare that we have no known financial, personal, or professional conflicts of interest that could have influenced the work, analysis, or conclusions presented in relation to COBIOT.

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