



# Deciphering microbial community robustness through synthetic ecology and molecular systems synecology

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Microbial ecosystems exhibit specific robustness attributes arising from the assembly and interaction networks of diverse, heterogeneous communities challenged by fluctuating environmental conditions. Synthetic ecology provides new insights into key biodiversity–stability relationships and robustness determinants of host-associated or environmental microbiomes. Driven by the advances of meta-omics technologies and bioinformatics, community-centered approaches (defined as molecular systems synecology) combined with the development of dynamic and mechanistic mathematical models make it possible to decipher and predict the outcomes of microbial ecosystems under disturbances. Beyond discriminating the normal operating range and natural, intrinsic dynamics of microbial processes from systems-level responses to environmental forcing, predictive modeling is poised to be integrated within prescriptive analytical frameworks and thus provide guidance in decision-making and proactive microbial resource management.

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**Current Opinion in Biotechnology** 2015, **33**:305–317

This review comes from a themed issue on **Environmental biotechnology**

Edited by **Spiros N Agathos** and **Nico Boon**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 14th April 2015

<http://dx.doi.org/10.1016/j.copbio.2015.03.012>

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## Introduction

From the enzymatic to the global scale, biological robustness is a key attribute of biosystems that guarantees the maintenance of structural organization and/or function performance in the face of disturbances and uncertainty. A brief survey of the Earth's biogeochemical history after the first stirrings of the Industrial Revolution shows a broad range of anthropogenic and natural perturbations that have been triggering specific biological responses and ecosystem state transitions, up to the ultimate point of sudden collapse [1]. The intrinsic principles and mechanisms of microbial robustness have drawn special

attention because microbial communities can provide host protection against diseases [2,3] and lie at the heart of biological processes that fulfill the premise of sustainable development. With the translation of the microbial resource management concept into practical applications [4], microbial communities also play crucial roles in the cradle-to-cradle approach by supporting the valorization and recycling of natural resources, man-made products and their wastes.

Microbial robustness has mainly been addressed from an autecological perspective by identifying the key features and biomarkers of clonal microbial populations that promote robust industrial and biotechnological processes, for example, modularity of metabolic networks, fault tolerance (enzyme redundancy and promiscuity), self-repair and protection systems (DNA repair and antioxidant activity) [5]. However, the metabolism, growth and robustness of individual microbial populations differ significantly when they are living within dynamic consortia characterized by intricate networks of intra-population and inter-population interactions. Because microbial community members are faced with a composite set of extracellular metabolic cues, display dissimilar or redundant functional traits and exchange genetic material and nutrients, the activities of most microbial communities cannot be exclusively attributed to any of its individual phylotype components. Many essential microbial partnerships occur in nature, such as the cooperative biodegradation of trichloroethene (TCE) through syntrophic associations and cofactor exchanges [6]. Because microbial consortia have the potential to achieve more diverse and robust functions than single taxa grown in isolation, there is a compelling impetus to move from population-based analysis to synecological (i.e., community-centered) approaches to study microbial resources within the context of natural or engineered systems. Cryoconservation strategies have recently been optimized for the stable preservation of ecologically-relevant and industrially-relevant microbial consortia to complement the vast collection of pure culture strains [7]. Supported by the experimental evidence of the link between microbial diversity, productivity and robustness, the production of next generation, polymicrobial probiotics (i.e., microbial ecosystem therapeutics [3]) to substitute for single-strain probiotic formulations is an elegant example of the quest for more robust and optimized microbial-driven services.

With the development of new molecular technology platforms and bioinformatic pipelines and the recent

advances in microbial ecological theory [8\*,9\*\*,10\*], new hypotheses can be formulated and tested to develop predictive models of microbial robustness in controlled, artificial communities and ultimately more complex natural ecosystems. Synthetic ecology, that is, the rational design and theory-driven manipulation of artificial microbial ecosystems [11], is an emerging approach for robustness prediction thanks to the analysis of replicate systems of lower complexity and higher controllability and reproducibility in the presence of specific perturbations. Similar to molecular (eco)systems- or community systems biology [12,13], molecular systems synecology seeks to achieve a systems-level understanding of community structure and function emerging from dynamic interactions and networks under different environmental scenarios. This holistic approach focuses on systems biology at the community level by integrating meta-omics techniques, computational systems bioinformatics and synecology (from the Greek *syn-* together, united and ecology, i.e., analysis of the activities of an entire natural or synthetic community as a whole and forming a unified functional entity). Engineered maintenance and perturbation studies in multiplexed continuous culture systems are particularly relevant to molecular systems synecology in order to single out and compare the effect of specific perturbations on microbial communities maintained under controlled, reproducible and environmentally-relevant conditions. The predictive models of robustness developed at the lab scale for synthetic and more complex communities can then be extended to natural microbiomes with the combination of multi-scale modeling of metabolic or hydrogeochemical processes [11].

This review provides a comprehensive overview of microbial community stability and robustness and is structured as follows: (i) dynamics and function of microbial communities under normal (undisturbed) conditions, (ii) the epistemology of microbial community robustness in the presence of disturbances, (iii) the mechanisms of microbial community robustness, (iv) the post-disturbance states of the systems and finally (v) the development of mathematical models to facilitate the assessment and prediction of microbial community robustness. We highlight the need for quantitative community-level benchmarks of multiple microbial ecosystems in confined and open systems to discriminate natural dynamics (baseline) from community changes under the impact of environmental forcing factors, either natural or anthropogenic. We also emphasize the multi-faceted dimension of microbial community robustness with the description of its epistemic framework and give an overview of the conceptual and mechanistic principles governing community robustness. Finally, the prediction of systems-level robustness of microbial ecosystems is discussed in the light of molecular systems synecology using network inference and dynamic modeling of meta-omics data sets.

### **Benchmarking in microbial ecology: microbial community dynamics and function under normal (undisturbed) conditions**

Before investigating the robustness of a microbial community towards a specific disturbance, its temporal stability (i.e., constancy in structure (see Box 1, [14]) and function over time) must be deciphered to define structural and functional pre-disturbance benchmarks (reference states) against which community robustness will be assessed (Figure 1). Perturbation-independent stability requires the description of the system (reference state of biological variables (descriptors) and environmental parameters) and the specification of its natural dynamics in terms of structure and function [15]. Similar to the normal operating range (NOR) concept of soil functioning [16], the normal limits of variation of microbial community processes under reference conditions are a prerequisite to properly assess the disturbance-specific responses of microbial ecosystems. A functional reference state with permissible limits of variation (i.e., engineering tolerance) can be obtained from (i) bulk chemical measurements (e.g., denitrification and nitrification rates [17,18]) or (ii) the definition of a functional core microbiome with quantifiable crucial traits using community-level functional diversity metrics [2,19]. A structural reference state defined on the basis of a core set of phylotypes identified for a target microbial habitat (i.e., a core microbiome in terms of specific microbial phylotypes) is more difficult to achieve because of the intrinsic dynamic nature of microbial communities (temporal and spatial structural variation). A set of shared metabolic traits across microbial habitats is frequently detected (e.g., human gut [2], activated sludge), notwithstanding high levels of variability in phylotype composition. As stated by Verstraete *et al.* [20], even under functionally stable conditions, microbial ecosystems display a cooperative community continuum with continuous fluctuations of community composition and population abundance. A comprehensive survey of the temporal variability of different microbial habitats using targeted sequencing of 16S rRNA genes (illumina-based 16S-tags (*iTags*) or 16S pyrosequencing (16S *pyrotags*)) demonstrated species-time relationships (STRs) with consistent temporal scaling exponents ( $\omega$ ) across similar environments ( $\omega$  ranging from 0.24 to 0.61, see Box 1) [21]. Comparable  $\omega$  values generated from pyrotags analysis were obtained for a full-scale activated sludge system (ranging from 0.38 to 0.45 as a function of the targeted 16S region) highlighting significant phylotype turnover rates [22].

Microbial communities also present intrinsic temporal variability in controlled lab-scale bioreactors under continuous or semi-continuous conditions. In a functionally-stable denitrifying continuous culture maintained in a chemostat for 50 days, Kraft *et al.* [23] observed that microbial communities can be highly dynamic in composition but achieve stable functional outputs thanks to the

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