COMMENTARY

Microbial self-recycling and biospherics

Matthias C. Rillig^{a,b,1}⁽, Janis Antonovics^c⁽, and India Mansour^{a,b}

Microbes are well known as potent recyclers of leftover biomass in ecosystems, preventing nutrient cycles from simply getting stuck (1). However, a lot less is known about how microbes can recycle themselves, their own biomass. This is highly relevant, because microbes don't often find themselves in front of a lavish buffet, but rather have to eke out a living at the edge of nutrient and energy starvation. In their paper in PNAS, Shoemaker et al. (2) examine the ability of populations of bacteria to recycle their own biomass, elegantly combining long-term experiments with modeling. The authors enclosed 100 populations from 21 different taxa individually and followed their fate for 3 y—all in the absence of matter or energy inputs. They find that almost all populations (except for one) survived, with extinction times estimated often in decades and far exceeding what would be expected from individual longevity under conditions of resource limitation. Thus, in many of the bacterial strains, when individuals die, living individuals can use the dead biomass of other individuals to increase their own survival and reproduction, thus greatly prolonging population persistence.

These results are relevant to many questions in environmental microbiology. For example, this recycling ability, and thus the ability to maintain oneself during periods of adversity, may be part of the remarkable resilience of microbially driven processes (3), which can frequently bounce back from a range of environmental insults. Necromass, that is, dead microbial cells, is increasingly a focus of work on soil organic matter storage (4, 5), an important ecosystem process, and it is very important to understand what factors control the maintenance or disappearance of these dead microbial remains, including how efficiently microbes can recycle themselves.

But there is another context in which these results are highly relevant, and which the authors themselves mention (2): the realm of microbial biospherics, that is, matter-closed energy-open microbial miniecosystems (6) (Fig. 1). A central question in such biospheres is



Fig. 1. Possible progression of studies of microbial biospherics (matter-closed microbial miniecosystems), taking the paper by Shoemaker et al. (2), which examines recycling of microbial necromass of single strains, as a starting point (*A*; living bacteria and necromass, i.e., dead bacterial cells). This approach could be extended to other microbial groups, for example, fungi or protists (*B*). Using simple environments, necromass recycling and system persistence could be explored for species pairs within (*C*; interacting bacteria and fungi) or across trophic levels (*D*; protists feeding on bacteria). Studies could eventually include more-complex environments (including, for example, artificial soils) and microbial consortia (*E*), and even explore the effects of aspects of global change (*F*; red, microplastic particles).

how cycling of matter can be maintained in the absence of external subsidies, and the present study is particularly interesting in this context. Granted, their systems were, by necessity, not strictly completely matter closed, because of the need to periodically sample the bacterial populations, but these quasiclosed systems can nevertheless provide insights into potential behavior of populations in the absence of any obvious inputs in terms of matter or energy, and that can help propel this field of research.

In their paper, Shoemaker et al. (2) characterize a rather large set of strains from 21 different species, and this is one of the features that sets this study apart in terms of scope and applicability of the results. Some

^aInstitut für Biologie, Freie Universität Berlin, D-14195 Berlin, Germany; ^bBerlin-Brandenburg Institute of Advanced Biodiversity Research, D-14195 Berlin, Germany; and ^cDepartment of Biology, University of Virginia, Charlottesville, VA 22904

Author contributions: M.C.R. designed research; J.A. and I.M. performed research; and M.C.R., J.A., and I.M. wrote the paper.

The authors declare no competing interest.

Published under the PNAS license.

See companion article, "Microbial population dynamics and evolutionary outcomes under extreme energy limitation," 10.1073/pnas.2101691118. ¹To whom correspondence may be addressed. Email: rillig@zedat.fu-berlin.de.

Published September 7, 2021.

exciting next steps would be to try to extend the approach to other organism groups. One group that immediately comes to mind is saprobic fungi, also extremely important decomposers. Would fungi also be able to "recycle" themselves for such a long time? Would evolutionary rates be rather different in these often effectively diploid eukaryotes?

An interesting open question in microbial biospherics research is the influence of evolutionary processes on system stability/ persistence. The degree to which "evolutionary novelty" will change the trajectory of such systems, and increase or decrease their stability, remains unknown, but this study reinforces the expectation that it is likely: The authors report clear evidence of evolutionary changes in five out of the seven strains where divergence among replicate populations was studied (2). Furthermore, rapid evolutionary changes under stressful conditions (7) are well documented in many systems, and the occurrence of a similar phenomenon here suggests that simple dynamical modeling may not be adequate to predict long-term persistence.

It would also be interesting to know the reason for the differences in the ability of different populations and species to recycle their own necromass. A logical extension would be to examine species mixtures, especially those with contrasting metabolic abilities (Fig. 1). Will pairs of strains be able to increase efficiency of necromass recycling, or will particular species interactions, such as cross-feeding, expand or contract the niche space of component taxa (in terms of, for example, utilizable necromass components), and how might these interactions affect their evolutionary trajectories (8)?

Another direction would be to take this approach to look at the effect of environmental heterogeneity on persistence, thus moving up to understanding a system colonized with a full complement of a microbial community of decomposers (Fig. 1). One example would be to introduce single soil aggregates, complex

In their paper in PNAS, Shoemaker et al. examine the ability of populations of bacteria to recycle their own biomass, elegantly combining long-term experiments with modeling.

microhabitats colonized by a range of microbes (9), into such biospheres and study their ability to maintain long-term activity in the absence of external inputs. Such work would go full circle to the classical experiments in biospherics (10) that used complex aquatic systems, like pond water, but scaled down to a much smaller size. Microbial biospherics systems are also ideal arenas in which to dig into mechanistic questions about the effects of global change factors because they can serve as miniature arenas in which to investigate changes in community dynamics and ecosystem functioning. Within such complex communities and miniecosystems, it will be fascinating to link ecosystem process rates to microbial recycling and the fate of individual populations (11).

Acknowledgments

This work was supported by European Research Council Advanced Grant 694368 (to M.C.R.) and a Humboldt Research Award (to J.A.).

- 1 R. Bardgett, The Biology of Soil: A Community and Ecosystem Approach (Oxford University Press, 2005).
- 2 W. R. Shoemaker et al., Microbial population dynamics and evolutionary outcomes under extreme energy limitation. Proc. Natl. Acad. Sci. U.S.A. 118, e2101691118 (2021).
- 3 A. Shade et al., Fundamentals of microbial community resistance and resilience. Front. Microbiol. 3, 417 (2012).
- 4 C. Liang, W. Amelung, J. Lehmann, M. Kästner, Quantitative assessment of microbial necromass contribution to soil organic matter. Glob. Change Biol. 25, 3578–3590 (2019).
- 5 K. M. Buckeridge et al., Environmental and microbial controls on microbial necromass recycling, an important precursor for soil carbon stabilization. Commun. Earth Environ. 1, 36 (2020).
- 6 M. C. Rillig, J. Antonovics, Microbial biospherics: The experimental study of ecosystem function and evolution. Proc. Natl. Acad. Sci. U.S.A. 116, 11093–11098 (2019).
- 7 A. A. Hoffmann, M. J. Hercus, Environmental stress as an evolutionary force. Bioscience 50, 217–226 (2000).
- 8 L. Oña et al., Obligate cross-feeding expands the metabolic niche of bacteria. Nat. Ecol. Evol., https://doi.org/10.1038/s41559-021-01505-0 (2021).
- 9 B. Wang, P. E. Brewer, H. H. Shugart, M. T. Lerdau, S. D. Allison, Soil aggregates as biogeochemical reactors and implications for soil-atmosphere exchange of greenhouse gases—A concept. *Glob. Change Biol.* 25, 373–385 (2019).
- 10 F. B. Taub, Closed ecological systems. Annu. Rev. Ecol. Syst. 5, 139–160 (1974).
- 11 E. K. Hall et al., Understanding how microbiomes influence the systems they inhabit. Nat. Microbiol. 3, 977–982 (2018).