PNAS COMMENTARY OPEN ACCESS

# When energy is scarce, evolution selects dormancy

Christopher P. Kempes[a,b,1]

Endospores represent one of the most fascinating strategies among bacteria. As resources become scarce, certain species are able to produce a dormant state in which a thick proteinaceous coat protects the core genome along with a small number of ribosomes and enzymes capable of "rebooting" the cell if conditions become favorable again. The endospore is remarkably resilient, capable of withstanding impressive levels of UV radiation and extreme temperatures, pressure, salinity, antibiotic levels, and caustic chemicals (1). This resilience confers very long environmental half-lives, with several documented cases of survival on the order of $10^4$ years and arguments that endospores can remain viable for up to 100,000 y (2). Endospore formation, and dormancy more generally, has long been argued to be an evolved bet-hedging strategy (3, 4). If this is the case, then what evolutionary trade-offs are associated with this strategy, and what evidence would confirm that the strategy is under positive selection? This is the framing that Karakoç et al. use in their paper on the evolutionary strategy of endospores (5).

There is a thread of evolutionary theory that emphasizes energy as a key limitation for all functions of an organism. The formal connection between energy and evolution traces back to Lotka, who said "… natural selection will so operate as to increase the total mass of the organic system, to increase the rate of circulation of matter through the system, and to increase the total energy flux through the system …" (6). Evo-energetic thinking had an explosive period of growth in the middle of the last century as bioenergetics was formalized as a field (7, 8), and has had a recent renaissance as many point to the need to catalog the connection between energy, traits, and evolution (9–13). In bacteria, successful applications of this framing have included bottom–up calculations of maintenance costs, the derivation of interspecific growth-rate scaling relationships, and work showing that even the minuscule cost of copying a nucleotide into the next generation is "visible" to evolution (11, 13–15). Microbial evolution under low-energy conditions, a common occurrence in competitive and variable environments, is also known to shape the evolutionary dynamics and the selected traits in these populations (16–18). In mammals and plants, metabolic scaling theory has argued that traits are optimized for metabolism under physical constraints (9), and explicit evolutionary work has shown that the observed scaling relationships are selectable (19, 20). Such diverse work points to a new field coupling energy and evolution.

Much work in theoretical biology accounts for the utility of particular strategies or traits in an abstract setting. Often general models identify key trade-offs and concepts and are applicable to systems ranging from bacteria to language evolution. Migrating these ideas to more quantitative predictions requires a coupling with explicit environmental and physical constraints. The connection with energy and matter, as key limitations, allows for new quantitative predictions. The paper by Karakoç et al. is a wonderful example of the added traction a connection with energy gives to an ecological and evolutionary question.

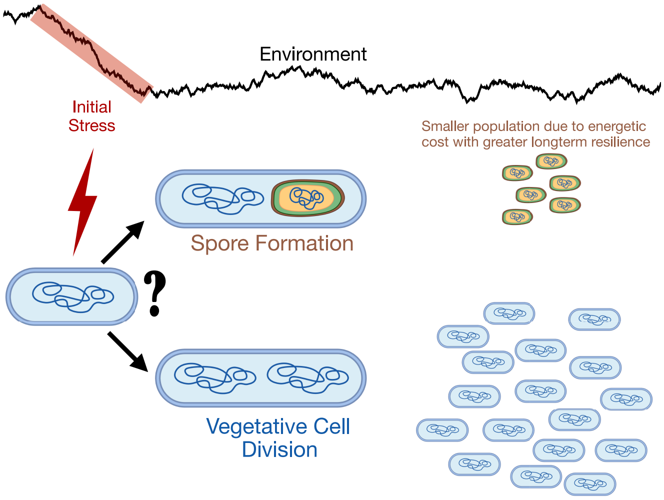

**Fig. 1.** The evolutionary trade-offs between spore-forming and vegetative cells under environmental energy limitations as presented by Karakoç et al. (5).

Karakoç et al. demonstrate that the entire spore life cycle accounts for 10% of the energy budget of a cell. In their comparison with other cellular traits, they show that spore costs are greater than the costs of membrane lipids and the flagellum, the next two costliest features in their analysis. The authors point out that the key question is whether such a costly investment is useful given that the spore-forming strategy is initiated when energy availability is most limited. The answer should be "yes" because we observe the strategy, but the burden of evolutionary bioenergetics is to show explicitly that the benefits outweigh the costs. The authors combine an impressive array of approaches to convince us that this trait has been selected for in the

Author affiliations: [a]The Santa Fe Institute, Santa Fe, NM 87501; and [b]Complexity Science Hub, Vienna 1030, Austria

---

Author contributions: C.P.K. designed research; performed research; and wrote the paper.

Competing interest statement: C.P.K. is a visiting faculty at Google. The company had no role in conceptualization, decision to publish, or preparation of the manuscript.

See companion article, "Evolutionary bioenergetics of sporulation," 10.1073/pnas.2524274123.

[1]Email: ckempes@santafe.edu.

context of environmental scarcity. First, they consider the cost comparison of cells with and without spore-forming strategies. A key result is that the majority of the cost of spore formation is the opportunity cost of diverting resources away from active growth. Even under this key trade-off, spores are still advantageous. They then develop a model for population dynamics that demonstrates the relative advantage of spore-formers. Finally, they perform quantitative evolutionary calculations and genome comparisons to argue for the benefit of the trait.

> **Karakoç et al. is a good example of the burgeoning field of evolutionary bioenergetics which is opening up an exciting new avenue where the concepts of evolutionary theory meet with physical constraints to make more detailed and quantitative predictions of physiology, traits, strategies, and cellular processes.**

The paper offers a variety of broad conceptual points and detailed quantitative predictions, which should not be completely repeated here, but I do want to highlight that the framework is immediately useful for many future directions. For example, a key metric that Karakoç et al. use is the break-even time between vegetative cells and spores, which is given by the ratio of the cost of spore formation to maintenance costs. We know that both of these costs should systematically change with cell size (11, 14, 15), and we should expect this ratio to follow a scaling relationship with cell size. Specifically, spore costs might be expected to be proportional to protein abundance, which scales with cell size with an exponent of 0.70 (11), while maintenance costs scale linearly with cell volume (14, 15). Thus the break-even time should scale with an exponent of $-0.30$, becoming shorter and shorter for larger-celled species. In the logic of Karakoç et al. this scaling calculation should imply the smallest bacterial cell size where spore formation is a viable strategy, and below this limit we should not observe spore-forming species. This is one simple example of the types of extensions that one can make with an energetic framework in hand.

The paper by Karakoç et al. is a good example of the burgeoning field of evolutionary bioenergetics that is opening up an exciting new avenue in which the concepts of evolutionary theory intersect with physical constraints to make more detailed and quantitative predictions of physiology, traits, strategies, and cellular processes.

**ACKNOWLEDGMENTS.** C.P.K. thanks S. E. Kern for useful comments. Aspects of Fig. 1 were produced using BioRender under license EZ29EIMDJZ.

1. P. Setlow, G. Christie, New thoughts on an old topic: Secrets of bacterial spore resistance slowly being revealed. *Microbiol. Mol. Biol. Rev.* **87**, e00080-22 (2023).
2. A. D. Williams *et al.*, Ancient environmental microbiomes and the cryosphere. *Trends Microbiol.* **33**, 233–249 (2025).
3. J. T. Lennon, S. E. Jones, Microbial seed banks: The ecological and evolutionary implications of dormancy. *Nat. Rev. Microbiol.* **9**, 119–130 (2011).
4. L. P. Morawska, J. A. Hernandez-Valdes, O. P. Kuipers, Diversity of bet-hedging strategies in microbial communities—Recent cases and insights. *WIREs Mech. Dis.* **14**, e1544 (2022).
5. C. Karakoç, W. R. Shoemaker, J. T. Lennon, Evolutionary bioenergetics of sporulation. *Proc. Natl. Acad. Sci. U.S.A.* **123**, e2524274123 (2026).
6. A. J. Lotka, Contribution to the energetics of evolution. *Proc. Natl. Acad. Sci. U.S.A.* **8**, 147–151 (1922).
7. H. J. Morowitz, *Energy Flow in Biology: Biological Organization as a Problem in Thermal Physics* (Academic Press, New York, 1968), p. 179.
8. M. Kleiber, *The Fire of Life: An Introduction to Animal Energetics* (Wiley, New York, 1961), p. 454.
9. C. P. Kempes, M. Koehl, G. B. West, The scales that limit: The physical boundaries of evolution. *Front. Ecol. Evol.* **7**, 242 (2019).
10. X. Yang *et al.*, Physical bioenergetics: Energy fluxes, budgets, and constraints in cells. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2026786118 (2021).
11. C. P. Kempes, L. Wang, J. P. Amend, J. Doyle, T. Hoehler, Evolutionary tradeoffs in cellular composition across diverse bacteria. *ISME J.* **10**, 2145–2157 (2016).
12. P. E. Schavemaker, M. Lynch, Bioenergetics and the evolution of cellular traits. *Annu. Rev. Biophys.* **54**, 81–99 (2025).
13. M. Lynch, G. K. Marinov, The bioenergetic costs of a gene. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 15690–15695 (2015).
14. C. P. Kempes, S. Dutkiewicz, M. J. Follows, Growth, metabolic partitioning, and the size of microorganisms. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 495–500 (2012).
15. C. P. Kempes *et al.*, Drivers of bacterial maintenance and minimal energy requirements. *Front. Microbiol.* **8**, 31 (2017).
16. M. A. Lever *et al.*, Life under extreme energy limitation: A synthesis of laboratory- and field-based investigations. *FEMS Microbiol. Rev.* **39**, 688–728 (2015).
17. 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).
18. W. R. Shoemaker, E. Polezhaeva, K. B. Givens, J. T. Lennon, Molecular evolutionary dynamics of energy limited microorganisms. *Mol. Biol. Evol.* **38**, 4532–4545 (2021).
19. F. Vasseur, C. Violle, B. J. Enquist, C. Granier, D. Vile, A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecol. Lett.* **15**, 1149–1157 (2012).
20. F. Vasseur *et al.*, Adaptive diversification of growth allometry in the plant *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 3416–3421 (2018).