or, at most, semiconductors), but also because they are expected to have unique electronic properties[19]. Meirzadeh and colleagues' findings hint that polar metals might have been under our noses all along, paradoxically on the surfaces of non-polar insulators.

Gustau Catalan is at Institucio Catalana de Recerca i Estudis Avançats, Barcelona 08010, Spain, and at Institut Català de Nanociència i Nanotecnologia, CSIC-BIST, Barcelona. **Beatriz Noheda** is at the Zernike Institute for Advanced Materials, University of Groningen, Groningen 9747AG, the Netherlands.
e-mails: gustau.catalan@icn2.cat; b.noheda@rug.nl

1. Whatmore, R. W. *Rep. Prog. Phys.* **49**, 1335–1386 (1986).
2. Meirzadeh, E. *et al. Adv. Mater.* **31**, 1904733 (2019).
3. Biancoli, A., Fancher, C. M., Jones, J. L. & Damjanovic, D. *Nature Mater.* **14**, 224–229 (2015).
4. Padilla, J. & Vanderbilt, D. *Surf. Sci.* **418**, 64–70 (1998).
5. Bhalla, A. S. & Newnham, R. E. *Phys. Status Solidi A* **58**, K19–K24 (1980).
6. Gehring, P. M., Hirota, K., Majkrzak, C. F. & Shirane, G. *Phys. Rev. Lett.* **71**, 1087 (1993).
7. Domingo, N., Bagués, N., Santiso, J. & Catalan, G. *Phys. Rev. B* **91**, 094111 (2015).
8. Hirota, K., Hill, J. P., Shapiro, S. M., Shirane, G. & Fujii, Y. *Phys. Rev. B* **52**, 13195–13205 (1995).
9. Jiang, Q. & Zegenhagen, J. *Surf. Sci.* **367**, L42–L46 (1996).
10. Sai, N., Meyer, B. & Vanderbilt, D. *Phys. Rev. Lett.* **84**, 5636 (2000).
11. Yamada, H., Kawasaki, M., Ogawa, Y. & Tokura, Y. *Appl. Phys. Lett.* **81**, 4793 (2002).
12. Tagantsev, K. *Phys. Rev. B* **34**, 5883–5889 (1986).
13. Narvaez, J., Vasquez-Sancho, F. & Catalan, G. *Nature* **538**, 219–221 (2016).
14. Stengel, M. *Phys. Rev. B* **90**, 201112(R) (2014).
15. Stanley, H. E. *Rev. Mod. Phys.* **71**, S358 (1999).
16. Santander-Syro, A. F. *et al. Nature* **469**, 189–193 (2011).
17. Anderson, P. W. & Blount, E. I. *Phys. Rev. Lett.* **14**, 217–219 (1965).
18. Shi, Y. *et al. Nature Mater.* **12**, 1024–1027 (2013).
19. Benedek, N. A. & Birol, T. *J. Mater. Chem. C* **4**, 4000–4015 (2016).

This article was published online on 18 November 2019.

Evolution

The balancing act of growth and expansion

Henry Mattingly & Thierry Emonet

Bacteria move along gradients of chemical attractants. Two studies find that, in nutrient-rich environments, bacteria can grow rapidly by following a non-nutritious attractant — but expanding too fast leaves them vulnerable. **See p.658 & p.664**

Bacteria can sense chemical attractants and use that information to navigate towards resources or away from harm — a process called chemotaxis. But why bacteria chase signals that often do not have much nutritional value has been a long-standing puzzle. Cremer *et al.*[1] show on page 658 that bacterial populations can use non-nutritious attractants as cues for rapidly expanding through nutrient-rich areas, ensuring that plentiful nutrients are available for their future growth. And on page 664, Liu *et al.*[2] build on this work to reveal an unanticipated rule of bacterial evolution: the safest way for a bacterial population to colonize a habitat is not necessarily to expand as fast as possible, because rapid expansion can leave the population vulnerable to invasion by competitors.

In the 1960s, the biochemist Julius Adler demonstrated that a group of cells consuming a chemical attractant can form a rapidly expanding wave that follows a moving concentration gradient that the cells create on their own[3]. That is, by consuming the attractant in their immediate vicinity, the cells create a gradient between their current location and the surrounding regions in which the chemical has not yet been consumed. The cells then chase the higher concentration — rather like a horse chasing a carrot on a stick. The wave's expansion speed is determined by how fast the travelling cells deplete the local attractant[4].

Cremer *et al.* examined how a cell population's use of chemotaxis to expand (defined as the occupation of more space), as in Adler's experiments, affects its growth (the increase in cell numbers). The authors seeded small colonies of bacteria in a Petri dish, and measured population size over time as the cells grew and filled the available space. As Adler had observed, the colonies formed expanding waves, and some cells fell behind the wavefront, seeding the newly covered ground.

Importantly, when Cremer and colleagues added small amounts of a non-nutritious chemical attractant that was different from the nutrient on which the cells were growing, the population capitalized on chemotaxis to expand before the local nutrient had become depleted. This increased the number of cells that had access to nutrients at a given time and allowed the population to grow much faster than it did without the directional cue of the attractant (Fig. 1). This gain relied on a separation between chemotaxis and growth: the attractant served as a cue, rather than as a nutrient source[5], to direct the cells towards unoccupied territory. When the attractant is the only nutrient, the population does not grow as fast; either the attractant is abundant, and the cells can't consume it fast enough for rapid expansion, or the attractant is limited, and expansion can be fast but the settlers behind the wavefront are starved and don't grow.

This work demonstrates that — in a nutrient-rich environment — the faster a single population expands, the faster it grows. But what happens when competitors (including spontaneously generated mutants in the population) expand into the same territory? Last year, we and our colleagues[6] showed that bacteria with different chemotactic abilities

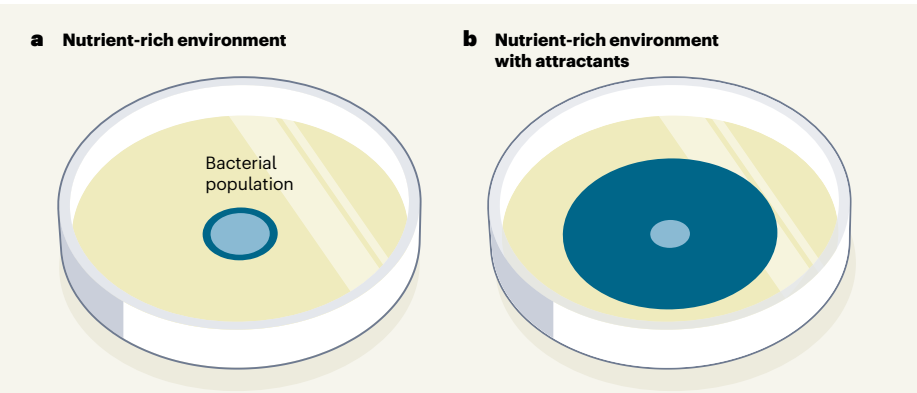

Figure 1 | How bacteria maximize growth in nutrient-rich environments. a, Populations of bacteria can spread out within a nutrient-rich habitat through cell division and random motion. But this approach causes most of the population to stay in a small location and deplete local nutrients — so, many cells starve (light blue) and only the outer edge grows (dark blue). **b**, Cremer *et al.*[1] grew bacteria in the same environment but included low levels of a non-nutritious attractant chemical (not shown). The cells chased the attractant through a process called chemotaxis, expanding rapidly across the dish before the local nutrients were depleted, so that most of the population had the nutrients needed to grow.

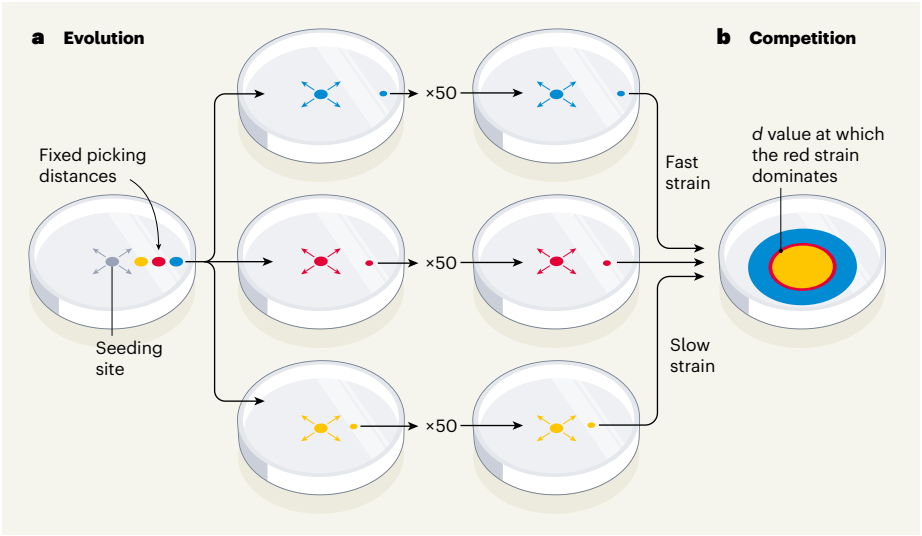

Figure 2 | An expansion strategy for protecting against competitors. Liu *et al.*[2] show that rapid expansion is not necessarily the best strategy if populations are competing for limited space. **a**, The authors seeded cells in the centre of a dish and let them expand across the dish (indicated by outward-pointing arrows). They then picked bacteria that had reached fixed distances from the seeding point (five distances were used, but only three are shown here, for simplicity). They reseeded cells picked from different distances in separate plates and repeated the process, picking cells from the same distance after the cells had filled the plate. Reseeding 50 times led to the evolution of strains that had expansion speeds that increased with picking distance. **b**, The team then seeded strains of different speeds together in a dish so that they would compete against one another. This revealed a simple rule for determining which strain will dominate at distance d from the seeding site — the one satisfying $d = u/\lambda$, where u is the strain's expansion rate when the population expands without competition and λ represents how quickly cells divide. Slow strains dominate close to the seeding site and fast strains dominate farther away, but at a particular value of d, the red strain cannot be outcompeted and is protected.

(but with the same genes) can travel together in the same expanding wave by spatially organizing themselves. High-performing cells travel at the front of the wave, where the attractant gradient is shallow; low-performing ones are found at the back, where the gradient is steeper because more of the attractant has been consumed. Steeper gradients are easier to navigate, so this spatial organization enables all cells to travel at about the same speed.

"The authors' strains had evolved to fill a niche in which they were stable when facing invasion by competitors."

However, cells at the back are more likely to fall behind the group and seed the covered ground. It has been unclear how this sorting mechanism affects the relative growth of multiple populations when they travel together.

Liu *et al.* addressed this question using an evolution experiment. As in Cremer and colleagues' study, the authors seeded a population of bacteria in a Petri dish and allowed it to expand and fill the available space. Then the authors picked bacteria that had reached one of five fixed distances from the starting point and seeded them in a new dish in which they expanded again (Fig. 2a). The researchers repeated the process 50 times, picking from the same distance each time.

Given that Cremer and colleagues found that faster expansion leads to greater growth, one might expect that Liu and colleagues' protocol would select for strains that showed increasingly fast expansion, regardless of the picking distance. Instead, as the cycles progressed, strains picked at locations close to the initial seeding site evolved to expand more slowly than their ancestors, whereas those picked farther away evolved to expand more quickly.

Liu *et al.* then performed a competition assay in which they seeded evolved strains of different expansion speeds in the same dish. The authors found that the strains occupied different regions: slow strains deposited settlers behind the wave more rapidly and therefore dominated close to the seeding point, whereas fast strains deposited settlers more slowly and dominated far from it (Fig. 2b). Each strain's fitness (quantified by its relative abundance) therefore depended on its distance from the starting point — a clue to the outcome of the evolution experiment.

Finally, through a combination of simulations and mathematical arguments, the researchers discovered a simple rule that predicts which strain is fittest at any given distance (d) from the seeding site. For expansion speed u (when expanding without competition) and growth rate λ, the strain that satisfies $d = u/\lambda$ will dominate at d. As a strain's expansion speed increases, fewer individuals of that strain fall behind to colonize the area, so it dominates at a greater distance (higher d), after other strains have lagged behind. By contrast, the higher a strain's growth rate, the sooner it becomes the predominant strain in the expanding wavefront, and so the earlier it deposits settlers.

Taken together, these fascinating results show how populations of bacteria can balance rapid expansion and growth with ensuring that competitors cannot invade their territory. Liu and colleagues' evolved strains were not the fittest in an absolute sense: they did not necessarily expand or grow the fastest when seeded in isolation. Rather, they had evolved to fill a niche in which they were stable when facing invasion by competitors.

The experimental systems developed in the two current studies are well suited for exploration of how the abilities of bacteria to shape and navigate their complex chemical environments affect ecological and evolutionary dynamics. These results should reach far beyond bacterial chemotaxis, and improve researchers' understanding of the behaviour of growing populations across many fields.

Henry Mattingly and **Thierry Emonet** are in the Department of Molecular, Cellular and Developmental Biology, Yale University, New Haven, Connecticut 06520-8103, USA.
e-mails: henry.mattingly@yale.edu; thierry.emonet@yale.edu

1. Cremer, J. *et al. Nature* **575**, 658–663 (2019).
2. Liu, W., Cremer, J., Li, D., Hwa, T. & Liu, C. *Nature* **575**, 664–668 (2019).
3. Adler, J. *Science* **153**, 708–716 (1966).
4. Keller, E. F. & Segel, L. A. *J. Theor. Biol.* **30**, 235–248 (1971).
5. Yang, Y. *et al. Mol. Microbiol.* **96**, 1272–1282 (2015).
6. Fu, X. *et al. Nature Commun.* **9**, 2177 (2018).

This article was published online on 6 November 2019.