Trends in Microbiology

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Opinion

What is microbial dormancy?

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Life can be stressful. One way to deal with stress is to simply wait it out. Microbes do this by entering a state of reduced activity and increased resistance commonly called 'dormancy'. But what is dormancy? Different scientific disciplines emphasize distinct traits and phenotypic ranges in defining dormancy for their microbial species and system-specific questions of interest. Here, we propose a unified definition of microbial dormancy, using a broad framework to place earlier discipline-specific definitions in a new context. We then discuss how this new definition and framework may improve our ability to investigate dormancy using multi-omics tools. Finally, we leverage our framework to discuss the diversity of genomic mechanisms for dormancy in an extreme environment that challenges easy definitions – the permafrost.

Highlights

The ability of microorganisms to resuscitate from dormancy has major implications for ecosystem function.

By conceptualizing the space of possible definitions of dormancy as a multidimensional trait space, we construct a pluralistic concept of dormancy that accommodates and allows intercomparison between distinct definitions of dormancy from a variety of disciplines.

Our framework for describing and comparing definitions of dormancy facilitates cross-communication between subfields of microbiology.

Our framework can be applied to extreme cases, such as permafrost, where it allows for discriminating between microorganisms that are adaptively dormant, and those that are simply stressed.

Microbial dormancy: it is complicated

Microorganisms survive and thrive in diverse and often harsh environments. Advances in molecular biology (e.g., next-generation sequencing technology) have greatly expanded our understanding of the breadth of habitable systems across the earth, with environments as varied as the atmosphere and the deep subsurface being dominated by microbes [1–3]. New insights into microbial activity in these systems are reshaping our understanding of the biosphere. Yet it is the microbial capacity for inactivity – for a physiological program of **dormancy** (see Glossary) – that allows many lineages to survive harsh environments and enables rapid response to changes in environmental conditions. Such adaptations may become increasingly important to organisms as anthropogenic climate change threatens to increase the variability and extremes of climate conditions [4].

What do we mean by dormancy? Certainly, microbes vary widely in their metabolic states, and what may initially seem like inactivity may actually be extremely slow growth (e.g., mycobacteria [5]). Historically, definitions of dormancy have varied across subfields [6–13], creating semantic differences and divergent subfield perspectives that hinder cooperative efforts in the increasingly interdisciplinary microbial sciences. Here, we build a conceptual framework that is capable of accommodating the different microbial survival strategies variously described as 'dormancy'.

Why do we need one framework to rule them all? Microbial dormancy is likely a feature of all terrestrial ecosystems, with common examples observed in systems as varied as **permafrost** [14–16], deep soils [17], deserts [18], marine sediments [19], and the human body [10,20] (Box 1). Common traits associated with the entrance into, maintenance of, and exit from dormancy across these biomes include specific DNA repair mechanisms [9], remodeled metabolic pathways for starvation persistence (e.g., mixotrophy, carbon monoxide consumption, glycogen accumulation and consumption, lower endogenous metabolism) [9,21], downregulation of biosynthetic pathway enzyme translation during persistence for antibiotic tolerance [22], membrane modifications for maintaining fluidity [14], and

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defense and stress-response pathways (e.g., antibiotic resistance [10], cold/heat-shock response proteins [23]). However, the specific combination of traits in one dormancy-capable microbe may be quite distinct from that in another. Furthermore, dormancy is not defined by any single trait in this set; rather, dormant microbes may employ a variety of pathways to increase their environmental resilience while decreasing their overall activity. In this perspective, we address this spectrum of microbial inactivity and resiliency through an updated conceptual framework for defining dormancy and provide a case study using permafrost to demonstrate how this framework can be used to understand dormancy in complex environments and across disciplines. In doing so, we give multidisciplinary teams of scientists a new theoretical toolset for forming hypotheses and understanding the implications of dormancy in their data. We see our **pluralistic approach** [24] as a powerful way to build connections between subfields in the microbial sciences.

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(Re)defining dormancy

Competing definitions of dormancy have arisen as different fields of study offer definitions relevant to their own driving questions. Few would argue for a definition of dormancy that excluded the **endospore**, a cell that has fully differentiated into a hardy, well-protected resting state from which it may germinate in the future [9]. But what about cells that undergo some less-dramatic degree of differentiation – for example, thickening the cell wall or increasing nutrient storage ([18], and citations within) while stopping short of forming a 'true endospore'? Nongrowing '**persister**' cells in a population can evade antibiotic treatment; are they then dormant [22]? What about cells that arrest growth using abortive infection systems that evade viral targeting [25–27]? Each of these physiological states, despite their differences, would be described as dormancy by at least one subfield of researchers and possibly excluded by others.

Previous definitions of dormancy have varied widely in their inclusivity. The broadest definition, set forth by Lennon and Jones in 2011 [8], following Sussman and Douthit [6], describes dormancy as 'any rest period or reversible interruption of the phenotypic development of an organism'. Others emphasize that dormancy is a state of reduced metabolic capacity [28,29], sometimes even deriving specific cut-offs for metabolic activity to differentiate nongrowing cells from truly dormant ones [21]. The most restrictive definitions require that dormancy explicitly provides increased resilience to external stressors, often only including endospore formation as a resilience mechanism [9,11].

These contrasting perspectives raise several questions relevant for defining dormancy. (i) Is a metabolic slowdown necessary, or is replicative arrest sufficient? (ii) Are there generalizable metabolic rate cut-offs for defining active versus dormant cells? (iii) Is dormancy necessarily adaptive? To answer these questions, we have conceptualized the capacity for dormancy as a **multidimensional** trait space, where subfield-specific definitions of dormancy occupy different regions. That is, different researchers place emphasis on distinct traits associated with dormancy, with some more focused on the absolute metabolic rate of the cell and others focused on how hardy the resting state is to environmental stressors, among a variety of other possible dimensions to consider.

We have outlined an example of a possible space for definition comparison in Figure 1, where after first characterizing a species within the bounds of our chosen dimensions, we can then debate and discuss the merits of its inclusion as an organism capable of dormancy. First, if we think of each trait as an individual value that contributes to a multidimensional vector of trait values, then the phenotypes of individual species can each be described by such a vector (Figure 1A). Each dimension of this space may be a summary of a multidimensional space in itself, such as hardiness/resilience in the example shown in Figure 1A, which may be further broken down as in Figure 1B. After deciding on trait dimensions to consider in the trait space, we can then define

regions that correspond to our particular dormancy definition of interest, or are specifically relevant to the environment of study. For example, we may only accept organisms capable of very low metabolic rates (Figure 1C) or able to remain in their resting state for relatively long periods of time (Figure 1D). Alternatively, we may set a high hardiness cut-off that excludes organisms whose resting states are susceptible to environmental stress (Figure 1E; though hardiness itself is a multidimensional trait, see Figure 1B). Importantly, the way we discuss dormancy will depend on the particular organism of interest and its environmental context (as with species concepts [24]; also see Figure 1A). For example, researchers studying persistence may focus on hardiness, whereas those studying sporulation may focus on features of cellular differentiation. Thus, the answers to each of these questions will depend on the region of trait space and specific adaptations a researcher is focused on.

Nevertheless, a common working definition of dormancy will help microbial scientists bridge disciplinary divides to address grand challenges – such as understanding the many roles microbes play in nature's response to climate change, where a common definition of dormancy can improve predictions of microbial contributions to ecological outcomes. Synthesizing previous work, we propose the following general-purpose definition:

> Dormancy is a temporary, adaptive state of reduced metabolic activity within an extended period of arrested growth that can enable a microbe to maintain viability under unfavorable environmental conditions.

This definition broadly answers our three earlier questions as (i) 'yes, metabolic slowdown is necessary', (ii) 'strict cut-offs are not necessary; rather, metabolic slowdown should be considered in relation to metabolic rate in an optimal, stress-free environment, which will differ by organism and environment', and (iii) 'yes, dormancy is necessarily adaptive'.

A related question is whether dormancy requires complete (reproductive) growth arrest, or whether a dramatic slowing down of reproduction in response to stress could be a form of dormancy. Our pluralistic approach [24] to defining dormancy – in which many coexisting definitions are compared and contrasted by explicitly locating them in trait-space – can accommodate this perspective. However, our working definition would exclude these forms of 'dormancy' because it refers specifically to 'growth arrest'.

It is important to note here that the specific adaptations chosen for the theoretical framework for dormancy shown in Figure 1 and described earlier are not meant to be interpreted as the only possible traits referenced by definitions of dormancy, but rather an example of common dormancy-related traits that help to demonstrate the utility of the framework. We invite readers to interchange these traits for those that they feel would be relevant to their environment of interest and to verify those traits as adaptations that should facilitate survival during slow-downs in metabolic and reproductive activity.

Must dormancy be adaptive?

Our working definition insists that the capacity for dormancy must have some adaptive value (i.e., must increase fitness in some sense). Why is this adaptive value necessary for dormancy? Not all aspects of an organism's phenotype – that is, traits – are necessarily adaptive [30,31]. Take the example of starvation. Replicative arrest under starvation is a result of nutrient scarcity, not an adaptation to that scarcity; thus, cells in replicative arrest may or may not be dormant or viable. While it may be possible to distinguish starvation-induced replicative arrest from 'true' dormancy-induced replicative arrest by setting stringent cut-offs for metabolic rate, these cut-

Glossary

Active layer: the layer of soil overlying permafrost that is seasonally frozen (less than 2 years) and regularly thaws during the summer months.
Akinetes: thick-walled, dormant cyanobacterial cells in the orders Nostocales and Stigonematales. They are often present in biological soil crusts.
Cryoturbation: the mixing of soil layers due to frost heaving.
Dormancy: a temporary, adaptive, state of reduced metabolic activity within an extended period of arrested growth that enables a microbe to maintain viability under unfavorable environmental conditions.
Endospore: a bacterial structure characterized by being dormant, hardy, and nonreproductive.
Multidimensional: as in 'multidimensional trait space', referring to the many axes of phenotypic diversity that species vary along, with each individual phenotypic value (e.g., cell size, metabolic rate, etc.) being a single dimension.
Permafrost: soil with a temperature continually below 0°C for at least 2 years.
Persisters: nondividing subpopulations of cells that tend to arrest both reproductive growth and the expression of genes for biosynthetic-pathway enzymes, yielding cell resistance to antagonistic compounds.
Pluralism: as in 'pluralistic definitions of dormancy', the recognition that no single conception of dormancy can cover the diverse set of phenotypes biologists use this term to describe, and that to adequately describe nature biologists need to flexibly apply the definition that is most appropriate for the questions, organisms, and environments they are studying. Similar to pluralistic species concepts [24].
Trait space: space of possible phenotypes where each dimension in this (typically multidimensional) space is a single 1D trait value (e.g., minimum metabolic rate).

Box 1. Microbial dormancy in diverse and harsh environments

The capacity for dormancy is central to microbial resilience in a wide variety of ecosystems. Each ecosystem presents a unique set of challenges for the survival of both active and dormant microorganisms. Microbial life has accordingly evolved a wide variety of survival traits [55]. For example, *Virgibacillus arcticus* survive for hundreds to thousands of years as endospores in harsh, yet low-disturbance permafrost soils [15] (Figure IA) alongside 'active' microbial species with slow metabolic activity, enzymatic tolerance to extreme cold, and exceptionally long doubling times (e.g., 62 years at –20°C, and modifications to cell-wall lipid saturation [16,56,57]). In deep subsoils (Figure IB) microbial adaptations have also led to expression of dormancy through the formation of endospores, reduced or altered metabolic activity, and potential activation of genes for use of internally stored energy [17]. In arid environments (Figure IC), lower metabolic activity may be combined with thickened cell walls and the accumulation of extracellular polymeric structures to form a hardy resting state that is operationally defined as dormancy ([18], and citations within). The formation of spore-like **akinetes** has also been observed for cyanobacteria isolated from the biological soil crusts that are a hallmark of many arid soil ecosystems. Within marine sediments (Figure ID), abundant endospores employ divergent strategies, and generally shape the deep biosphere by guiding community assembly and enabling slow-growth mechanics in this harsh environment [19]. Last, within the human body (Figure IE), infectious bacteria exposed to a new environment can form nondividing subpopulations of cells called persisters [22]. Complicating antibiotic treatment, persister cells tend to arrest both reproductive growth and the expression of genes for biosynthetic pathway enzymes, yielding cell resistance to antagonistic compounds. The reduced metabolic and nonreproductive growth state of persisters makes them operationally dormant until they resuscitate within their host to cause disease [20,22].

Despite clear differences in the functions and expressions of dormancy across environments, in all cases there is a strong fitness benefit to being capable of entering dormancy – so long as it is also possible to leave dormancy. This is especially true for environments such as permafrost soils, where the advantageous conditions needed to resuscitate dormant cells may not occur for millennia. It should be noted that the examples presented here are a simplification of the broad challenges faced by microorganisms in these environments, and thus also do not represent all the forms of dormancy that may be present.

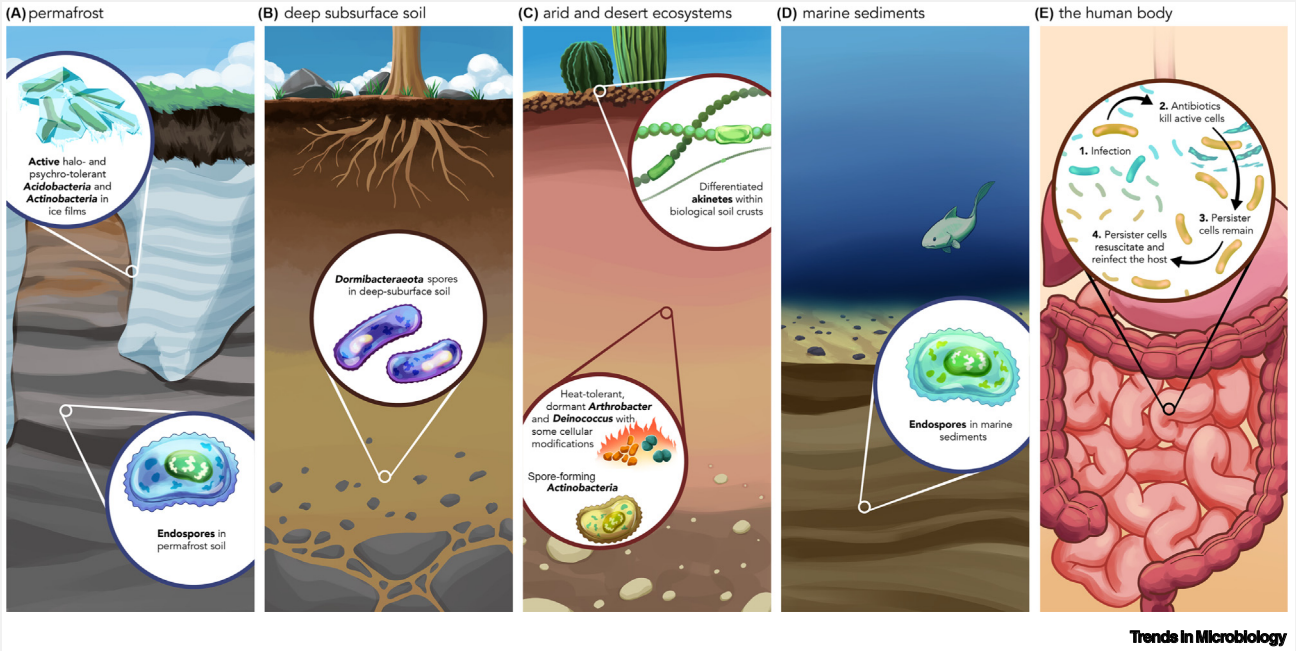

Figure I. Examples of microbial dormancy in harsh environments, including (A) permafrost, (B) deep, subsurface soil, (C) arid and desert ecosystems, (D) marine sediments, and (E) the human body.

offs are unlikely to apply across species. Instead, we appeal to what we think biologists actually want to talk about when they talk about dormancy: commitment to a specialized metabolic state that serves as an adaptation to wait out stressful conditions. In another example, the loss of reproductive function with DNA damage is not necessarily dormancy, and the loss of replication may be directly related to the damage incurred. However, the cell's response to the damage can be a function of dormancy. If the cell, after loss/halting of replicative function from DNA damage, invests in mechanisms to become hardier to reduce future damage, the response to damage may then be a key component of that cell's dormancy response. This adaptive nature of dormancy can be visualized in trait space (Figure1A) where the combination of a specific species'

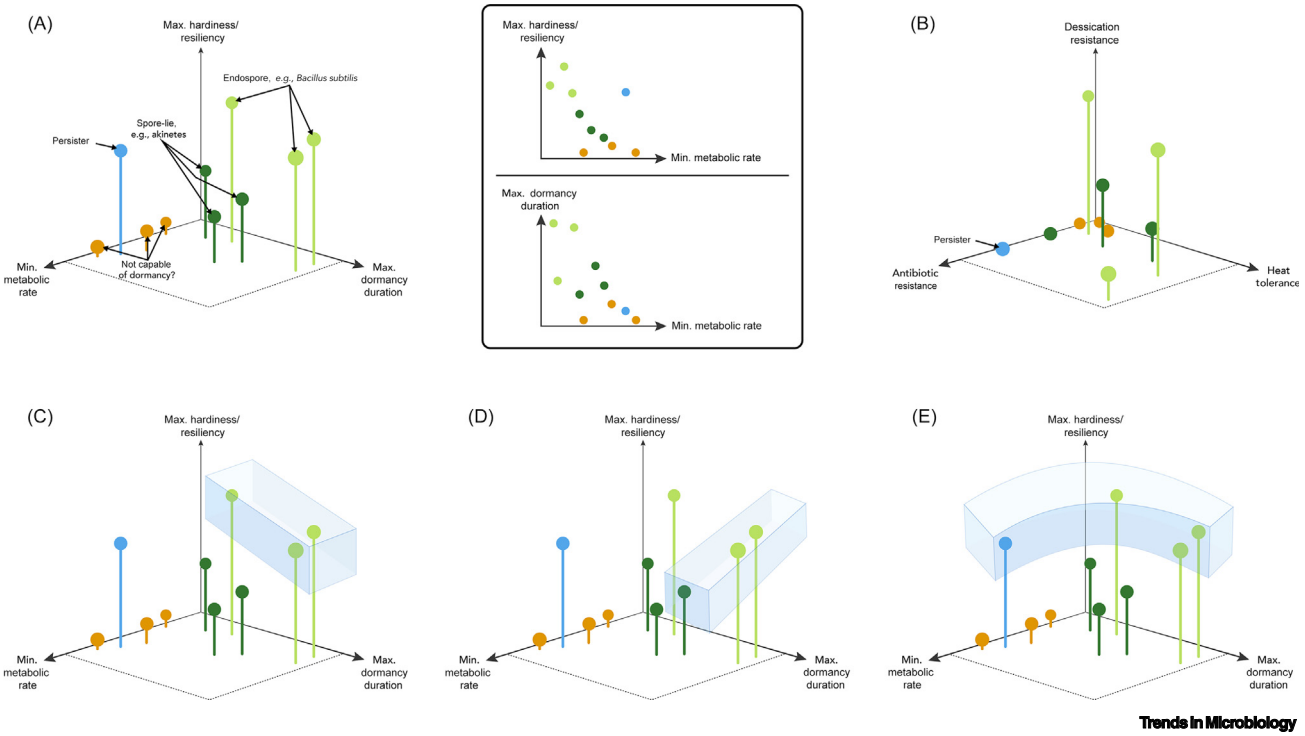

Figure 1. Conceptualization of species in multidimensional trait space to illustrate how distinct definitions of dormancy may be interrelated. Points represent theoretical placement of organisms in trait space on the basis of different possible kinds of dormancy they may exhibit. (A) Species' traits vary along multiple axes related to their ability to go dormant. Here we highlight three traits of particular importance: how low a species can push its metabolic rate and for how long, and how resilient the dormant state is to outside stressors. These trait axes are expected to be generally, but not always, correlated. (B) 'Resiliency' can be thought of as many independent traits that may not be correlated with one another. For example, a persister cell may be tolerant to antibiotics that a spore is not, even as the spore has a higher resilience to desiccation and heat stress. Finally (C–E), different subfields conceptualize dormancy as different regions of trait space. For example, the hardy, long-lasting resting state with a low metabolic rate in (C) is characteristic of endospore-forming Firmicutes. On the other hand, definition (D) which allows for a greater range of metabolic rates would include other resting states with a less severe metabolic cut-offs. Finally, panel (E) illustrates a definition that relies primarily on hardiness, that is, how resistant a dormant cell is to stress, rather than being concerned with its degree of inactivity, and would include persister populations.

traits within the stressful environment may or may not classify it as dormancy-capable depending on the specific environmental conditions (Figure 1C,D).

We note that entry into dormancy may not follow a particular environmental cue, but often happens stochastically as a bet-hedging strategy [32,33]. These forms of dormancy still fall under our working definition of dormancy because bet hedging is an adaptation that effectively mitigates the risk of a changing environment for a population of cells [34,35], increasing the long-term fitness of that population. Given the clonality of microbial populations, inclusive definitions of fitness apply well to these cases for assessing whether or not a trait is an adaptation (and would similarly apply in nonclonal bet-hedging populations, e.g., of plants, where seeds often germinate stochastically [34,36]). For instance, persister cells stochastically enter a dormant state, and their presence allows populations to recover from subsequent antibiotic exposure (Box 1).

Furthermore, dormancy as an adaptation is always defined with respect to the environmental stressors it evolved to respond to. A persister cell may tolerate antibiotics that a spore cannot, even as the spore has a higher resilience to desiccation and heat stress (Figure 1B). Indeed,

dormancy may even reduce resilience to nontarget stressors: for example, UV exposure may be a heightened risk for cells whose dormancy mechanisms include inactivation of some DNA-repair mechanisms [37].

Potential implications for 'omics: genetic modules for dormancy

What are the potential genomic implications of letting many definitions of dormancy coexist? First, if we define dormancy as distinct regions of trait space, that is, as coevolved sets of phenotypic adaptations, we should be able to distinguish different kinds of dormancy on the basis of the genomic adaptations underlying these traits. In other words, it will likely be possible to distinguish different kinds of dormancy on the basis of their associated genetic programs and the distribution of these pathways across organisms. Second, environment-specific stressors may enrich for organisms capable of different kinds of dormancy. However, it is important to note that to confirm these genes' contribution to dormancy in the environment of interest, additional measurements that verify metabolism and reproduction rates with and without the stressor are necessary. Many genes may be broadly associated with cellular stress, including dormancy-related genes, meaning that not all such genes will show such environment-specific correlations.

In addition, knowledge about gene distributional patterns may ultimately aid in *de novo* functional annotation. The benefit of leveraging gene proximity and co-occurrence signals across genomes and metagenomes in this way has been demonstrated in other areas such as novel antiviral defense systems [38,39] and could potentially be adapted for other cellular functions such as dormancy [40]. Thus, a pluralistic conception of dormancy that allows for many, domain-specific definitions may better align with how we analyze and understand genomic patterns. Genes for adaptation/stress response to an environmental stressor may form modules with other expected dormancy-related traits. However, it is important to note that to confirm these genes' contribution to dormancy in the environment of interest, additional measurements that verify metabolism and reproduction rates with and without the stressor are necessary. Another complication for looking for ecological correlations is that, in many senses, an organism's niche defines its environment [41]. Thus, two organisms with different survival strategies effectively experience different environments, and will have different adaptations, complicating any search for simple environment–trait correlations.

Pushing definitions to the extreme – dormancy in the permafrost

Our flexible framework for thinking about dormancy allows us to consider the complexities of microbial life in a new light. In the final section of this perspective, we demonstrate the utility of our framework for future studies of permafrost and overlying soils – a harsh environment that harbors microbes with diverse life-history strategies and that will be subject to dramatic near-term change.

Permafrost-affected soils are composed of two distinct layers, an **active layer** and the permafrost below. Active-layer soils, at the surface, are noted for their seasonal freeze–thaw cycles [14], while the underlying permafrost is consistently frozen (below 0°C) for long periods of time (at least 2 years [42], but often several thousand years). The permafrost contains a large store of carbon-rich organic matter which has a high potential to be mineralized to carbon dioxide and/or methane by the microbial population when thawed [43–46]. In a process known as **cryoturbation** [47], the permafrost and active layer can interact through frost heaving, which can introduce fresh material to the permafrost or bring permafrost material into the active layer. Mixing material means mixing microbes too: injecting active-layer microbes adapted to seasonal freezes into the permafrost, and lifting permafrost microbes adapted to long-term freezes into the relatively permissive conditions mentioned earlier. What happens to these microbes next? Which

organisms are poised to make use of newly thawed permafrost material, and what are the climate consequences of different groups' survival? Improving our ability to recognize and describe microbial dormancy should also improve the predictability of microbial and environmental responses to thaw.

Where in our multidimensional trait space (Figure 1) do permafrost microbes sit? These organisms contain a diverse range of adaptations to the cold, saline unfrozen fluid channels where they reside [48,49]. They persist through long periods without reproduction and exhibit adaptations to the environment, including altered membrane fluidity [50], genes responsive to thermal, osmotic, and nutrient-limitation stresses [51], and cold-adapted enzymes [52]. Previous studies have revealed that permafrost microbes often toughen up mechanically, variously thickening their outer walls, encysting, or sporulating ([40,41], and references therein). These forms likely all move these cells up a hardiness/resiliency axis and out a dormancy duration axis, though notably spores represent a larger fraction of cells recovered from older permafrost samples (≥27 vs. 18 thousand years ago; [53]). Isotope uptake experiments place these organisms toward the minimum on a metabolic activity axis at permafrost temperatures [16], whereas their metabolic activity and reproductive rates can increase greatly upon thaw/warming [16,54]. Different scientists might apply different dormancy criteria to such organisms and decide that only a few of these organisms are dormancy-capable in permafrost (e.g., only the spore-formers, see [9] and [11]), or that most or even all are. Applying our framework, we argue that most may be. Understanding which of these classifications is right is critically important to predicting thaw outcomes – not only near-term metabolism and C outputs but also community succession and the fates of microbial seedbanks [32].

So, how do we figure out which of these conclusions is right? Two challenges point the way to a solution. First, given the observation of very slow metabolic rates under *in situ*-like conditions, a useful definition of dormancy has to be able to tell the difference between a passive slowdown (e.g., imposed by temperature constraints on enzyme kinetics) and a deliberate, adaptive switch to a low-activity state that confers resilience. Second, consider the potential effect of permafrost incorporation on nutrient acquisition. Microbes mixed into the permafrost might exhibit reduced metabolic activity simply because they are starving, or they might be able to reduce activity to a level that can be supported by adaptations to maintain minimal nutrient acquisition or storage. Here again, the distinction is whether a microbe's odds of resuscitation upon warming are a matter of luck or of strategy, and a definition of dormancy must distinguish between the two. That is, dormancy must be adaptive. Its mechanisms must be specific to the stressors of the environment, and therefore the combination of activity assays with environment- and genome-resolved 'omics analysis can reveal, for the permafrost and for other systems, which microbes are capable of dormancy and how dormancy is achieved in that system. Redefinition matters because we predict different outcomes when adaptively dormant organisms experience environmental change than when non-adapted ones do, and our capacity to predict permafrost ecosystem outputs is a critical piece of global climate modeling.

Concluding remarks

In this perspective, we have aimed to address the definition of microbial dormancy. Our unified definition reintroduces dormancy as an adaptive trait with a multidimensional spectrum of contributing characteristics that combine to enable the capacity for dormancy in a microorganism. From a genome-science perspective, this conceptual framework allows us to expand the scope of our search for dormant organisms and should lead to a better understanding of microbial assembly upon resuscitation of dormant organisms within the community [36] (see Outstanding questions).

Outstanding questions

Using our pluralistic framework for defining dormancy, how well can we better understand microbial community assembly upon permafrost thaw?

How well does this framework perform in other environmental scenarios?

What does our definition of dormancy mean for how we interpret microbial life in other extreme environments?

What other common terms would benefit from a pluralistic approach to definition?

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Declaration of interests

No interests are declared.

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