

Expanding the Pulse–Reserve Paradigm to Microorganisms on the Basis of Differential Reserve Management Strategies

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The pulse–reserve paradigm (PRP) is central in dryland ecology, although microorganismal traits were not explicitly considered in its inception. We asked if the PRP could be reframed to encompass organisms both large and small. We used a synthetic review of recent advances in arid land microbial ecology combined with a mathematically explicit theoretical model. Preserving the PRPs core of adaptations by reserve building, the model considers differential organismal strategies to manage these reserves. It proposes a gradient of organisms according to their reserve strategies, from nimble responders (NIRs) to torpid responders (TORs). It predicts how organismal fitness depends on pulse regimes and reserve strategies, partially explaining organismal diversification and distributions. After accounting for scaling phenomena and redefining the microscale meaning of aridity, the evidence shows that the PRP is applicable to microbes. This modified PRP represents an inclusive theoretical framework working across life-forms, although direct testing is still needed.

Keywords: microbes, plants, aridlands, adaptations, theoretical ecology

Drylands, which encompass deserts, shrublands, grasslands and savannas, account for 40% of the terrestrial surface (Pravělie 2016) and 30% of global carbon fixation (Field et al. 1998) and explain most of the interannual variability of the global carbon cycle (Poulter et al. 2014). In addition, drylands are home of 30% of the human population and to some of most vulnerable groups of people, who are often immediately dependent on resources from the natural environment (Reynolds et al. 2007). However, theoretical frameworks of dryland functioning are scarce. This is particularly relevant when inclusive management of multiple ecosystem services is desired (Yahdjian et al. 2015, Hoover et al. 2020), including conservation of biological diversity as one such desired service. For example, to inform managed relocation efforts in the face of global climate change (Richardson et al. 2009), it would be relevant to have theoretical underpinnings of general applicability at the organism level. In addition, microbial physiology, if not microbially mediated processes, is underrepresented from the formulation of dryland ecological theory. A reasonable way to remedy this situation is to evaluate if current plant-based theoretical frameworks would accommodate the inclusion of microbes.

Arguably, the pulse–reserve paradigm (PRP) constitutes the most important and enduring paradigm in dryland ecology since its postulation by Noy-Meir (1973) almost 50 years ago. It holds that dryland ecosystems undergo cyclical dynamics in which rare rainfall events trigger a flow of resources, mostly carbohydrates and nutrients from reserves (seeds or perennial plant organs) to an existing plant. During the pulse, the plant grows new leaves and roots devoting most of the acquired resources through photosynthesis and absorption from the soil to new growth. Next, the plant starts sending resources to reserve organs that are replenished toward the end of this pulse to prepare for dormancy between pulses. As a new cycle starts with the next pulse, a new flow from reserves to growth will be triggered. The PRP was largely based on keen observations of the climatic rigors typical of drylands and on insightful naturalistic observations of plant life strategies, and it has been subject to subsequent refinements and derivations relating to specific aspects such as the importance of response thresholds (Schwinning et al. 2004), functional plant types (Ogle and Reynolds 2004), and interactions with nutrient pulses (Collins et al. 2014). It remains one of the most cited works in the field, although microbes and microbial processes were underrepresented

at inception: It is plant centric (Collins et al. 2014). But the roles that microbes and their assemblages (microbiomes) play in dryland ecology have become ever more patent during the last decades (Bashan and de-Bashan 2010). Not only are microbes influential as agents of disease, for which there is a long history of recognition, but they are now understood to be ubiquitous, sometimes intricately integrated partners in mutualisms with both plants and animals. They are also responsible for much of the biogeochemical cycling, and, in the face of limits to plant cover and productivity imposed by aridity, they can take on some basic ecosystem processes such as primary productivity and soil stabilization. Logically, efforts to bring microbial processes into the fold of the PRP eventually followed (Collins et al. 2008, 2014, Štoviček et al. 2017). As is so much in microbial ecology, however, these contributions were based on analyses of microbial communities and microbial processes. However, they did not directly consider differential adaptations in particular microbial taxa (i.e., trait-based analyses; Martiny et al. 2015) in a way that parallels the core autoecological foundation of the Noy-Meir (1973) PRP for plants. The microbially based contributions remain a self-contained black box that offers none of the interpretive granularity that can be ascribed to plant communities. For example, the time scale for pulse responses is known to be much shorter for microbial than for plant processes (Collins et al. 2014), but although we can explain differential plant response times and thresholds on the basis of plant rooting depth, no such granularity can yet be described for microbes.

A successful strategy of scientific progress has been the borrowing of pieces of theory and their mathematical models from sister disciplines. Noy-Meir (1973) developed his PRP simultaneously under the intellectual influence of the International Biological Program. Early on, concepts borrowed from the cost–income theory from economics were applied to the evolution of resource allocation between leaves and roots in plants of arid environments (Orians and Solbrig 1977a). The cost–income theory is implicitly embedded in the PRP. Organisms need to use resources in the form of stored nutrients and energy to support a shift from quiescent to active state, to prepare for an eventual safe return to dormancy, and to mitigate environmental insults during the inactive state. Plants deploy new roots and leaves to capture resources after a rainfall pulse; their seeds germinate on the basis of carbon reserves accumulated preemptively during the times of plenty. The PRP predicts that the resources acquired during the pulse will be enough to replenish storage to be able to restart the cycle at the onset of the next pulse, and result in some net growth during the pulse. Variability of the duration of the pulses determines whether enough resources are acquired to fulfill these dual needs. Short pulses may end up in the consumption of more resources than can be acquired, leading to organismal or population demise. Long pulses will certainly offset the initial investment and yield a positive effect on storage. Thresholds for shifts from quiescence to

active state interacting with the length of pulses determine the outcomes for individuals and populations.

It is our intention in the present article to probe if the core tenets in the PRP find applicability in microbial biology, a discipline that has become much more conspicuously important for the ecology of drylands than might have been surmised at the time of Noy-Meir's (1973) publication, and one that now has experienced at least some advances to attempt such an exercise. Recent contributions show that it is indeed possible to attain general theoretical frameworks that are applicable to both micro- and macroorganisms when they are derived from basic, universal core tenets, as is the case with the principles of biological seed banks (Lennon et al. 2021). Broadening the PRP beyond plants has been very important in guiding integrative research in drylands and developing new tools for holistic dryland management. Our central questions are these: Is the PRP applicable to microbes? Is there a universal PRP that can be applied to microbes and plants? And what are the organismal adaptations in plants and microbes that allow them to manage different sized pulses? Because the PRP was first developed with plants in mind, we highlight plant–microbe contrasts in the process. In the present article, we introduce a new conceptualization: the importance of reserve management style as the basis for organismal adaptations to cope with resources that come in pulses. We frame it with a mathematical model, evaluate its predictions in the light of knowledge of organismal biology, and explore the consequences and applicability of the generalized paradigm.

Modeling the PRP: Nature and consequences of pulsed resources

We reframed the PRP to make it generically applicable while preserving its basic tenets. Succinctly, biological activity in drylands is strongly determined by pulses of water availability (Noy-Meir 1973), and this challenge is met by organisms through the accumulation of reserves during the pulse that are then used to power transitions into and out of dormancy. The reframing is still based on the tenet that all organisms base their response to pulses on the accumulation of reserves (Collins et al. 2008), but we introduce the concept that organisms can differ in their reserve management style along a continuum between two strategies. At one end of the continuum, what we call *nimble responders* (NIRs) are organisms that transition swiftly in and out of pulse use mode. To achieve this, however, they allocate a certain proportion of their metabolism and resources to maintain a constant, constitutive physiological readiness for interpulse conditions, and to ensure that metabolic systems are inherently hardy and protected at all times. Such level of constant readiness comes at the cost of building permanent, constitutive reserves, depressing their growth potential (and rate) from a theoretical maximum; they are inherently slow growers. At the opposite end, although they do allocate portions of their resources as reserves to prepare for quiescence, *torpid responders* (TORs) only do so as a pulse nears

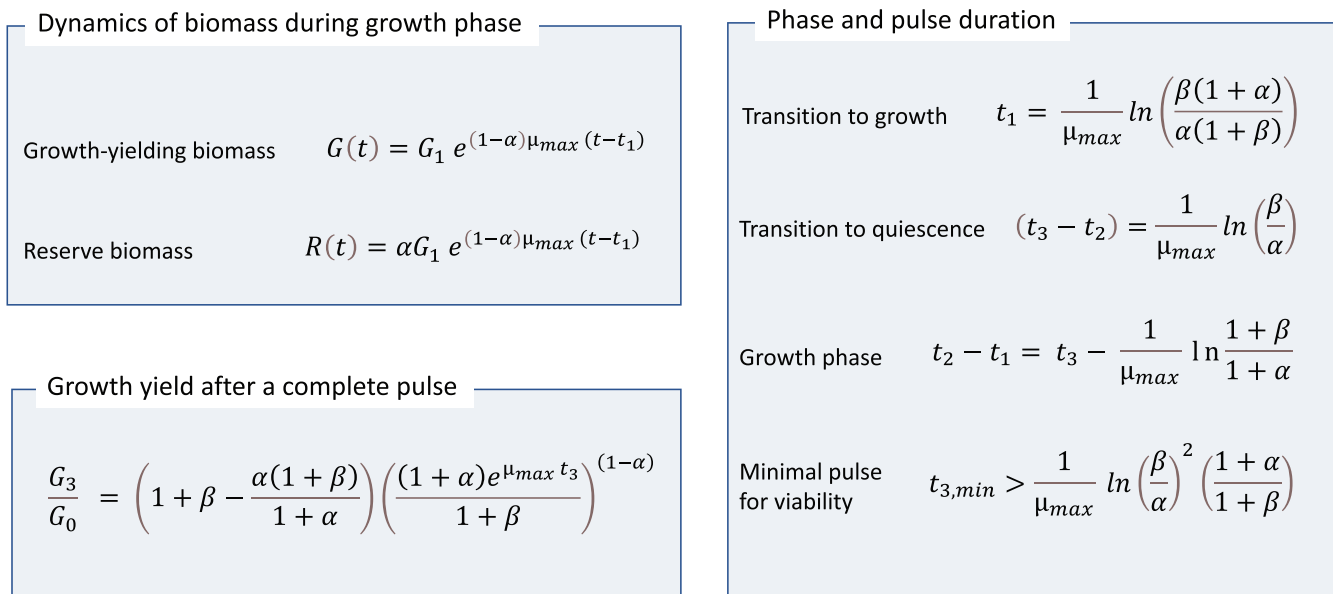


Figure 1. Formulations for growth dynamics and main output parameters.

an end. These can be understood as late-pulse investments. Consequently, they can allocate recently acquired resources fully to growth processes during much of the pulse unconstrained by allocation to reserves, and they grow swiftly during it. Because of their low level of constitutive readiness, the lag times for transition to dormancy and back into growth among TORs are long, in that reserves need to be mostly synthesized from scratch toward the end of a pulse and then retrofitted into growth-promoting biomass at the beginning of the next pulse. To continue the financial metaphor, NIRs can be understood as conservative investors, focused on certainty of returns that are not high but are frequent (i.e., they will grow some regardless of the pulse length), whereas TORs would be akin to risky investors whose strategy relies on high returns that occur rarely (they will grow a lot if the pulse happens to be long, at the risk of failing it is short). It is important to realize that specific organisms will fall within the continuum between the extremes exemplified in the NIR and TOR acronyms. The distinction will be most properly used when comparing the relative position of an organism along this continuum, and probably most useful when comparing the relative character of pairs of organisms.

An explicit mathematical model based on the ideas in the previous paragraph is presented in the supplemental materials, the main formulations of which are gathered in figure 1. Its input parameters, outputs and predictions are discussed in the following paragraph.

The duration of the pulse is divided into three periods: transition from quiescence, growth phase, and transition to quiescence. The level of constant readiness for quiescence is gauged by the parameter α , which constitutes the central parameter in the model, defined and calculated as the ratio of reserve biomass and growth-yielding biomass maintained during the growth phase in the pulse. It remains

constant within it, and as growth must be positive, the level of constant readiness will vary between 0 minimally and maximally approach 1. Organisms approaching the NIR end with high constant readiness will have high α , and TOR-like organisms will be characterized by low α . The level of investments in reserves needed to ensure successful transitions in and out of dormancy is gauged by the parameter β , which is defined and calculated as the ratio of growth-yielding biomass to reserve biomass reached at the end of the pulse. Organisms that do not reach β by the end of a pulse will not be viable at the next iteration. Nothing prevents an organism to invest very heavily in β , and its maximal values are principally not constrained, but if these reserves are retrofitted into growth structures at the next pulse with reasonable efficiency (i.e., above 30%), β will typically take values below 3. The instantaneous growth rate (μ) that is possible at any one time during the growth phase in a pulse is dependent on α , being depressed from its maximal value by the resources allocated to constant readiness. The net yield of growth, defined as the ratio of growth enabling biomass at the end of a pulse to that at its beginning is, however, dependent on both α and β . The dynamics of growth-enabling biomass and reserve biomass during a pulse under this framework model are depicted in figure 2a. A comparative depiction of the dynamics of growth during a pulse for end-member organismal types is in figure 2b. Again, NIRs are characterized by low μ , but high α , whereas TORs by high μ but low α .

Relevant model outputs are the duration of the transition periods and growth phase, the net new growth yield after completion of a pulse cycle, and the minimal duration of a pulse required for viability. Their formulation as a function of input parameters is in figure 1. The duration of the growth phase is determined by the duration of the pulse minus the duration of the necessary transitions. Pulse duration must

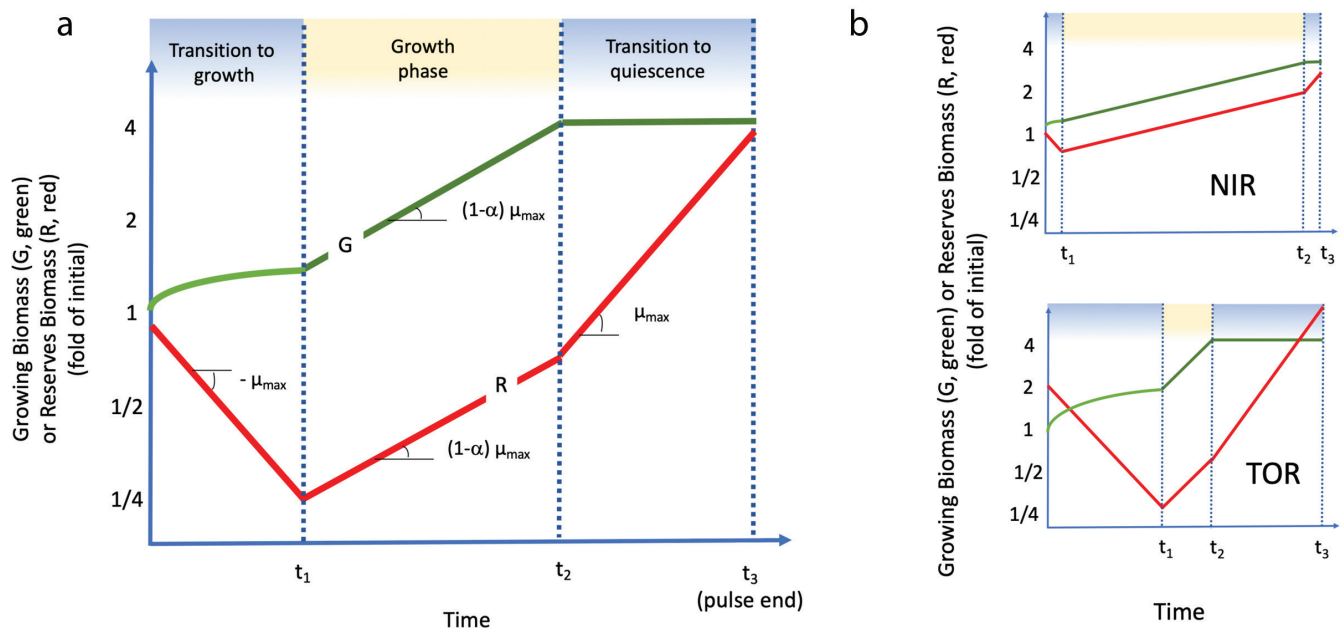


Figure 2. (a) Modeled dynamics of growth-yielding biomass (G) and reserves (R) during a pulse of resources with explicit transitions between quiescence and growth and back to quiescence. Important parameters are intrinsic maximal growth rate (μ_{max}), the ratio of biomass allocated constantly to reserves over that allocated to growth during growth (constant readiness, α), and the ratio of biomass allocated to support transitions over that allocated to growth at the end of the pulse. Times for transition are dependent on the previous parameters. (b) Differential strategies of management of reserve investment result in distinct functional adaptations: NIRs and TORs. NIR organisms invest conservatively in preparation for quiescence (high α), and can respond swiftly (short transition times), at the expense of lower growth rate (μ), whereas TORs invest with higher risk (low α), need longer transition times but can grow fast during favorable times. Explicit mathematical model equations are in the supplemental materials.

exceed the duration of transitions for organisms (or populations) to attain net growth. Although the point has been made that transitions are energetically costly for both plants (Gremer and Sala 2013) and microbes (Schimel 2018), they are also costly in terms of time, particularly when active time is at a premium. Therefore, we also define a *minimal pulse duration* that allows for completion of the necessary transitions. Should a pulse last less than this minimal duration, viability will be compromised and the resuscitation strategy will fail.

The model predicts that transition times decrease with increasing constant readiness reserves (α) and increase with increasing end-of-pulse reserves (β), only in the case in which α tends to β , they tend to 0, which biologically corresponds to the case in which virtually all reserves needed for transition are always present. It also predicts that the minimal duration of the pulse needed for viability decreases with increasing constitutive readiness (figure 3). Finally, it predicts that increasing the amount of end-of-pulse reserves (β) lengthens minimal pulse duration for viability.

In terms of growth yields as a function of pulse duration (figure 4), the model predicts that the more an organism tends to the NIR end member, the more it will benefit from a regime of short pulses whereas tending to the TOR end, will benefit from longer pulses. It also predicts that investments

in end-of-pulse reserves (β) result in advantages in growth yield regardless of pulse duration, as long as the minimal pulse duration is exceeded. Finally, it predicts that the return of late-pulse investment becomes increasingly negligible for very long pulses. In general terms, the constant readiness of NIRs is only beneficial when pulses are short, whereas late-pulse investments matter more when pulses are intermediate in duration. When pulses are so long as to lose their pulsed character neither type of adaptation is beneficial, consistent with the PRP tenet that the gathering of reserves is a characteristic selected for only under pulsed regimes of growth.

Although we have expressed pulse duration, rather unintuitively, as the inverse of μ_{max} , these units have a biological meaning. In exponential growth $1/\mu_{max}$ represents the time it takes for a population to grow by a factor of e . It is related to the (minimal) doubling time, D , as $D = \ln 2/\mu_{max}$. So, in biological terms, NIR organisms will have an advantage in pulses that are shorter than some $6D$ (below some 10 times $1/\mu_{max}$; figure 3). For bacteria, although there is considerable variability, average doubling times are around 5 hours (Weissman et al. 2021). Therefore, for bacteria, recurrent pulse durations shorter than a day will benefit only NIRs, and above that, TORs will do better, but pulses exceeding a week, will not benefit either type. For plants, the analogous whole-plant relative growth rates vary between 0.1 and 0.4 per day (Price

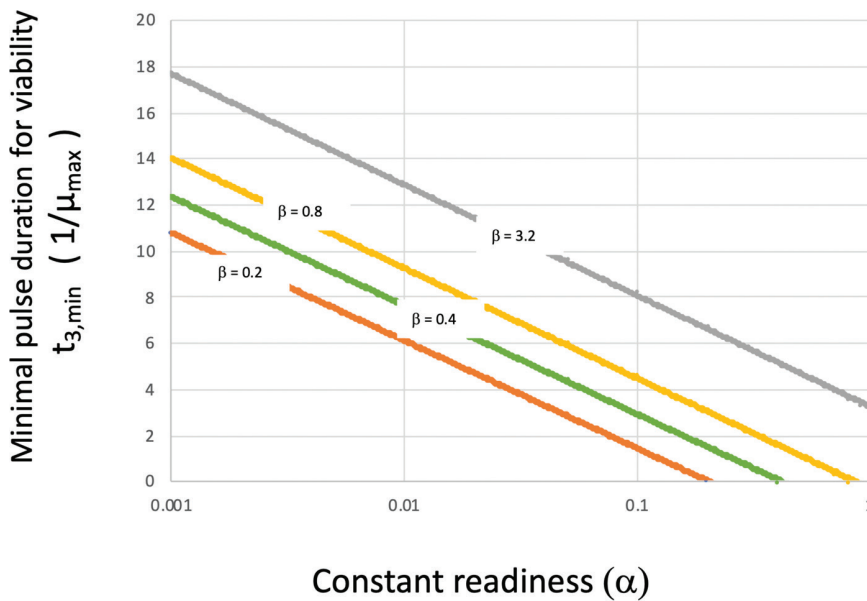


Figure 3. Minimal pulse duration for viability ($t_{3,min}$ expressed as multiples of the inverse of μ_{max}) as a function of level of constant reserve investment (constant readiness, α) for various values of late-pulse reserve investment (β).

and Munns 2020), and we can take 3 days as a typical doubling time. NIR plants will benefit from (soil) water pulses shorter than 18 days, but that will be insufficient for TOR plants. Pulses of water availability that exceed many months will not yield differential benefits to either type.

Importantly, however, all these predictions are derived from very simple, generic tenets that do not involve specific plant functional traits, so that they are therefore universally applicable. Pulse duration or size bestows benefits differentially between NIRs and TORs, and its variability can principally drive organismal specialization, in turn supporting differentiated ecosystem-level outcomes, which is a fundamental characteristic of the PRP (Schwinning et al. 2004). The predictions logically imply that shifts in pulse size distribution range will affect the functional types of organisms that can effectively grow, the spatial extent of their populations and their dynamic fate under climates changing in time or space. Experimental evidence consistent with this prediction has been presented: Imposed treatments with decreased average rain pulse size result in swift and very marked shifts in community composition of primary producers of biological soil crusts, favoring cyanobacteria over mosses (Reed et al. 2012), and favoring some species of cyanobacteria over others. Similarly, the predicted shift in plant species composition under regimes of differing pulse size have been presented (Jones et al. 2016). Traits that might implicate differential management of reserves among losers and winners, however, were not directly quantified in any of those cases.

On the other hand, it is not difficult to find principally NIR-like and TOR-like cases among arid-land plants. For example, perennial grasses such as *Bouteloua gracilis*

that dominate enormous areas of North America have shown a remarkably fast response to precipitation pulses. Not only leaf water status and photosynthesis but also root growth (Lauenroth et al. 1987) rapidly shift in a few hours after a rain event into an active state, returning to quiescence a few days after. These grasses invest constitutively in nonstructural carbohydrate reserves (Menke and Trlica 1983), lignocellulose, and in hardy crown tissue structures containing buds and tillers that together allow fast onset of growth. However, they produce only moderate amounts of seeds. Annual grasses that dominate California grasslands, by contrast, are examples of TOR-like plants: Comparatively, they grow swiftly without conspicuous investments in structures dedicated to improving survival under interperiod conditions, but they do so only during rather large pulses of precipitation (Huenneke and Mooney 2012). Toward the end of the pulse their

physiology quickly turns into the all-out production of reserves in the form of large amounts of seeds. The ultimate question for us remains this: Is there evidence that microorganisms also fit in this framework? Because its premises are only a pulsed nature of growth, the reliance on reserves as strategies, and the differential management of reserves by specific types, the question translates essentially to finding evidence that microbes rely centrally on reserve building and to find a functional differentiation between NIRs and TORs among them.

Microbial traits in drylands

Before we embark on the attempt to characterize traits of dryland microbes, we should consider that climatic definitions were not made with them in mind. Some microbes greatly exceed the perceived limits of temperature and water availability that underlay climatic cutoffs (Rothschild and Mancinelli 2001, Schulze-Makuch et al. 2018), and spatial environmental variation within a single climatic region can create noncompliant microniches. Texturally coarse soils of mesic climates, for example, unable to retain meteoric water inputs for very long do often sustain microbial communities typical of deserts in temperate climates (Smith et al. 2004). In hyperarid settings, the presence of surface pebbles that locally retard soil water evaporation allow the formation of hypolithic microbial communities, embedded in an otherwise barren landscape (Schlesinger et al. 2003, Warren-Rhodes et al. 2006). Therefore, paradigms that may ensue from the study of microbial adaptations to aridity will find full applicability outside of climatically understood drylands and will fail to apply in some instances within them. One should apply the concept of aridity in agreement

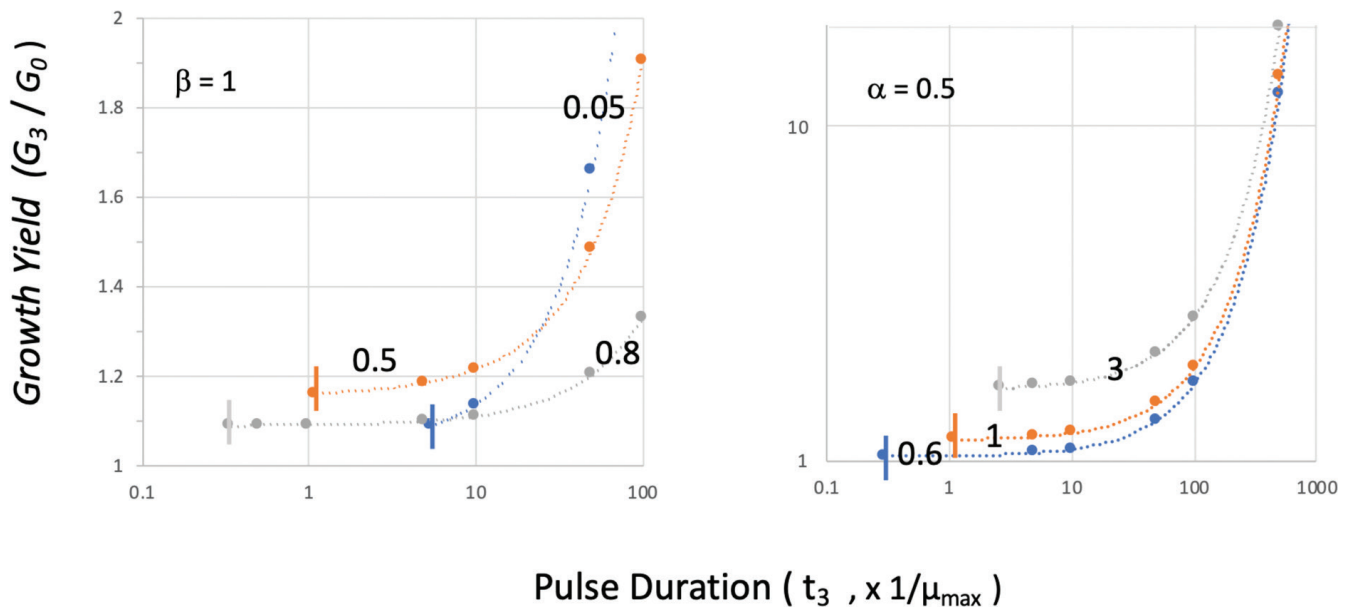


Figure 4. Dependence of growth yield (defined as fold increase in G over the duration of a pulse) on pulse duration (expressed as multiples of the inverse of μ_{max}), for various values of constant readiness α (left) and late-pulse investments β (right). Vertical bars indicate minimal pulse duration as per figure 3. Only moderate yields are ever attained with high α but positive growth is attained even with very short pulses. Higher yields can be attained by increasing β , but at the expense of higher thresholds for viability, and the beneficial effects become irrelevant for very long pulses.

with the implied outcome of biological activity hindrance by water scarcity. Still, several representative characteristics of dryland plant communities do in fact find parallels in their microbial coinhabitants. A direct evaluation of differential genomic capabilities as well as comparative surveys of microbial distributions reveal that microbial communities and their member microbes are uniquely adapted to arid conditions, as are desert plants and animals. Global distributional surveys of soil bacteria clearly point to a compositional differentiation in drylands from those in other climates (Angel et al. 2013, Neilson et al. 2017, Delgado-Baquerizo et al. 2018, Schulze-Makuch et al. 2018), a pattern that seems to involve preferentially rare species (i.e., species with a narrow niche; Bickel and Or 2021). These are traits they share with plant and animal communities. In fact, for a few specific microorganisms, we have sufficient evidence that their distribution is constrained to arid environments, implying a maladaptation to other climates (Hector and Laniado-Laborin 2005). Although it is true for microbes in most environments, we know relatively little about the specific nature of these differential adaptations, given that most microbial ecology efforts are not geared to establishing the natural history of particular microbes, their autoecology, but rather to establish emergent properties of microbial communities taken as black boxes. But it is precisely these organismal auto ecological traits that comprise the central pillars of the PRP. At most, changes in community composition can be used to infer trait-based patterns assuming that some traits have a phylogenetic correlation. But this exercise is fraught with perils, in that phylogeny seems to underpin certain

traits more strongly than others and also differentially so among major microbial groups (Martiny et al. 2015). The opposite concept is that of convergent evolution in which similar traits evolved along different evolutionary paths both in plants (Orlans and Solbrig 1977b) and microbes (Garcia-Pichel and Wojciechowski 2009)

Microbes in arid conditions do lead a life characterized by rare pulses of activity embedded in a regime of suspended animation (Lennon and Jones 2011, Schimel 2018). Because of the short generation times of microbes, community composition can change dramatically even within the duration of a single pulse, based on the resuscitation of dormant, rare species (Aanderud et al. 2015). This implies that selective forces acting on traits that sustain transitions from dormant to active states are at play. Metagenomic (Le et al. 2016) and metatranscriptomic (Rajeev et al. 2013) analyses of arid soil bacterial populations speak of the crucial importance of the capacity to repair genetic damage accumulated during inactive periods for an effective recovery from dormancy. Activation of DNA repair genes seems to be the absolute priority inasmuch as they constitute the very first wave of gene expression on microbial rehydration (Setlow 2007). The studies carried out on two desiccation-resistant model bacteria, *Deinococcus* (Cox et al. 2010) and *Chroococciopsis* (Billi et al. 2000) tell us a similar story about the relevance of damage repair. Adaptations to avoid photodamage, such as the synthesis of passive sunscreen compounds (Garcia-Pichel et al. 1992) or the increase in cellular ploidy to attain genomic redundancy (Cox et al. 2010, Sukenik et al. 2012), also speak of the importance of adaptations to increase

overall fitness by decreasing mortality during quiescence. Although synthesis of these components is accomplished during active periods of growth, their contribution to fitness takes place under metabolic dormancy, when active repair does not take place. The sunscreen scytonemin, for example, is common in cyanobacteria that thrive under pulsed growth conditions, including those from soil crusts and epilithic environments (Garcia-Pichel and Castenholz 1991) but has been recurrently lost through the evolution of the phylum Cyanobacteria in clades that adapted to more constant environments (Garcia-Pichel et al. 2019). The decoupling of light-harvesting systems from reaction centers in desert microbial phototrophs constitutes another example of a preventative strategy (Bar-Eyal et al. 2015), and so does the migration toward environmental refugia in anticipation of desiccation (Pringault and Garcia-Pichel 2004). Similarly, significant investment into spore formation (Setlow 2007) is common in saprophytic fungi and in at least two phyla of bacteria, the Firmicutes and the Actinobacteria (Lennon et al. 2021). These examples clearly speak for an anticipatory, integrative coordination between the system states of quiescence and active growth, a shift that can occur rather rapidly at the physiological and genetic levels (Rajeev et al. 2013, Oren et al. 2019). Therefore, microbes adapt to the pulsed nature of their environment, rather than to either the active or inactive phases in it. This brief review of microbial life strategies suggests that a preemptive accumulation of reserves (in the form of cellular machinery and energy reserves to fuel repair on activation, or as investment in costly secondary metabolites to avoid damage) could well play a role in the swift and effective use of short pulses of hydration and activity and may in fact underpin the adaptation of microbes to life in arid lands.

Size differentially affects how microbes and plants cope with a pulsed environment. The small size of microbes imposes constraints and opportunities that differ significantly from those affecting plants. Relevant processes scale with size (L), often because of the differential scaling of body volume (L^3) to surface area (L^2). In any attempts to test how the PRP applies to microbes, one should take those effects into account. For example, because the usefulness of sunscreens depends directly on the thickness of the teguments they are laid onto, plants can use sunscreens much more efficiently for photoprotection than microbes can (Gao and Garcia-Pichel 2011). Because conductive heat transfer scales inversely with size (Planinšič and Vollmer 2008), very small organisms equilibrate temperature with its surrounding virtually instantaneously. Temperature homeostasis simply cannot be a microbe's forte: Microbes must evolve to endure temperature shifts unscathed instead. Mass transport is very strongly scale sensitive. At small scales, a microbe's environment becomes essentially stagnant, diffusion becoming the main mass transport vehicle, but diffusion's effectiveness scales inversely with the square of distance. This is why bacteria do not need internal transport structures, and why

metabolite exchange among microbes at short range is quite effective, requiring little metabolic effort. Desiccation can be understood in similar physical terms, as the diffusional loss of water in a gradient of water potential, and therefore fractional water loss scales inversely with the square of linear size (Jakubczyk et al. 2012, Carrier et al. 2016). Again microbial cells will tend to equilibrate with their immediate surroundings virtually instantaneously and microbial cells will be as wet as their environment is. Attempting to keep water inside a microorganism by retarding evaporation using nondiffusive teguments (as some plants do using cuticular waxes) is principally a lost cause.

An important caveat for the generalizations above, however, is that aggregation of microbial cells into larger, coherent structures such as colonies or biofilms can reverse these physically imposed opportunities and limitations. Nutrient supply can be limited by diffusion when microbes come together into millimeter-sized aggregates or biofilms (Garcia-Pichel et al. 1999). When they do, they typically create microenvironments around such aggregates (Garcia-Pichel and Belnap 2001) because diffusion is insufficient to release their metabolic byproducts. In some extreme cases, such macroscopic aggregates can cause turbulent transport of nutrients through motility (Fenchel and Glud 1998), increase the albedo and equilibrium temperature of soil surfaces (Couradeau et al. 2016), or retain moisture for some time after a rain event (Scherer and Zhong 1991). Macroscopic aggregates of microbes must be independently evaluated for the relevance of such effects.

Do microbes also use activity pulses to gather reserves in preparation for quiescence? Microbes do produce organic and inorganic storage reserves, typically in the form of polymers that help them avoid high cellular turgor pressure: Polyglucose (glycogen, starch) and poly-beta-hydroxyalkanoates (PHAs) are carbon reserves. These type of reserves are prevalent among microbes (Mason-Jones et al. 2021). More specialized polymers, such as cyanophycin, store carbon and nitrogen, and polyphosphates store inorganic phosphorous (Kolodny et al. 2006). Colorless sulfur bacteria can even accumulate electron donors such as polymeric sulfur and acceptors such as nitrate (Schulz et al. 1999). Polymerization and mobilization of all of these reserves is responsive to pulses in availability of the respective nutrient (Dawes and Senior 1973), in patterns suggestive of a prioritization of storage over growth when resource depletion is imminent (Mason-Jones et al. 2021). The gathering of reserve polymers is generally considered a major physiological trait enabling microbial dormancy and the formation of seed banks (Lennon and Jones 2011). A genetic ability to produce abundant reserves, correlates in specific microbes with resistance to stress conditions (Madueño et al. 2018) and can demonstrably support resuscitation from dormancy (Klotz et al. 2016). Recent studies of gene expression in field populations of the cyanobacterium *Microcoleus vaginatus* from soil crusts during wetting or desiccation pulses showed

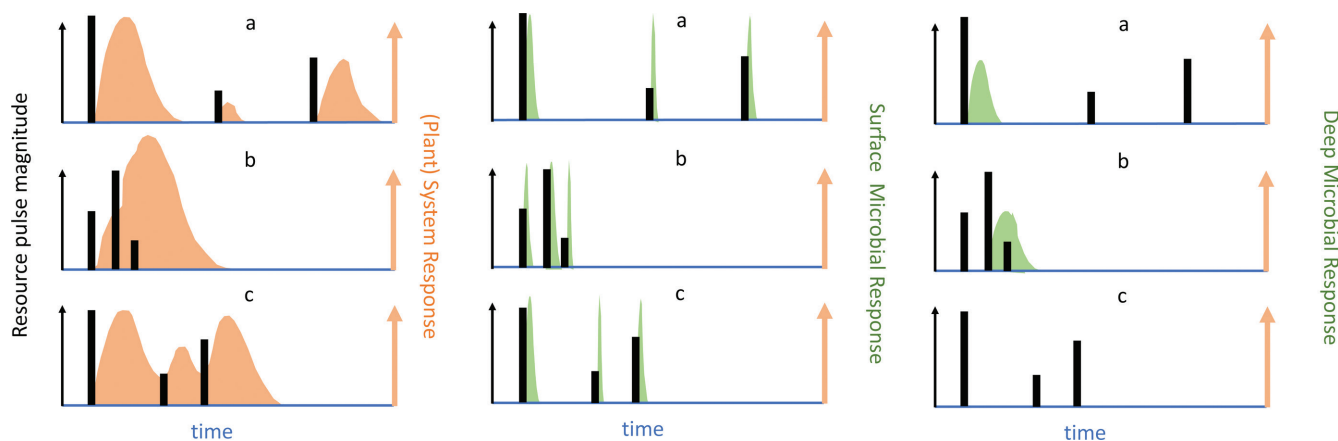


Figure 5. Noy-Meier's (1973) concept of the plant-system responses (shaded areas) to pulsed water resources (black bars) in the left panel, with its translation to microbial responses for NIR-like microorganisms close to the soil surface (middle panel) and for TOR-like microorganisms deeper in the soil profile (right panel). Panels (a) to (c) represent different pulse regimes.

the importance of reserve compounds in the context of overall gene regulatory acclimation: Genes for cyanophycin and polyphosphate synthesis were expressed heavily during the growth and wet phase (see figure 2), whereas those for the mobilization of both glycogen and polyphosphate reserves were strongly upregulated with the onset of desiccation, in the transition to quiescence phase of figure 2. Direct measurements and metabolic simulation have shown that *M. vaginatus* allocates more fixed carbon to polymers constitutively than other cyanobacteria (Jose et al. 2018), indicating that this microbe tends to be a NIR type, which is consistent with field experimentation. Both these facts are consistent with the pulse-reserve hypothesis as it pertains to carbon and nutrients, the reserves accumulated during wet times allowing the preparation for successful dormancy (i.e., anticipatory regulation) during drought. Other microbes are known for the accumulation of specific resources in preparation for desiccation or exit from quiescence phases (Klotz and Forchhammer 2017). The soil actinobacterium *Rhodococcus* upregulates the formation of ectoin (a compatible solute), and proteins to detoxify oxygen stress (LeBlanc et al. 2008). Such investments can be significant. UV sunscreen compounds, such as cyanobacterial scytonemin, can make up investments in the order of several percentage points of a cell's dry mass, becoming useful in comparison to active repair mechanisms only during quiescence (Gao and Garcia-Pichel 2011) and its biosynthesis is enhanced by desiccation (Fleming and Castenholz 2007). Glycogen or PHA can be accumulated to more than half of a cell's dry weight (Klotz and Forchhammer 2017, Madueño et al. 2018). Such level of accumulation would speak for associated values of the parameter β in our model easily exceeding unity.

The developmentally sophisticated formation of desiccation-induced spores (Sukenik et al. 2015), a strategy shared by fungi and several bacterial phyla, represents perhaps an extreme case of all-out late-pulse allocation to reserves (typical of TORs with low α) that enables extremely long

quiescence periods. The trade-off is that a relatively long new pulse with copious resources is needed to allow for an equally complex process of germination (Stewart et al. 1981, Dworkin and Shah 2010) before new resources can be effectively tapped, as is predicted by our model. Therefore, as in plants, not only do microbes prepare for dormancy through the gathering of resources, but examples of microorganisms adapted to either short or long pulses that manage these reserves differently can also be found.

Soil segregates between microbial NIRs and TORs

In Noy-Meier's (1973) framework, soil acts as a water repository that significantly extends water availability beyond the precipitation pulse, for organisms that can tap it (figure 5) and is a central consideration in the original and subsequent refinements of the paradigm (Ogle and Reynolds 2004). As one proceeds down the soil profile, water content suffers from diminished inputs (infiltration inputs will require larger pulses) but benefits from more moderate evaporative losses, so less water reaches deep layers but there it lingers over longer periods. So, pulse duration increases with soil depth (Sala et al. 1992). This differential distribution of water in the soil profile translates into a force for plant diversification, where NIR-tending functional types specialize in tapping surficial resources whereas TOR-like shrubs use mostly deeper water (Jackson et al. 1999). But how does this translate to soil microbial populations? We have seen how in principle the duration of a pulse for a microbe will tend to be as long as the water is available in its immediate surroundings. Undoubtedly, system responses that rely on microbially mediated processes are much faster than those mediated by plants (Austin et al. 2004). Consistent with long known empirical evidence (Linn and Doran 1984), soil microbial activity should follow the dynamics of soil water content along the profile and in time (figure 5). We can therefore expect that microbes will function for short periods at the surface (NIR territory), and for longer periods

as they move down the profile (increasingly, TOR turf). In fact, it is those spore formers in the Firmicutes and the Actinobacteria (TOR-like organisms) that tend to dominate zones deep in the soil profile (Fierer et al. 2003), where high water content episodes are rare but once they happen, they last for long time. In soil surface communities such as biocrusts, by contrast, TOR spore formers are typically exceedingly rare under normal conditions (Garcia-Pichel et al. 2003), although veritable blooms of spore formers can be brought about by long flooding of these crusts (Karaoz et al. 2018). Typical soil-surface communities, such as biocrusts, are inhabited by communities that respond swiftly, within minutes, to pulses (Scherer and Zhong 1991, Garcia-Pichel and Belnap 2001). The point has been made that the ecosystem contributions to carbon cycling of such communities is particularly important under regimes of short pulses (Cable and Huxman 2004). Furthermore, even within surface communities, plant interspaces are prone to experience more intensely pulsed conditions than the soil under plant canopies. Trait-based comparisons of microbial communities in these two contrasting environments from an arid setting show a significant enrichment of spore-forming microbes in soil under plants (more TOR-like in our framework), even when generic traits to resistance to desiccation were more enriched in the interspace soils (Goberna et al. 2014).

The mechanisms by which this is accomplished differ between plants and microbes. The shorter generation times of microbes allow this to take place at the level of community assembly, rather than just as evolutionary ecophysiological diversification. In fact, experiments show that even short-term variations in aridity can exert rather swift microbial community shifts in a variety of settings (Rothrock and Garcia-Pichel 2005, Castro et al. 2010, Barnard et al. 2013, Liu et al. 2019). In a mesoscale experimental set up, soil crust cyanobacterial communities suffered stark shifts in organismal dominance within a few years of either a decrease in overall precipitation or a 2-month delay in the onset of the rainy season (Fernandes et al. 2018), promoting dominance of NIR-like, drought-resistant *M. vaginatus* over other cyanobacteria. These dynamic compositional shifts find consistent parallels in the geographical distribution of the same cyanobacterial taxa along varying climates (Fernandes et al. 2021). The patterns reviewed above indicate that although the effects on diversification operate through alpha diversity in plant communities, they do so through beta diversity along the soil profile in microbial communities. In summary, both in plants and in microorganism, the pulsed nature of water distribution in the soil is a force for niche partitioning and evolutionary diversification, as was postulated by Noy-Meir (1973).

Formally testing the model

We have sought in the present article to assess the NIR or TOR model for consistency with current organismal knowledge. Although the phenomenology reviewed is consistent with its predictions, it is only indirectly and qualitatively so,

and it encompasses only the few organismal types whose biology was informative enough. It will be important in the future to test the model more formally, quantitatively, and generally. A conceptually simple experimental test could make use of imposed variations in pulse duration and pulse number as the cumulative pulse time is kept constant, as has been previously used to assess effect at the community or ecosystem level (Jones et al. 2016) but with a focus on quantitative determination of the main parameters in the model: μ , α , and β . The expectation is that experimental increase in pulse frequency and reduction in pulse duration will result in changes in microbial community composition that favor the presence of organisms with elevated α and lower μ . Alternatively, one could seek a correlative validation by comparing the average NIR versus TOR character in locales selected along geographical gradients of pulse size distribution. Naturally the duration of experimental treatments will have to allow for differences in generation times between plant and microbes. In the case of microbes, determination of α , β , and μ can be best performed using relevant isolates in culture. For plants, single-species specimens for analyses can be easily obtained from the field (Gremer and Sala 2013). Quantification of α and β is rather straightforward using biochemical analyses for known reserve compounds (Del Don et al. 1994, Martínez-Vilalta et al. 2016) during the appropriate time (growth phase for α , or initial quiescence phase for β).

Organismal traits can also be principally derived from (meta)genomic information directly from natural microbial communities. For example, genomically coded information can be used to indirectly gauge habitat breadth (Barberán et al. 2014), maximal growth rates (Weissman et al. 2021), or nutritional modes (Chen et al. 2021) of specific phylotypes. Furthermore, comparative analyses of genomic complexity in the genes underlying particular traits provides proxies for the relative importance of a given trait in a given setting (Cao et al. 2020). In some cases, organismal traits can be assigned to particular phylotypes on the basis of sequence similarity to known organisms (Goberna et al. 2014, Couradeau et al. 2019), making it principally possible to derive organismal traits from the most common form of community data analyses (i.e., 16S rRNA amplicon sequencing), although this requires assumptions of phylogenetic conservation that are far from guaranteed (Martiny et al. 2015). Metagenomic approaches are much preferred in this context. To test predictions regarding the NIR–TOR continuum, genomic or transcriptomic proxies for its three main parameters (μ , α , and β) can be readily envisioned. Ribosomal codon use bias can be used to gauge the maximal growth rates commonly realized by an organism in its habitat, as it reflects adaptations of the protein synthesis machinery to those maximal rates. This will gauge our parameter μ (rather than our μ_{\max} , which defines a theoretical maximal growth rate for any organism under a given set of conditions and resources). Although the relative importance of reserves in a given microbe can potentially be ascertained by the presence,

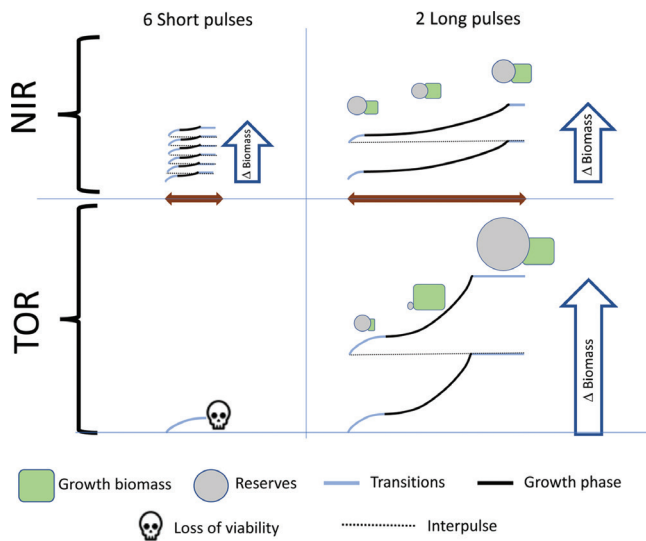


Figure 6. Conceptual model of the organismal strategy continuum for the management of reserves under pulsed activity regimes of varying pulse length. Most organisms will find themselves in the continuum between nimble responders (NIR) and torpid responders (TOR). Graph compares the net biomass yield under constant total pulse time, with either two large pulses or six short pulses one-third as long, for NIRs and TORs. If pulses are short enough, TOR types cannot accommodate their long transition times and fail to complete the transition (lower left) but NIR types can (albeit with low yield; top left). If pulses are long, faster growth rates result in higher biomass yields for TORs than for NIRs. The differential levels of reserve and growth biomass through a pulse in each type are also indicated.

relative abundance and complexity of the genes that code for their synthesis and mobilization (Rajeev et al. 2013), the direct derivation of proxies for α and β , is probably more complex, if not impossible, because the genetic underpinning of constitutive (α) and end-of-cycle (β) reserves is likely shared. An assessment of relative gene expression levels during growth and transition phases will be required, which will necessitate the use of time-resolved (meta)transcriptomics during actual pulse experiments.

Conclusions

Yes, on the basis of available evidence, the PRP works in microbes and plants, although direct rigorous testing would be desirable. However, the mechanisms that evolved to cope with an environment characterized by resource pulses followed by prolonged periods of quiescence are different for microbes and plants. Size determines the mechanisms that make organisms thrive in this highly variable and extreme conditions. We do find examples approaching NIR and TOR organisms in both plants and microbes. In many regards, Noy-Meir's (1973) vision of the pulse-reserve dynamics shaping the natural history of desert organisms is applicable

to microbes, which show a diversity of adaptations much richer than he could have envisioned when he lumped microorganisms under the term *poikilohydric*. These adaptations are in many regards convergent with those of plants, although they are often modulated by scaling constraints. The PRP clearly holds across levels of biological organization for carbon reserves and for specialized structures when understood as a function of strategies to manage necessary reserves (figure 6). The consequences of a pulsed water regime for functional diversification hold across organismal boundaries but operate largely through organismal diversity in plants and more intensely through community assembly in microbiomes.

Although the current formulation of our model suffices to predict many of the predicted outcomes of the PRP, it does not explicitly include two aspects of arid land organismal adaptations that may *a priori* be considered relevant: the capacity for acquisition of water reserves and the length of periods in between pulses. Acquisition of water reserves serves the purpose of effectively lengthening the pulse duration and is a common adaptation among dryland plants such as cacti and euphorbias. The issue with water reserves is much tougher for microbes than for plants, because of the size constraints discussed above, although extracellular polysaccharide investments may slow rates of water loss (Roberson and Firestone 1992, Chenu 1993, Hart et al. 1999). This is clearly so in microbes that build macroscopic thalli such as *Nostoc commune* (Scherer and Zhong 1991), or in microbial assemblages that attain sufficient mass, but are unlikely to make much of a difference for single, typical microbial cells. This may be the reason why only small organisms (or small independent parts of plants, such as seeds) can truly be anhydrobiotic (Potts 2001, Alpert 2005), surviving a temporary loss of all (or most) of their water. Reliance on anhydrobiosis is apparently the only viable solution for small beings. Drought resistance in macroorganisms, by contrast, is always dependent on preventing water loss. Increasing length of pulse interperiods will decrease the capacity of dormant cells to resuscitate as they accumulate environmental insults that will have to be repaired. In our framework, this will mean that organisms faced with long droughts will experience a decrease in the efficiency with which reserves can be retrofitted into growing biomass, which we had assumed to remain constant and high. This is likely to be countered by increases in β to make up for the loss in efficiency, which in turn will increase the minimal pulse size for viability and, therefore, likely affect NIR types more negatively than TOR types. These aspects should be given more detailed attention in future work.

Given that continental microbial ecosystems similar to those now present in drylands are known to have existed (Simpson et al. 2013, Beraldi-Campesi et al. 2014) and to have driven global biogeochemical cycles (Thomazo et al. 2018) since the mid-Precambrian, long before the advent of land plants, perhaps the fact that microbes follow the PRP should not come as a big surprise, because opportunity

makes the thief. An apparently universal differential aspect of the biology of living organisms under arid regimes is that fitness under pulsed conditions in a background of water scarcity becomes a strong function of strategies to prevent death during periods of quiescence, whereas mechanisms geared toward promoting fast growth become less relevant than they might be in mesic environments. In other words, desert organisms, including microbes, can be expected to be hard to grow but hard to kill. Microbes probably found that out first, the hard way.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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