1 Title 2 Microbiome Rescue: Directing resilience of environmental microbial communities 3 Author 4 5 Ashley Shade\*, ORCID 0000-0002-7189-3067 6 7 Affiliations 8 1. Univ Lyon, CNRS, INSA Lyon, Université Claude Bernard Lyon 1, École Centrale 9 de Lyon, Ampère, UMR5005, 69134, Ecully cedex, France. (Present address) 2. Department of Microbiology and Molecular Genetics, Michigan State University, 10 11 East 12 Lansing, MI 48824 USA 13 3. The Plant Resilience Institute, Michigan State University, East Lansing, MI 48824 14 4. Department of Plant, Soil and Microbial Sciences, Michigan State University, East 15 Lansing MI 16 48824 USA 17 5. Program in Ecology, Evolution, and Behavior, Michigan State University, East 18 Lansing, MI 48824 USA 19 6. The Great Lakes Bioenergy Research Center, Michigan State University, East 20 Lansing, MI 48824 USA

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Abstract

Earth's climate crisis threatens to disrupt ecosystem services and destabilize food security.

Microbiome management will be a crucial component of a comprehensive strategy to maintain

stable microbial functions for ecosystems and plants in the face of climate change. Microbiome

rescue is the directed, community-level recovery of microbial populations and functions lost

after an environmental disturbance. Microbiome rescue aims to propel a resilience trajectory for

community functions. Rescue can be achieved via demographic, functional, adaptive, or

evolutionary recovery of disturbance-sensitive populations. Various ecological mechanisms

support rescue, including dispersal, reactivation from dormancy, functional redundancy,

plasticity, and diversification, and these mechanisms can interact. Notably, controlling microbial

reactivation from dormancy is a potentially fruitful but underexplored target for rescue.

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# Introduction

altered by a disturbance and is a critical component of ecological stability [11–13] (**Figure 1**). Environmental microbiomes provide critical functions that feedback on Earth's climate[1–4]. Therefore, understanding and predicting how disturbances alter microbiome functions is a

Resilience is the capacity of a system (plant, soil, or microbiome) to recover after being

requisite part of a comprehensive strategy to stabilize systems and adapt to climate change. Also,

because microbiomes are synergistic components of soil and plant systems [5–7], microbiome

management [8–10] will become essential to preserve ecosystem services and food security by supporting soil and plant resilience.

Across many ecosystems, microbiomes are repeatedly observed to be highly sensitive but often also highly resilient to various disturbances[11–13], even after those disturbances that seem intense, extreme, or unnatural (e.g.[14–18]). Despite decades of research in microbiome disturbance ecology, there remain critical knowledge gaps about the ecological and evolutionary mechanisms that drive resilience and their relative contributions to microbiome responses to disturbance. How can the field advance from simply identifying and describing patterns of microbiome responses to disturbances? How can the field move toward prediction, forecasting, and microbiome management to maintain critical microbial functions on a rapidly changing planet?

Microbiome rescue is the successful recovery of multiple functional populations that were compromised during a disturbance. Thus, the collective rescue of disturbance-sensitive populations can drive a community trajectory of functional resilience. By advancing the understanding of the ecology of microbiome resilience via rescue, microbiome interventions can be directed, developed, and tested for utility in soils and plants, including crops. Several excellent recent pieces have offered synergistic ideas to those presented here (e.g., [12,19–21]). While acknowledging and bridging from these works, this work's emphasis will be to explore a conceptual framework that can be investigated to inform the ecological mechanisms of resilience. These mechanisms can support plants and soils facing climate change by directing the rescue of microbial communities.

A distinction with *microbiome rescue* is the emphasis on the resilience of the microbial community and its functions as a system. In contrast, previous works have focused on the rescue

of host-supportive microbial populations and outcomes for the host ("microbial rescue," e.g.,[19]. Related, "community rescue" has been specified as populations that evolve in response to a lethal disturbance (e.g. [21]), with subsequent research progressing to consider the possibility of ecological adaptation alongside evolution (e.g., [16,17]).

Main Text

The microbiome rescue framework (**Figure 2**) is inspired by evolutionary concepts to alleviate populations at risk of extinction due to dwindling sizes and bottlenecks [22]. Microbiome rescue connects to the ecological concept of temporal turnover, which is the replacement of some populations with others over time [23]. Different types of rescue, and the mechanisms that support them, could interact or synergize to maximize the community trajectory of resilience toward complete functional recovery (**Figure 2**). Key parameters to consider for rescue include the degree and discretion of mortality imposed by the disturbance (*disturbance selectivity*, **Box 1**) and the most probable rescuers to support the most likely mechanism in the post-disturbance environment (**Figure 2**).

Demographic rescue (Figure 2) is the reintroduction of microbial populations that were fully sensitive to the disturbance. Mechanisms of demographic rescue include the dispersal of cells across a regional landscape and reactivation from the local dormant pool. Conspecific populations are the rescuers because they are likely to offer similar functions. For simplicity, conspecific refers to populations with highly similar or identical genotypes to the disturbance-sensitive populations, though it should be acknowledged that there can be within-population heterogeneity in function. The success of demographic rescue relies on the ecological selection of the original microbiome populations and functions in the post-disturbance environment.

Notably, the post-disturbance environment may not be identical to the pre-disturbance environment, and microbial activities may facilitate environmental recovery or redirect to a different environment.

Microbiomes facing short-term (pulse) disturbances that temporarily alter the environment may be more likely to recover via demographic rescue than microbiomes facing long-term (press) disturbances that alter the environment enduringly. Short-term environmental disturbances prime for demographic rescue include weather-related events like drought, flood, heat waves, and cold snaps. Because demographic rescue is a straightforward replacement of lost microbiome populations with the same populations, it may be reasoned that it has the lowest difficulty and highest potential compared to the other rescue types. Thus, demographic rescue may be effective even in situations of an incomplete understanding of microbiome functions, as the original functions may be expected to be retained given the recovery of the pre-disturbance membership. One example of demographic recovery (of many in the literature) was an observation that temperate soil microbiomes exposed to multiple years of elevated temperature recovered in their structure after the local temperature returned to normal [14].

Functional rescue (Figure 2) is the supplementation of functional redundancy in the community. In other words, heterospecific members are (re)introduced or activated, leading to a different composition but equivalent functionality after the disturbance. As true for demographic rescue, mechanisms of functional rescue include regional dispersal and local reactivation, plus the mechanism of local functional redundancy. The most likely rescuers of the sensitive populations include heterospecific populations that are not genetically like the lost population but provide similar functions, potentially at similar rates and efficiencies. Depending on the function(s) of interest to recover, possible rescuer populations may be predicted by

(meta)genomes or traits that can inform as to overlapping functional pathways and responses. For example, some microbial genes that support transformations within the nitrogen cycle are broadly distributed taxonomically and biogeographically [24,25], and so it has been suggested that their high redundancy may lead to stable functioning despite changes in the environment (see [26]). Functional rescue may support recovery after either press or pulse disturbances and may be especially useful in situations of point environmental pollution (e.g., chemical spill). For example, pollution-induced community tolerance (PICT) considers how community tolerance to a pollutant may improve with exposure and support stable maintenance of functions, despite the inevitable loss of pollutant-sensitive populations [27]. The success of functional rescue relies on the ecological selection of the functionally equivalent microbiome populations in the post-disturbance environment. As a directed microbiome intervention, it may be reasoned that functional rescue has medium-high difficulty due to the requirement first to understand and target specific, desired functions to ensure maintenance in the post-disturbance microbiome.

Adaptive rescue (Figure 2) is when the surviving individuals of disturbance-sensitive

populations adapt phenotypically to the disturbed conditions and persist but maintain their original genetic background. Thus, the rescuers are the surviving members of disturbance-sensitive populations. An example of adaptive rescue is phenotypic heterogeneity within a population that *a priori* manifests both sensitive and resistant phenotypes to the impending disturbance. In this case, the resistant phenotypes survive the disturbance, and the sensitive phenotypes do not, but in the end, the population can recover. Adaptive rescue can also include phenotypic plasticities, such as temporary entry into protected states like spores, cysts, or other resistant phenotypes (e.g., persister cells that are insensitive when exposed to antibiotics and

remain viable [28]). Adaptive rescue also could manifest as resistance and may be common among microbial populations that inhabit ecosystems that experience disturbance regimes.

The success of adaptive rescue relies on the ecological selection of the surviving cells in the post-disturbance environment, which can be driven by non-lethal exposure to the disturbance, building plastic tolerance before a subsequent exposure of greater intensity [16,17,21]. As a directed microbiome intervention, adaptive rescue may be relatively challenging to direct due to the need to understand and responsively control molecular cues for the phenotypic adaptations, either responding before or immediately following the disturbance.

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While phenotypic mechanisms underpin adaptive rescue, genotypic mechanisms underpin evolutionary rescue. Evolutionary rescue (Figure 2) is when multiple local populations genotypically diversify to have a selective advantage over kin sensitive to the disturbance or disturbance regime, with no cost to functional performance (also called "community rescue" [21]). Diversification occurs in microbiomes via horizontal gene transfer [29,30] or beneficial mutations [30,31], leading to selective sweeps. The most likely rescuers are surviving individuals of partially sensitive populations that have diversified with positive selection in the postdisturbance environment but without cost to function. In addition, rescuers could be non-kin contributors of advantageous genes via horizontal gene transfer. Evolutionary rescue may be more likely following a press disturbance, within a disturbance regime, or in co-selection with a host also experiencing the disturbance. Indeed, previous studies have demonstrated the potential for evolutionary rescue given exposure to compounded press disturbances [16,21]. Evolutionary rescue may be difficult to achieve as a directed microbiome intervention. However, recent work suggests that in specific situations, such as when high-diversity communities are dominated by competitive interactions, diversification via horizontal gene transfer of resistance genes may

increase community stability after disturbance [32]. In addition, there is excitement about the potential of directed microbiome engineering or co-evolution ex-situ to contend with anticipated disturbances [33]. Host-engineered or co-evolved microbiota could be applied as probiotics or bio-inoculants to test their efficacy for rescue *in situ*.

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Within the range of potential microbiome responses to disturbance, there are several junctures that could support microbiome resilience via rescue (Figure 1, blue stars indicating potential intervention opportunities). Specifically, demographic and adaptive rescue could be used to promote resilience in structure (single-state "engineering" resilience), and functional and evolutionary rescue could be used to promote functional redundancy. According to the ecology literature, interventions to prevent a regime shift (i.e., a fundamental change in the community structure and function apparent by a shift in dominant nutrient and energy sources) are possible if they occur before the system crosses a critical threshold, past which ecological forcing will inevitably lead to a regime shift [34–37]. In the case of a successful rescue intervention before the critical threshold, the trajectory of recovery can proceed toward either resilience in structure or functional redundancy. With sufficient knowledge of system dynamics, the microbiome could be rescued after a regime shift with a radical intervention (ecological resilience), likely an intervention that will couple ecosystem restoration with microbiome rescue. Fecal transplants in the human gut microbiome are exemplary microbiome interventions (of a notable few) given regime shifts [38].

While microbiome resilience could proceed "naturally" without intervention as the outcome of ecological assembly processes [30,39,40](and often does after a relatively minor perturbation), the aspiration is to understand those deterministic mechanisms and to leverage them to achieve maximal effectivity and efficiency in resilience via rescue. Several general

strategies could be favorable as rescue interventions. Each of these general strategies would need to be tailored and tested to enrich populations that offer the functions lost after disturbance. As one strategy, rescue could be directed with non-biologically active additives that enrich particular microbiome members or functions. This strategy is perhaps best demonstrated in the human gut ecosystem with prebiotics, which are typically non-human-digestible foods that enrich bacterial fermenters to support gut health [41]. In agriculture, "prebiotics" may include plant or waste products that enrich community members to improve soil, such as biochar, treated wastewater effluent, and others [42]. As another rescue strategy, reactivation from the dormant reservoir could be directed with environmental or molecular signals; for example, free amino acids could reactivate endospore-forming Bacillota lineages, and resuscitation promotion factors (rpf) could reactivate exospore-forming Actinomycetota lineages [43,44]. Also, microorganisms could be supplemented into the system directly as bioinoculants, such as in the case of a plant growth-promoting bacterial strain discovered for wheat [45] or as considered with native arbuscular mycorrhizal fungi for plant community restoration [46]. However, bioinoculation approaches often are challenged by a lack of persistence or activation of the added microorganisms [47]. Additionally, more complicated rescue strategies may include repressing competitors or enriching cooperators (see, for example, the biotic interactions section in [48]), engineering plant hosts to improve microbiome recruitment [49,50], or restoration of the environment to support conditions that select for the desired microbial populations (e.g., [51]).

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When considering how to direct rescue, it is important to consider whether microbiome rescue towards recovery to its pre-disturbance state is aligned with the desired functional outcome. Take caution that a pre-disturbance functional state of a microbiome may not

necessarily be "natural" (e.g., without the legacy of anthropogenic influence) or optimal to achieve the desired microbial functions.

205 Start Box 1

Box 1. Who is resistant, who is lost, and who should be rescued? Considerations of mortality after disturbance to inform rescue strategies.

(Figure A.)

Microbiomes are comprised of many populations that collectively exhibit a range of susceptibilities to a disturbance, and the degree of loss of microbiome populations or functions will directly affect determining effective rescue strategies. For rescue, it is important to consider which microbiome populations are *selected against*, given the disturbance. These are the populations that may need to be rescued as a cohort. Here, terms are proposed to describe the disturbance's community-level mortality, including the many comprising populations and their responses. The terms combine concepts of fitness and selection with that of disturbance intensity and can inform how complicated it may be to initiate a resilience trajectory via rescue.

Selective mortality is the complete or nearly complete loss of disturbance-sensitive populations. The disturbance is lethal to a subset of the microbiome populations but inconsequential to other populations, which retain full viability. Examples of disturbances that can result in selective mortality include selective antibiotics or heavy metals or changes in temperature, pH, or other abiotic gradients that explain the principal niche axes of microbial habitats. Selective mortality can disrupt or reorganize biotic interactions among surviving microbiome populations. Indeed, reconstituting biotic interactions may be necessary for microbiome resilience [52] if those interactions evoke inter-dependencies that are relatively more important than environmental drivers for preserving functions. There also are potential indirect

losses or gains among the insensitive populations, for example, due to release from competition or loss of a synergistic partner [53,54]. Therefore, understanding how the network of microbiome interactions determines community functions could be critical for directing rescue.

Partial mortality is when a disturbance acts equitably on all populations such that all populations decrease in size, but few are entirely lost to extinction. Partial mortality can occur if there are physical protections for the microbiome, as in a structurally heterogeneous environment. For example, a forest fire that burns only the top five centimeters of soil may be reseeded by protected microbiome members that survived at lower depths. A disturbance resulting in partial mortality may be the best-case scenario for rescue, as the pre-disturbance populations persist and may collectively recover with minimal intervention as the environment recovers.

Notably, several studies report that a low-intensity disturbance that results in partial or selective mortality can equip enduring populations for survival upon subsequent exposure to a high-intensity event that would otherwise be expected to induce lethality (e.g., recently, [16,21,32]). This scenario also has relevance in contexts of compounded disturbances [55].

Finally, *mass mortality* is all microbiome populations' complete or nearly complete local extinction. Mass mortality may occur after an extreme, intense, or unnatural disturbance, such as a volcano eruption, highly toxic chemical spill, or severe radiation exposure. In the case of mass mortality without intervention, primary succession proceeds from a "blank slate" environment [39,40], typically seeded by immigrating cells dispersed from the regional metacommunity. A disturbance event that results in mass mortality offers the maximum control and potential for the orchestration of microbiome rescue because there are no biotic contingencies in the disturbed environment, like competition or invasion resistance. After mass mortality, microbiome rescue

would likely need to be paired with ecosystem restoration to facilitate the functional resilience of the microbiome.

250 End Box 1

Controlling microbial activation is an underexplored target for rescue

Dormancy is a reversible state of low metabolic activity employed by diverse microbial lineages as a bet-hedging strategy in unfavorable conditions [56]. Furthermore, dormant states are standard among microbial populations in the environment, with soil reported to have >80% of cells and >55% of taxa persisting in a dormant state at any time [56]. The dynamics of microbial dormancy include the process of inactivation (also called initiation into dormancy) and reactivation (also called resuscitation) (**Figure 3**)[57]. Both inactivation and reactivation can be either stochastic or deterministic processes. In cases of deterministic dynamics, environmental or biological signals may cue the start of the process. There is also the case of scout cells, in which a stochastic reactivation of one cell is followed by a microbial-mediated cue to reactivate dormant kin in a conducive environment [58].

Though studies that consider microbiome activation dynamics remain few, the studies that report activity have observed signals of both reactivation and inactivation during and after environmental changes [56–60], suggesting that responsive switches in activation may be common. In addition, there is a vast literature on soil "priming," which shows that some microbiome members are more prone to respond readily to resource inputs, which is attributed to differences in their initial activity statuses as well as to their resource preferences (e.g., [59–64].) Our soil warming experiment showed that reactivation alone contributed 18% to microbiome resilience [65]. In this study, the activating taxa were different from those active before the warming, suggesting the potential for functional redundancy.

Reactivation offers potential advantages as a mechanism for either demographic or functional rescue. It could leverage existing local microbiome diversity without the need to introduce nonnative populations and thus target local dormant populations likely to be adapted to the recovered environment (if so, before the disturbance). While the long-term persistence of desired microbiome populations can be a challenge for bio-inoculation (e.g.,[47]), reactivated cells may likely persist in the local environment because they offer dormant phenotypes that survived the disturbance. Cue-responsive dynamics offer an apparent environmental- or signal-based intervention to control the activation. Finally, reactivated populations may be more likely to fit into the recovered biotic context because of legacy interactions within the microbiome. For these reasons, intensified research efforts toward understanding reactivation as a directed rescue mechanism to support a resilience trajectory are critical.

#### Conclusions

Microbiome research is at a critical moment to accelerate fundamental, ecological knowledge of microbiome resilience that will direct the development of microbiome-enabled solutions for ecosystems and hosts facing climate change. Foremost, high-quality and extensive microbiome time series that capture disturbances are requisite. For comparisons and to draw out generalities, representative time series are needed from communities and ecosystems that scale in complexity from controlled mesocosms in the laboratory to the highest-diversity field ecosystems. When analyzing these time series, there is a need to measure and quantify resistance and resilience using metrics that are transferrable and comparable across systems and studies, and a need to adopt and adapt quantitative modeling of dynamic systems, including Bayesian approaches to enable adjustment of priors as new data points are observed over time. For a time

series, it is also crucial to assess active taxa and to determine how activity status may switch during and after disturbance. Several technologies offer a range of precision for determining the active microbiome populations (e.g., bio-orthogonal non-canonical amino-acid targeting with cell sorting and sequencing (BONCAT-FACs) [66], quantitative stable isotope probing (qSIP) [67,68], 16S rRNA:DNA ratios [61]), but DNA-based microbiome sequencing alone is limited, and especially for environmental communities that harbor many inactive cells and taxa, like soils.

There are ample gaps in our understanding of the biology and ecology of dormant strategies of environmental microbial. Within an ecosystem, what is the composition and structure of its dormant pool, and how does this compare to the active pool? How does the dormant pool change over time and space? What is the distribution of longevity and viability of cells in the dormant pool? For a population, how variable is the timing of their reactivation? Do they have signals for switching between active and inactive, and what are they? These fundamental questions are yet-unanswered for the majority of environmental microbial taxa.

In addition, we need to improve our understanding of the role of eco-evolutionary dynamics in microbiome disturbance responses and, specifically, to better account for the different contributions of bacterial diversification (via plasmids, phage, and transformation) to resilience and different types of climate disturbances. This knowledge will enhance insights into the evolutionary mechanisms of resilience and their utility for rescue.

Finally, it will be critical to prioritize which microbiome functions and taxa are useful for resilience, including which will be critical or supportive of functions given future climate projections. Some loss of microbial biodiversity is inevitable, but many populations are inactive or offer redundant functions. When samples for microbiome analysis are collected and stored

appropriately, rich data from long-term ecological research or long-term climate experiment sites (e.g., [69,70]) can offer insights into which microbial taxa are likely to survive or thrive under different climate scenarios. It will be critical to continue to couple insights from gradually changing conditions (e.g., elevated mean temperature and atmospheric carbon dioxide) with scenarios of extreme pulse disturbances (e.g., heat waves, drought) to provide "worst case" assessments of the most enduring microbial populations and their functions. Together, these directions will complement the understanding of microbiome resilience and rescue efforts to retain or recover critical microbiome functions for plants and soils, given climate change.

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- Competing interests
- 335 The author declares no competing interests.

## Data Availability Statement

No new data or code was generated to produce this work.

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- 529 Figure Legends
  - Figure 1. An overview of microbiome responses to disturbance as expanded from Allison and Martiny 2009 [71]. Resistance, resilience, functional redundancy, and regime shift are possible microbiome outcomes after disturbance (orange lightning bolt). The two microbiome response variables are structure (composition and relative contribution of taxa, squares) and function (performance or output from the community, ovals). Gray arrows show disturbance-induced microbiome trajectories. Potential points of intervention that may be conducive opportunities for microbiome rescue are shown with blue stars, with alternative trajectories as intervention outcomes shown in yellow lines with directional arrows. The first microbiome outcome, resistance, is when the microbiome is insensitive to the disturbance in structure and function and remains unchanged after the event. The second outcome, resilience (a.k.a. "engineering resilience"), is when the microbiome is altered in both structure and function in response to the disturbance but eventually recovers in both variables. The third outcome, functional *redundancy*, is when the microbiome structure remains altered after a disturbance, but the function recovers fully. Redundancy is attributed to different microbial populations capable of replacing one another functionally without measurable consequences for performance and is arguably expected for highly diverse microbial communities. An additional outcome, regime shift, is when structure

and function are fundamentally altered and do not recover, often with apparent changes in the energy and resource availability or utilization that indicate an alternative state assumed by the community. The inset "ball and socket" diagrams show the conceptual relationship between (a) "engineering resilience," which occurs within a single state, and (b) "ecological resilience," which transverses multiple states. The critical threshold (green dashed line) is the point past which a regime shift is inevitable and is often predicated by increased variance/decreased temporal stability in the system. Interventions before the critical threshold are thought to be more likely to be successful (dark blue star), while interventions after the critical threshold are thought to be more radical to have a chance of success (light blue star). However, more empirical research is needed in microbial systems to understand multi-state dynamics and their potential generalities.

Figure 2. A framework for microbiome rescue to recover critical functions after disturbance. Disturbances can lead to the mortality of sensitive populations. Demographic, functional, and adaptive rescues rely on ecological selection. Evolutionary rescue relies on diversification (gain of new genetic material) that offers an advantage given the disturbance but has no functional cost. Microbial shapes that share the same color and shape represent individuals from the same populations. Microbial shapes with filled color and solid lines represent active individuals, and shapes with no fill and dashed lines represent sensitive/dead individuals.

Figure 3. Microbial dormancy transitions can be stochastic (blue arrows) or deterministic (black arrows). For both inactivation and reactivation, microbes can (a) respond to

environmental changes (orange lightning bolt symbol) or (b) change to the other activity state stochastically. For reactivation, there is also the potential for receiving cues from scout cells (c, cue indicated by the triangles), in which some members of the dormant pool reactivate stochastically (c-1) but, if finding a favorable environment, produce a released signal to reactive kin cells (c-2) and initiate collective reactivation (c-3). Deterministic cues for reactivation may be targets for managing microbiome resilience rescue; deterministic cues for inactivation also may promote population persistence during a disturbance. However, dormancy strategies and their drivers are unknown or not well understood for most environmental microbial taxa.

Figure A (Box 1). Understanding disturbance selectivity can inform rescue strategies and their likelihood of success. In this diagram, different microbial populations are represented by different shapes and colors. Filled shapes and solid lines represent active members, and unfilled shapes with dashed lines are members sensitive to the disturbance and deceased. Disturbances that act indiscriminately on a microbiome can cause *mass mortality* (A) of all populations, leading to their local extinction. In heterogeneous environments or with disturbances of moderate intensity, *partial mortality* (B) can occur, in which most populations suffer some loss of members to the disturbance but retain other viable members locally. Finally, *selective mortality* (C) results when disturbances remove or severely reduce the membership of a subset of sensitive populations while at the same time leaving viable resistant populations. Examples of potential recovery outcomes of the microbiome are presented for each rescue type in Figure 2.

Annotated references (alphabetical)

Coyte et al. 2022 bioRXiv investigated the eco-evolutionary outcomes of mercury resistance gene transfer using theoretical and experimental approaches and related these transmissions to the stability of the community as an average, as well as to recipient and donor populations. Thus, this work has implications for understanding different population responses to mechanisms that support resilience and rescue within disturbances that cause selective or partial mortality.

Díaz et al. 2021 provide one of the few comprehensive studies of success in the discovery and application of a crop-beneficial bacterial bioinoculant. Here, a wheat-associated pseudomonad strain is identified in culture, genomically and functionally characterized, tested in the laboratory, and finally brought to field trials to demonstrate yield-promoting traits.

Fugère et al. 2020 have applied evolutionary concepts of population rescue, focused on the adaptive and evolutionary mechanisms that can rescue collective taxa within a phytoplankton community via an initial low-dose exposure of glyphosate prior to a more intense exposure. This work examines how communities in "deteriorating" conditions may survive via rescue and considers the average fitness of populations as the community fitness, which was manifested as total biomass.

Graham et al. 2020 have reinforced conceptual frameworks from ecology that have been applied to microbiome resilience, focusing on understanding the various disturbance characteristics that drive microbiome outcomes.

Mueller et al. 2019 introduced the concept of *microbial rescue* to benefit host physiology or behavior, provided a primer on population rescue from ecology and evolutionary biology, and recommended to readers unfamiliar with the concept of rescue. Palmer and Foster, 2022 assertively discuss that competitive interactions, and not cooperative ones, are the most common microbial engagements; this work and contradicting references cited therein (see also Kehe et al. 2021) provide a helpful foray into the hot debate of the nature and contribution of microbial biotic interactions for community outcomes and thus has baring for directing resilience via rescue. Philippot et al. 2022 discussed the implications of compounded disturbances for microbiome resilience with an excellent and ample overview of key disturbance ecology terminology and concepts, including the multiple usages of the term resilience (see section therein: "Resilience: a fuzzy concept"). Sorensen and Shade 2020 performed a mesocosm experiment in which temperate soils were exposed to high, durable heat before returning to ambient temperatures. The experiment included

a treatment that excluded microbial dispersal and allowed for assessing the contributions of both

dispersal and reactivation to post-disturbance assembly.

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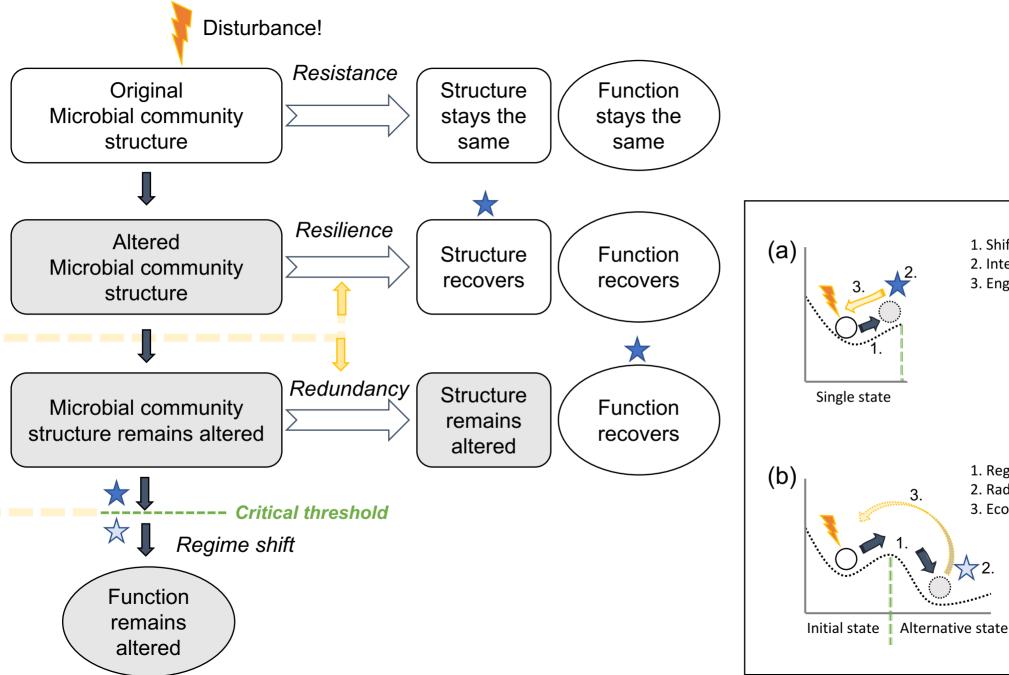
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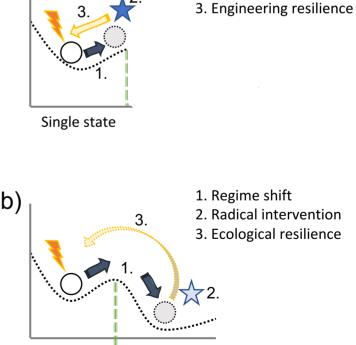
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## Shade- MicroRescue

## Highlights

- 1. Microbiome management can maintain functions for systems facing climate change.
- 2. Microbiome Rescue reintroduces functional members lost to disturbance.
- 3. Rescue can be demographic, functional, adaptive, and/or evolutionary.
- 4. Deterministic rescue mechanisms can direct interventions to stabilize functions.
- 5. It is urgent to assess microbial reactivation from dormancy as a rescue strategy.





1. Shift within a state

2. Intervention

