

Microbial rescue effects: How microbiomes can save hosts from extinction

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Abstract

1. Rescue effects arise when ecological and evolutionary processes restore positive intrinsic growth rates in populations that are at risk of going extinct. Rescue effects have traditionally focused on the roles of immigration, phenotypic plasticity, gene flow, and adaptation. However, species interactions are also critical for understanding how populations respond to environmental change.
2. In particular, the fitness of plant and animal hosts is strongly influenced by symbiotic associations with the bacteria, archaea, microeukaryotes and viruses that collectively make up a host's microbiome. While some are pathogenic, many microorganisms confer nutritional, immunological, and developmental benefits that can protect hosts against the effects of rapid environmental change.
3. Microbial rescue occurs when changes in microbiome abundance, composition, or activity influence host physiology or behaviour in ways that improve host fitness. If these microbial attributes and their beneficial effects are transmitted through a population, it may stabilize growth rates and reduce the probability of extinction.
4. In addition to providing a framework to guide theoretical and empirical efforts in host-microbiome research, the principles of microbial rescue may also be useful for adaptively managing at-risk species. We discuss the risks and rewards of incorporating microbial rescue into conservation strategies such as probiotics, assisted migration, and captive breeding.

KEYWORDS

adaptation, biodiversity, conservation, dispersal, global change, symbiosis

1 | INTRODUCTION

Environmental change is occurring across the globe at an unprecedented rate. With atmospheric CO₂ concentrations now exceeding 400 ppm (Blunden, Arndt, & Hartfield, 2018), global mean surface temperatures are rising (Stocker et al., 2013) and the world ocean is becoming more acidic (Gattuso et al., 2015). Habitat is being degraded and homogenized via land-use change while nutrient runoff from industrial-scale agriculture is expanding anoxic dead zones in coastal ecosystems (Foley, 2005; Stocker et al., 2013). Meanwhile, altered precipitation regimes are creating more intense and prolonged

periods of drought and flooding that threaten our ability to reliably feed the growing human population (Trenberth, 2011). These and other global changes pose severe threats to the biodiversity of virtually all ecosystems on Earth.

For species to persist in the face of widespread and rapid environmental change, it is important to identify biological mechanisms that can reverse trends of population decline. Some populations can achieve this by moving into more favourable habitats, for example, through the migration of heat-stressed individuals to sites at higher latitudes with cooler temperatures (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Parmesan & Yohe, 2003).

However, many taxa are unable to disperse sufficiently well to keep up with the pace of global change (Schloss, Nunez, & Lawler, 2012). While these populations are at risk, they are not necessarily doomed to extinction. Vulnerable taxa can be rescued through various ecological and evolutionary processes that change the intrinsic growth rate of a population from negative to positive, promoting long-term persistence. These processes, collectively known as rescue effects, can be leveraged to enhance conservation efforts and improve predictions of species persistence in response to global change.

2 | RESCUE EFFECTS: AN OVERVIEW

As an environment changes, some species rapidly approach extinction while others decline at slower rates (Kuussaari et al., 2009). A delayed response to environmental change provides an opportunity for natural processes or human interventions to stabilize a population. Specifically, the probability of extinction can be minimized by rescue effects, which include ecological and evolutionary processes that restore positive intrinsic population growth to an at-risk population (Derry et al., 2019).

2.1 | Ecological rescue effects

Rescue effects can occur by purely ecological processes, where changes in population sizes or non-heritable shifts in traits buffer against extinction. One type of ecological rescue effect is demographic rescue. This long-recognized phenomenon is rooted in fundamental processes such as births, deaths, and immigration that collectively determine population size. Demographic rescue occurs when immigration from distant sites stabilizes the abundance of a focal population (Figure 1a). First considered in the context of island biogeography (Brown & Kodric-Brown, 1977), demographic rescue was subsequently integrated into metapopulation theory (Hanski, 1982) to emphasize that the movement of individuals from a source population could prevent local extinction in a sink population (Gotelli, 1991; Stacey, Taper, & Johnson, 1997). Since then, demographic rescue has been documented in a range of systems, including the golden-mantled ground squirrel (*Spermophilus lateralis*) in the Rocky Mountains of Colorado (USA), where after a four-year period of steep decline, immigration from nearby sites restored population sizes to previous levels and prevented local extinction (McEachern, Van Vuren, Floyd, May, & Eadie, 2011).

Another type of ecological rescue is plastic rescue, where non-heritable phenotypic changes contribute to the increased growth rate of a population in an unsuitable environment (Figure 1c; Snell-Rood, Kobiela, Sikkink, & Shephard, 2018). For example, populations of the pipevine swallowtail caterpillar (*Battus philenor*) throughout the southern United States exhibit two environmentally determined colour morphs: a black form at temperatures up to 36°C and a red form that dissipates heat more efficiently at elevated temperatures.

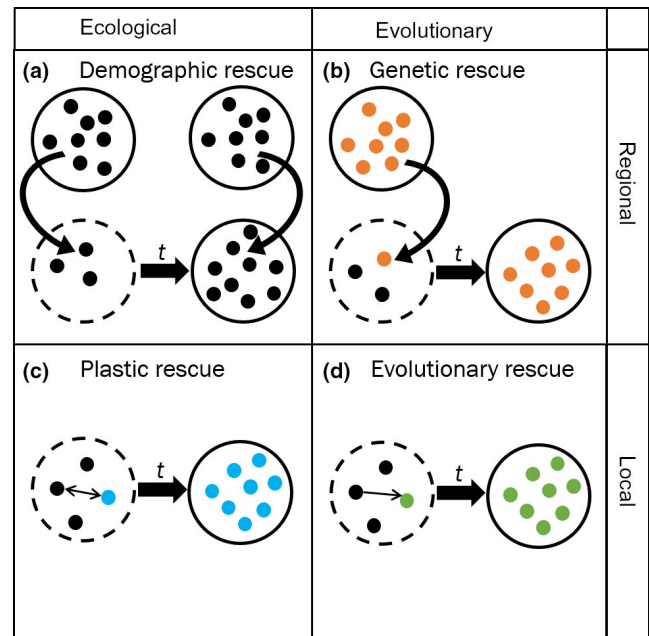


FIGURE 1 Rescue effects are a set of ecological and evolutionary processes that over time (t) can restore positive intrinsic growth in at-risk populations (dashed line circles represent at-risk host populations and solid line circles represent stable host populations). Demographic rescue (a) occurs when increases in population size through immigration reduce the risk of population extinction. Genetic rescue (b) occurs when adaptive gene flow from neighbouring populations (orange symbols) reduces inbreeding depression in at-risk populations. Plastic rescue (c) occurs when non-heritable phenotypic changes in response to changing environments prevent extinction. Blue symbols represent a different phenotype arising from the same genotype within a population. Evolutionary rescue (d) occurs when a beneficial allele (green symbols) increases in frequency via adaptive evolution and directly reduces that population's risk of extinction

At higher latitudes and cooler temperatures, individuals retain the ability to produce the red morph, suggesting that plasticity in body colour could rescue these populations if temperatures exceed 36°C (Nielsen, 2017). While these demographic and plastic ecological rescue effects can temporarily enhance population growth, they are unlikely to prevent extinction in the long run without evolutionary change.

2.2 | Evolutionary rescue effects

Populations can also be rescued by evolutionary processes. Evolutionary rescue occurs when local adaptation from standing genetic diversity or de novo mutation is rapid enough to prevent extinction under new environmental conditions (Figure 1d; Bell & Gonzalez, 2009; Gomulkiewicz & Holt, 1995). The signature of evolutionary rescue is an increase in the frequency of an adaptive allele that leads to a rebound in the size of an at-risk population (Bell, 2017; Carlson, Cunningham, & Westley, 2014). The likelihood of evolutionary rescue for a population depends on

population size, standing genetic variation, and the rate of beneficial mutation among other factors (Bell, 2013). For example, rodent populations in cities are often controlled with anti-vitamin K-based rodenticides, such as warfarin, which inhibits blood coagulation (Vander Wal, Garant, Festa-Bianchet, & Pelletier, 2013). In Baltimore, Maryland (USA), pesticide application initially led to a 60% decline in rodent populations. However, mutations eventually accumulated in vitamin K epoxide reductase, the enzyme that is targeted by warfarin. It seems that these beneficial mutations enabled the evolutionary rescue of some rodent populations back to pre-rodenticide levels in as little as two years (Rost et al., 2009).

Genetic rescue is another type of evolutionary rescue effect that occurs when gene flow helps a population recover from inbreeding depression (Figure 1b). As a population shrinks, inbreeding results in the accumulation of deleterious mutations and decreased heterozygosity that cannot be purged via recombination. As a result, population size continues to decline due to positive feedbacks that further reduce fitness (Gabriel, Lynch, & Bürger, 1993). Genetic rescue provides an influx of alleles from elsewhere in the landscape, supplying the population with enough genetic variation to avoid extinction. For example, the Rocky Mountain bighorn sheep (*Ovis canadensis*) in the National Bison Range (Montana, USA) suffered from a genetic bottleneck in 1922 that led to severe inbreeding for several generations. The introduction of sheep from neighbouring Montana herds between 1985 and 1994, allowed gene flow and introgression of several loci that restored positive population growth through increased lifespan and reproductive success (Miller, Poissant, Hogg, & Coltman, 2012). As a result, evolutionary rescue provides opportunities for populations to adapt to environmental conditions associated with global change.

3 | MICROBIAL RESCUE EFFECTS

Thus far, we have discussed how rescue effects within a species can reverse population declines and promote species persistence. However, population survival is highly dependent on interactions with other species. In particular, the fitness of plants and animals can be strongly influenced by interactions with their microbiomes, i.e., the bacteria, archaea, microeukaryotes and viruses that live on and inside of hosts, (David et al., 2019; Gould et al., 2018; Pillai, Gouhier, & Vollmer, 2017). Collectively, these microorganisms can affect host nutrition, behaviour, physiology, and development in various ways (Lynch & Hsiao, 2019). Due to the importance of host-microbiome interactions for host survival, we introduce the microbial rescue effect, which reflects the ability of modified microbiomes to increase host fitness and population densities, thereby preventing host extinction. In the following sections, we outline the microbial rescue effect framework by emphasizing the three basic stages of microbial rescue, which include: (1) environmentally induced changes in host microbiome attributes, (2) a subsequent increase in a host's fitness conferred by microbiome attributes, and (3) transmission of beneficial interactions among individuals leading to rescue of the host population (Figure 2).

3.1 | Stage 1: Changes in microbiome attributes

Microbial rescue is initiated when environmental change leads to an alteration in host microbiome composition, abundance, or activity (Figure 2). A variety of ecological processes including environmental filtering, species sorting, and ecological drift can all lead to shifts in these microbial attributes (Christian, Whitaker, & Clay, 2015; Costello, Stagaman, Dethlefsen, Bohannan, & Relman, 2012;

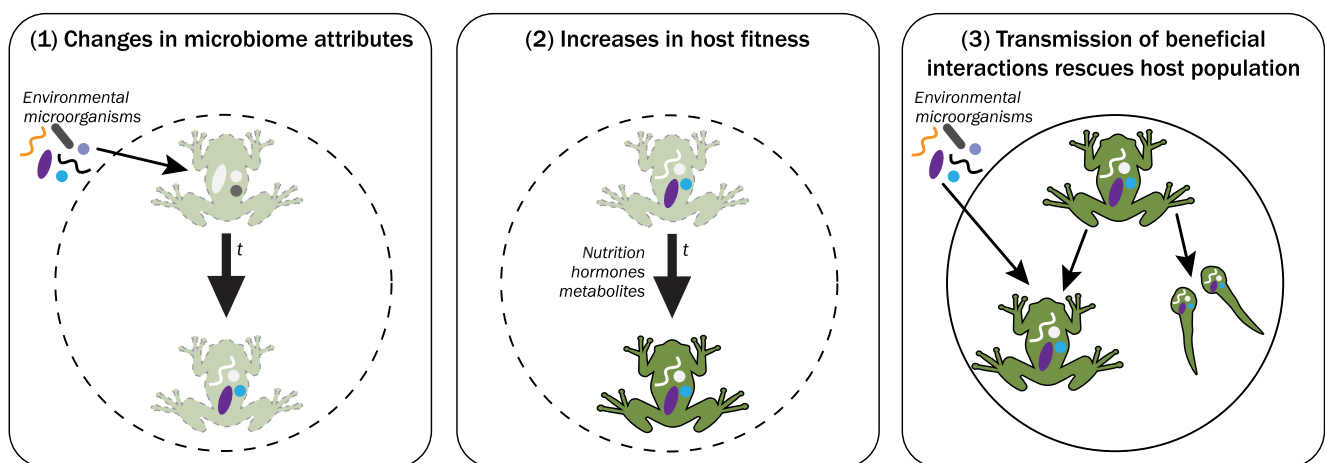


FIGURE 2 Microbial rescue effect occurs when low-fitness individuals (light green hosts) in an at-risk population (dashed line circles) experience (1) changes in the composition, abundance, activity or traits of their microbiome. These changes in microbiome attributes can cause (2) increases in individual fitness (dark green hosts) through host-microbiome interactions, which improve performance via enhanced nutrition, hormonal regulation, or metabolite exchange in the host. When these increases in host fitness spread through the population either through horizontal or vertical transmission (3), the host population growth rate can increase and the population is rescued (solid line circle)

Koskella, Hall, & Metcalf, 2017). Microorganisms are also affected by rapid evolutionary processes, owing to their short generation times and large population sizes. As a result, new traits can arise in microbial populations via de novo mutation or horizontal gene transfer. Importantly, feedbacks often arise between these ecological and evolutionary processes, which can influence the performance of a host within its lifetime (Gould et al., 2018; Macke, Tasiemski, Massol, Callens, & Decaestecker, 2017).

3.2 | Stage 2: Increases in host fitness

A shift in microbiome attributes sets up the second stage of microbial rescue, a corresponding change in host phenotype and fitness caused by host-microbiome interactions (Figure 2). For example, microorganisms can produce metabolites that regulate gene expression of the host during key stages of development (Blacher, Levy, Tatirovsky, & Elinav, 2017; Goldberg, Allis, & Bernstein, 2007). A high-fibre diet in mammals favours a microbiome that produces increased short-chain fatty acids (SCFAs), which consist of fermentation products including acetate, propionate, and butyrate (Thorburn et al., 2015). In addition to serving as the source of energy, SCFAs influence immune cell function and decrease instances of asthma in adults by inhibiting histone deacetylation of the Foxp3 promoter, which can be passed on to offspring (Thorburn et al., 2015). As development of the immune function is tightly linked to host fitness, epigenetic effects like these can be important for microbial rescue.

Microorganisms can also regulate resource acquisition, a critical aspect of host fitness. In the mammalian gastrointestinal tract, bacteria can degrade aromatic amino acids, bile acid, choline, polyphenol, protein, and carbohydrates as well as synthesize essential vitamins (Yadav, Verma, & Chauhan, 2018). Gut microbiomes may also help define a host's dietary niche and determine its performance when exposed to novel food sources. In plants, rhizosphere microbiomes play an analogous role by increasing the turnover and availability of growth-limiting nutrients. In addition, root-associated microbiomes can aid in plant nutrition when challenged by environmental stress. For example, plants can form new associations with drought-tolerant rhizobia and mycorrhizae, which stabilize mutualisms that would otherwise fail to establish (Rubin, van Groenigen, & Hungate, 2017).

Changes in microbiome attributes can also alter hormone regulation, which has important consequences for the behaviour and metabolism of hosts (Bercik et al., 2011; Neuman, Debelius, Knight, & Koren, 2015). In plants, microbially produced hormones can result in increased levels of indole-acetic acid, reducing plant stress response to salt conditions (Abdelaziz et al., 2019). In animals, microbially produced hormones are known to influence mood, behaviour, and even brain development (Lynch & Hsiao, 2019; Sampson & Mazmanian, 2015). In critically endangered black rhinos (*Diceros bicornis michaeli*), the microbiome is thought to be important for breeding success given that their gut bacteria are associated with

hormone production (Antwis, Edwards, Unwin, Walker, & Shultz, 2019). Because reproductive behaviours are integral to the fitness of many host populations, microbially mediated hormone regulation is a potentially important mechanism of microbial rescue.

3.3 | Stage 3: Transmission of beneficial interactions

While microbiomes are clearly important for host fitness, beneficial interactions must spread throughout the population for microbial rescue to occur (Figure 2). This can be facilitated by horizontal transmission, but requires that microorganisms tolerate environmental conditions (pH, temperature, moisture, and oxygen) that are quite different from those associated with hosts (Mendes, Kuramae, Navarrete, van Veen, & Tsai, 2014). Traits such as dormancy (Lennon & Jones, 2011) and dispersal (Martiny et al., 2006) enhance microbial survival in variable environments. Nevertheless, in small at-risk populations where the frequency of host-host encounter is minimized, horizontal transmission may be less effective at spreading beneficial interactions conferred by microbiomes.

Microorganisms can also be vertically acquired via parent-offspring transmission during birth. In this way, the microbiome is considered by some to be a partially heritable trait of a host population (Vliet & Doebeli, 2019). For example, in mice, most beneficial gut microorganisms are vertically transmitted, while pathogenic microorganisms are encountered via contact with sick members of the population or other contaminated materials (Moeller, Suzuki, Phifer-Rixey, & Nachman, 2018). Therefore, horizontal transmission may allow beneficial interactions to spread through and rescue a population at a faster rate (e.g., within a generation), but with more inter-host variability (Adair & Douglas, 2017). In contrast, vertical transmission may be a slower (e.g., multiple generations), but more reliable, avenue of microbial rescue.

3.4 | Examples of microbial rescue

Altered precipitation patterns are a major threat to plant communities around the world. The increased frequency and duration of drought will likely have negative effects on the productivity, phenology, and geographic distribution of many plant species (Hughes, 2000). Microbial rescue may be one overlooked mechanism that could improve fitness of water-stressed plant populations. For example, microbial community composition can affect the strength of natural selection on flowering time and biomass in *Brassica rapa* (Lau & Lennon, 2011). This means the below-ground microbiome could determine whether plants can adapt to novel environments, a possible mechanism for microbial rescue. To test the microbiome's ability to mitigate water stress in plants, *B. rapa* populations were maintained for multiple generations in either wet or dry conditions in a controlled greenhouse environment (Lau & Lennon, 2012). These populations were then replanted with soil bacteria and fungi that were previously exposed to wet and dry

conditions to determine how microbial history affected plant fitness. Contemporary drought decreased fruit number by ~60%, yet when planted with dry-adapted microorganisms, fruit number decreased by only 20% (Lau & Lennon, 2012). The microbiome's capacity to mitigate water stress in plants may lead to microbial rescue if the beneficial interactions spread to neighbouring individuals (horizontal transmission) or to offspring seedlings (vertical transmission).

Warming oceans are one of the primary factors contributing to the disappearance of coral reefs around the world. When elevated temperatures exceed the thermal limits of zooxanthellae (*Symbiodinium* sp.), a coral symbiont essential for carbon acquisition, the zooxanthellae are expelled from the coral host. This expulsion results in a phenomenon known as bleaching, which reduces the coral's ability to acquire nutrients, eventually leading to death (Bourne, Morrow, & Webster, 2016). Coral microbiomes can undergo compositional and genetic changes that lead to microbial rescue of the host that may spread through the coral population at different rates depending on the mode of symbiont transmission (Mieog et al., 2009). For example, in a transplant experiment in the Indo-Pacific stony coral (*Acropora millepora*), a species that experiences horizontal transmission of symbionts (Mieog et al., 2009), the abundance of thermally tolerant clades of zooxanthellae increased over time, changing the composition of the microbiome and leading to increased fitness of coral hosts in the warmer waters. In contrast, corals lacking symbionts from the thermally tolerant zooxanthellae clade bleached and died (Berkelmans & van Oppen, 2006). Experimental evolution of the symbiont suggests that the zooxanthellae can evolve to keep up with warming oceans through adaptation to higher temperatures (Chakravarti, Beltran, & van Oppen, 2017). These heritable changes in zooxanthellae prevented their expulsion by the coral, increasing host fitness and promoting rescue (Chakravarti & van Oppen, 2018). In this case, a single trait in a single microbial genus is responsible for increasing host fitness and rescuing coral populations through nutrient acquisition under increasing water temperatures.

4 | MICROBIAL RESCUE IN CONSERVATION BIOLOGY

The accelerating pace of environmental change often requires the intervention and management of at-risk populations. Most modern-day conservation efforts leverage ecological information including habitat quality, behavioural characteristics, and species interactions (Mawdsley, O'Malley, & Ojima, 2009). Often, conservation biologists also consider evolutionary processes such as inbreeding depression, gene flow, and adaptation (Aitken & Whitlock, 2013; Derry et al., 2019). Historically, less attention has been paid to the role of the microbiome when attempting to manage plant and animal species (Trevelline, Fontaine, Hartup, & Kohl, 2019). Recently, however, microorganisms have been attracting more attention in conservation biology (West et al., 2019). In

this section, we discuss the benefits and consequences of using microbial rescue as a framework for the management of microbially reliant hosts (Figure 3).

In some cases, important aspects of host fitness can be managed with easily identifiable and culturable groups of microorganisms. When this happens, microorganisms can be used in conservation efforts as probiotic supplements, which can shift microbiome attributes and promote interactions that reduce the risk of extinction. For example, beneficial bacteria have been used to address global amphibian declines caused by the chytrid fungus pathogen *Batrachochytrium dendrobatidis* (Bd), which has been implicated in an estimated 90 amphibian extinctions around the world (Scheele et al., 2019). One particular bacterial species that has been used to protect amphibians against Bd is *Janthinobacterium lividum* (Figure 3). Close relatives of this species have been recovered not only from the skin of healthy amphibians, but also from ponds and soils, suggesting it is adapted for survival in a range of conditions. Importantly, many species of *Janthinobacterium* are capable of producing violacein, a purple-coloured pigment derived from tryptophan that has anti-fungal properties. When *J. lividum* is applied to amphibian skin, hosts become less susceptible to Bd infection (Becker, Brucker, Schwantes, Harris, & Minbiole, 2009). While there are still practical challenges to using probiotics to address global-scale epidemics, the *Janthinobacterium* case study demonstrates that the principles of microbial rescue may be used, perhaps in combination with other conservation efforts, to protect local populations from pathogens that have the potential to drive hosts to extinction.

In most cases, microbial rescue will likely involve consortia of microorganisms possessing a range of traits that are more difficult to identify and manage. One solution to this challenge involves microbiome engineering, an approach that selects for microbial assemblages that correspond with desirable host traits or performance (reviewed in Mueller & Sachs, 2015). For example, microbiome engineering has been used to select for and propagate microorganisms that remove organic pollutants that threaten coral reef health (Figure 3). A microbial sample from a coral colony (*Mussismilia harttii*) was grown in a medium supplemented with oil (Santos et al., 2015). After incubation, the 10 fastest growing morphotypes were isolated and combined to create an oil-degrading consortium. This engineered microbiome was then applied to corals, which led to an increase in host growth rate both in the presence and absence of the water-soluble oil fractions (Santos et al., 2015), showing that the benefit to host fitness occurred even when the environmental stress was removed. The ability to engineer a community of microorganisms that have a collective benefit to the host will allow for microbial rescue in cases where specific microbiome attributes or mechanisms of increased host fitness are not known.

One promising aspect of microbial rescue is its ability to be combined with other traditional conservation efforts to help improve success of managing at-risk populations. For example, assisted migration involves the relocation of a species into

Microbial Rescue in Conservation Biology


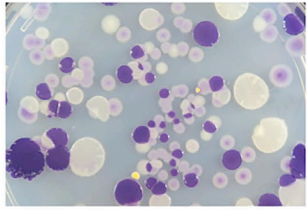

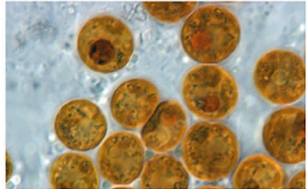




Example	At-risk host	Microbial rescue strategy
<p>Probiotic supplements & captive breeding: Chytrid fungus <i>Batrachochytrium dendrobatidis</i> (Bd) infects a range of amphibian hosts worldwide. Treating Bd-infected at-risk amphibian populations with antifungal producing bacteria such as <i>Janthinobacterium lividum</i> could lead to microbial rescue in the wild.</p>		
<p>Microbiome engineering: Engineered microbiomes with enhanced pollutant degradation functions can increase coral fitness to keep pace with environmental change and pollutant contamination. Microbially engineered probiotics can provide a potential route to microbial rescue.</p>		
<p>Assisted migrations: <i>Phaeocryptopus gaeumannii</i> is the causative fungal pathogen responsible for Swiss Needlecast disease in Douglas-fir populations. Assisted migration of Douglas-fir populations with associated ectomycorrhizal fungi can increase establishment success in novel environments.</p>		
<p>Captive breeding: White-sided dolphins housed in aquaria have microbiomes that are dissimilar to microbiomes of natural seawater. Probiotics such as <i>Lactobacillus</i> sp. increase microbial community composition stability in the captive dolphins.</p>		

FIGURE 3 Examples of conservation strategies that may improve success when the microbiome and microbial rescue are considered

a habitat that is projected to support net-positive population growth under future environmental conditions (McLachlan, Hellmann, & Schwartz, 2007). In identifying suitable habitat, scientists often consider climatic variables, migration corridors, and vegetation types. Often overlooked, however, is the role that microbiomes may play in the success of relocating plants or animals into a novel environment. Some evidence suggests that assisted migrations may be more successful if both hosts and their microbiomes are relocated together (Bothe, Turnau, & Regvar, 2010). For example, Douglas-fir (*Pseudotsuga menziesii*) seedlings and their soil microbiomes were experimentally migrated to common glasshouse environments of differing climates within its natural range in the Pacific Northwest of North America (Figure 3). In the experiment, half of the individuals retained their intact soil microbiomes while the other individuals were chemically treated to remove below-ground fungal symbionts (Pickles, Twieg, O'Neill, Mohn, & Simard, 2015). As a result, 18 of 32 soil and seedling

combinations showed evidence of local adaptation mediated by the intact soil microbiome (Pickles et al., 2015). Additionally, above-ground growth was higher for seedlings transplanted with their microbiome compared to those treated with fungicide demonstrating that transplantation of the microbiome with the target host population may increase success of assisted migration (Pickles et al., 2015).

Another conservation strategy that may benefit from a microbial perspective is captive breeding, which often involves moving individuals into human-controlled environments, such as zoos or conservation centres. While such efforts can be used to address extinction threats in the wild (e.g., lack of mates), host microbiomes have a tendency to become depleted when hosts are maintained in captivity owing to shifts in diet, social interactions, and immune function (Clayton et al., 2016). For example, white-sided dolphins (*Lagenorhynchus obliquidens*) housed in aquaria have a microbiome that is quite dissimilar to the microbiomes of wild dolphins from

Sarasota Bay (Florida, USA) or San Diego Bay (California, USA; Cardona et al., 2018). This may be due to the lower diversity of microorganisms that are sustained in the artificial seawater of the aquarium but could also reflect a reduction in host-to-host transmission of beneficial microbes. Some evidence suggests, however, that the administration of probiotics (e.g., *Lactobacillus* sp.) can stabilize the composition of the dolphin microbiome, indicating that there may be ways to better manage marine mammals in captivity (Figure 3).

While there is reason to be optimistic about integrating microbial rescue into conservation efforts, these strategies should be cautiously implemented. Microbiomes are complex and consist of many co-evolved interactions among microorganisms and their hosts. In some cases, the introduction of novel microbial populations or assemblages through probiotic supplements or microbiome engineering could disrupt host function in ways that exacerbate the stress of global change (Cheng et al., 2017). There are also cases where microbial manipulation can cause harm to ecosystems despite improving the fitness of the target host. For example, the grass strain tall-fescue Kentucky 31 was inoculated with *Neotyphodium coenoccephalum*, a fungus that improves the fitness of the grass, to improve host fitness but it has actually become an invasive species (Saikkonen, 2000) that causes declines in biodiversity (Clay & Holah, 1999). A similar sort of invasion can occur if transplanted microbial species have a competitive advantage over members of the native microbial community (Litchman, 2010). For example, when an entire microbiome is relocated with the host (e.g., assisted migration), some populations may become pathogenic to naïve hosts in the new environment (Ricciardi & Simberloff, 2009).

Fortunately, strategies for microbial rescue-based conservation can be improved with insights from biological control. Biological control and microbial rescue-based conservation are similar as they both involve the manipulation of one organism to control the fitness of another organism. While there are examples where biological control has been successful, a recent study suggests positive effects of biological control have been overstated in the literature (Havens, Jolls, Knight, & Vitt, 2019). In some cases, failure of biological control agents can be attributed to a lack of proper agent screening (Myers, 2000). The screening process is complicated as it emphasizes the need to balance many criteria such as financial costs and safety (Köhl, Postma, Nicot, Ruocco, & Blum, 2011). In the context of microbial rescue-based conservation, this means balancing the need for targeted conservation of host species with the need to maintain or promote ecosystem services. Failure can also come from a lack of understanding of the unintended consequences associated with biological manipulation (Myers, 2000). For microbial rescue applications, new theory is being developed to predict the effects of modifying complex microbial networks (Angulo, Moog, & Liu, 2019). Tools such as these allow for the identification of species that have a greater than expected ability to modulate community structure (Gibson, Bashan, Cao, Weiss, & Liu, 2016). This means that despite failures associated with past biological control and food-web manipulation, microbial interventions

in complex microbiomes may be able to be better predicted, developed, and controlled with the help of new insights and tools. Thus, our current understanding may be sufficient to start directing microbial rescue-based conservation strategies in a productive direction as long as appropriate cautions are taken by well-trained multidisciplinary teams.

5 | CONCLUSIONS

Mounting evidence suggests that microbiomes play an important role in host fitness. Our microbial rescue effect framework outlines a number of ecological and evolutionary processes that may stabilize plant and animal populations that are threatened by environmental change. Hosts can be colonized by microorganisms from multiple pools including the resident host microbiome, the environmental microbiome, and from the microbiomes of other hosts through contrasting modes of transmission. Gaining theoretical and empirical insight into when and how microbial rescue effects occur in nature may also allow conservation biologists to better incorporate the microbiome into management strategies. Further work must be done to evaluate how complexities such as eco-evolutionary feedbacks influence the strength and predictability of microbial rescue. Nevertheless, microbial rescue has the potential to stabilize host dynamics and improve our understanding of population persistence in a changing world.

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AUTHORS' CONTRIBUTIONS

All authors conceived and wrote the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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