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Preparing for the worst: Utilizing stress-tolerant soil microbial communities to aid ecological restoration in the Anthropocene

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Abstract

1. Multiple drivers of environmental change pose a significant challenge for ecological restoration, including climate change, soil salinization and environmental pollution. Due to the important role that soil biota play in enabling plants to cope with a variety of abiotic stressors, there is growing interest in the use of microbial inoculations to facilitate native plant restoration in the face of such change.

2. Recently, novel methods have begun being explored in agriculture to harness stress-conditioned soil biota for improving abiotic stress tolerance in crop species. Similar applications in ecological restoration – where plants are inoculated with indigenous soil microbial communities that are preconditioned to various abiotic stressors – could potentially increase our capacity to restore degraded ecosystems under global change.

3. In this paper, we aim to (1) outline the ways in which soil microbial communities might be conditioned in order to confer greater stress tolerance to plants that are targets for restoration; (2) highlight successful (and unsuccessful) examples where stress-tolerant soil microbial communities were utilized to improve plant performance; (3) describe the ways in which stress-conditioned soil biota could be deployed in order to assist ecological restoration; and (4) discuss the potential risks and outstanding questions associated with such an approach.

4. If restoration practitioners are able to harness the soil microbiome to improve plant stress tolerance as is currently being explored in agriculture, this could revolutionize methods for the restoration of degraded lands in the Anthropocene.

KEYWORDS
ecological restoration, plant–soil feedbacks, rhizosphere, soil biota, soil inoculation, stress conditioning, stress priming, stress tolerance

1 | INTRODUCTION

Anthropogenic activities continue to exert a profound impact on the environment, resulting in wide-scale habitat degradation (Hoekstra, Boucher, Ricketts, & Roberts, 2005), accelerated biodiversity loss (Pereira et al., 2010), severe environmental pollution (Brusseau, Pepper, & Gerba, 2019) and global climate change (Diffenbaugh & Field, 2013). Such extreme environmental perturbations both necessitate and complicate ecological restoration (Hobbs & Cramer, 2008), and there is a growing need for developing techniques that improve
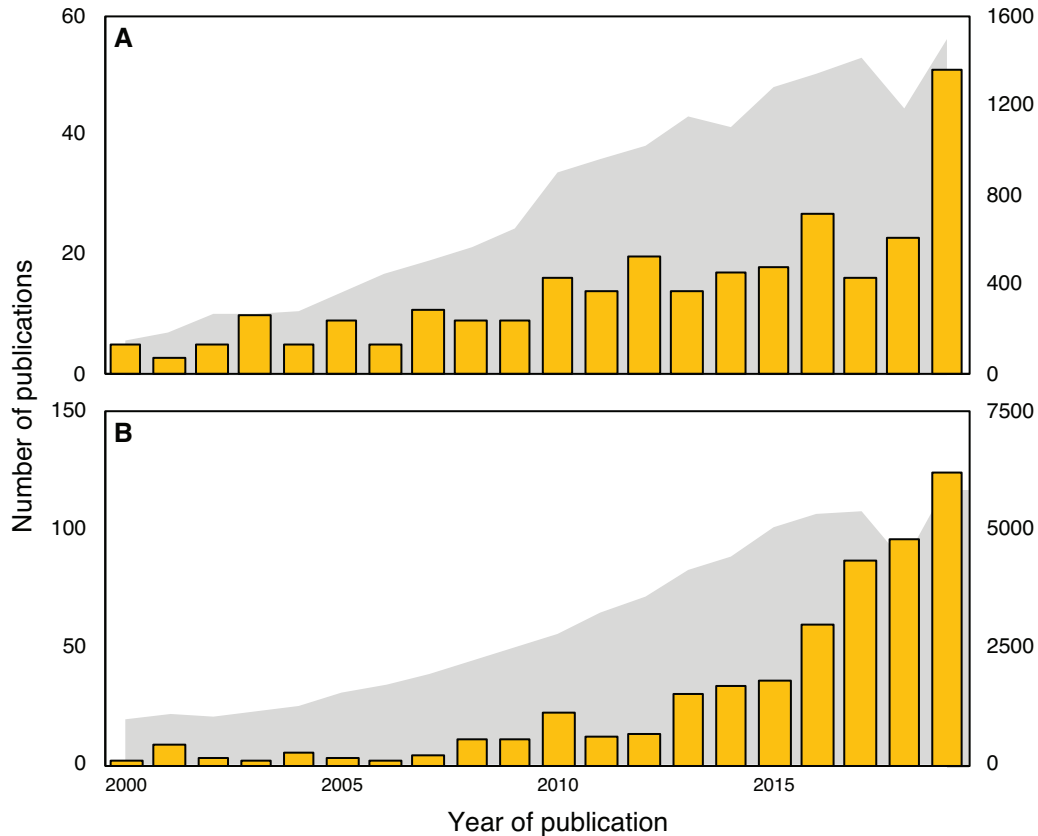
FIGURE 1 Research interest in the use of soil inoculation in ecological restoration (A) and the role of soil microbes in plant stress tolerance (B) as evidenced by the number of publications per year from 2000 to 2019. To quantify research interest in soil inoculation in ecological restoration over time (A), we queried Web of Science (http://www.webofknowledge.com) for the terms 'soil', 'inocul*' and 'restor*' and limited search results to those published since the year 2000 in the categories of ecology, environmental science, forestry and biological conservation ($n = 274$). The number of publications returned using the search term 'ecological restoration' is shown in grey for comparison ($n = 15,018$). To quantify research interest in the role of soil microbes in plant stress tolerance (B), we included the search terms 'soil', 'microb*', 'plant', 'stress', and 'tolerance' ($n = 564$). The number of publications returned using the search term 'plant stress tolerance' is shown in grey for comparison ($n = 59,423$)

our ability to re-establish resilient ecosystems in the face of this ongoing change. This is particularly important given the scale of ecosystem degradation, the urgency of restoration efforts needed and the associated costs of restoration activities (United Nations, 2019). While human activities have also substantially altered soil microbial communities in agricultural and natural systems worldwide, the rich reservoir of biodiversity belowground may hold the key to preserving and restoring ecosystem functioning and environmental sustainability in the Anthropocene (Geisen, Wall, & van der Putten, 2019; Singh, 2015).

Plants have a variety of mechanisms to mitigate the adverse effects of stress, including developing close associations with beneficial soil microbes. Soil microorganisms (e.g. bacteria, archaea and fungi) are found around, on, and in plant roots, and play an important role in determining plant performance, including responses to biotic and abiotic stressors (Rodriguez & Redman, 2008; Yang, Kloepper, & Ryu, 2009). As such, there has been growing interest in utilizing soil microbial inoculations in ecological restoration (Figure 1a). Most of this work has focused on mycorrhizal fungi (Heneghan et al., 2008; Koziol et al., 2018), but also plant growth-promoting rhizobacteria (PGPR) and nitrogen (N)-fixing bacteria (e.g. De-Bashan,

Hernandez, & Bashan, 2012; Thrall et al., 2005). There are numerous examples of soil microbes successfully facilitating ecological restoration (De-Bashan et al., 2012; Heneghan et al., 2008; Koziol et al., 2018). However, while an understanding of plant–soil feedbacks and aboveground–belowground linkages may greatly improve our ability to restore degraded ecosystems, such an approach has yet to be fully integrated into the field of restoration ecology (Kardol & Wardle, 2010), and much uncertainty remains regarding how to best utilize such manipulations to achieve desired outcomes due to the complexity of these dynamics (Harris, 2009; Neuenkamp, Prober, Price, Zobel, & Standish, 2019). There is good evidence to suggest, however, that indigenous soil microbial communities are more beneficial than commercially available inoculants in a restoration context (Maltz & Treseder, 2015), as allochthonous microorganisms may be poorly suited to local edaphic and environmental conditions and/or native plant hosts.

There is also growing research interest in the important role soil biota may play in driving plant stress tolerance (Figure 1b) in both agricultural and natural systems. One promising method for assisting ecological restoration under global change is the use of

TABLE 1 Case studies from natural systems exploring the effects of stress-conditioned soil biota on plant performance under various abiotic stressors including drought, heat, salinity and different types of environmental pollution

Reference	Stressor	Key findings
Kaisermann et al. (2017)	Drought	Drought-conditioned soil communities contributed to negative intraspecific plant–soil feedbacks in a grass and forb species, reducing plant growth
Lau and Lennon (2012)	Drought	Plant fitness was greatest when environmental conditions (wet vs. dry) matched the historical environmental conditions experienced by the soil microbial community
Marulanda et al. (2007)	Drought	Native arbuscular mycorrhizal fungi isolated from dry sites improved plant drought tolerance of a Mediterranean shrub more than fungi from non-dry sites
Marulanda et al. (2006)	Drought	Indigenous drought-tolerant soil bacterium and arbuscular mycorrhizal fungi improved water uptake and root development in a native shrub species
Rubin et al. (2018)	Heat	Heat-conditioned soil inoculum reduced plant growth and did not influence heat wave survival in the field in two native grass species
Hashem et al. (1998)	Heat	Heat-tolerant Rhizobium strains identified through laboratory screening successfully nodulated tree seedlings and fixed N under elevated temperatures
Estrada et al. (2013)	Salinity	Inoculation with native arbuscular mycorrhizal fungi isolated from saline soils enhanced growth, survival and physiological performance of a native halophyte under salt stress
Zhang et al. (2011)	Salinity	Arbuscular mycorrhizal fungi isolated from patches of vegetation growing on saline-alkaline soils improved the reestablishment of a native perennial grass in a degraded grassland impacted by salinity and low pH
Thrall et al. (2008)	Salinity	Growth rate of individual rhizobial isolates was reduced with increasing salt tolerance in culture, rhizobial salt-tolerance had no impact on host (*Acacia* spp.) growth and salt-tolerant rhizobia did not perform better in saline environments
Bois et al. (2006)	Salinity	Ectomycorrhizal species selected for salt tolerance in vitro improved growth and reduced salt stress in two conifer species in a pot study
Doty et al. (2017)	Environmental pollution	Inoculation with bacterial endophytes of *Populus* trees that metabolize TCE improved plant growth and reduced phytotoxicity in trees grown in TCE-contaminated soils
Jourand et al. (2014)	Environmental pollution	Ectomycorrhizal fungi isolated from nickel-rich ultramafic soils enhanced growth and mineral nutrition and reduced uptake of toxic metals in two plant species
Babu and Reddy (2011)	Environmental pollution	Arbuscular mycorrhizal fungi isolated from soils contaminated by fly ash (a by-product of coal mining) improved plant growth in *Eucalyptus* seedlings via increased P nutrition and decreased accumulation of Al, Cu, Fe and Zn

indigenous soil microbes that are pre-conditioned to various abiotic environmental stressors such as drought, increasing temperatures, salinity and environmental pollution. The importance of stress conditioning of plant material for restoration projects is widely appreciated (Valliere, Zhang, Sharifi, & Rundel, 2019; Walter, Jentsch, Beierkuhnlein, & Kreyling, 2013), but there is also growing recognition of stress conditioning in soil microbial communities in ways that could ultimately improve plant fitness under environmental change (Marulanda, Barea, & Azcón, 2009; Lau & Lennon, 2012). While much of this work is being applied to agricultural systems (Dessaux, Grandclément, & Faure, 2016; Grover, Ali, Sandhya, Rasul, & Venkateswarlu, 2011; Hussain, Mehnaz, & Siddique, 2018; Zachow, Müller, Tilcher, Donat, & Berg, 2013), this approach also has the potential to contribute to improving the success and applicability of ecological restoration in the Anthropocene.

The purpose of this review is to (1) outline the ways in which soil microbial communities might be conditioned in order to confer greater stress tolerance to plants that are targets for restoration; (2) highlight successful (and unsuccessful) examples where stress-primed soil microbial communities were utilized to improve plant growth and

stress tolerance in managed and natural systems (Table 1); (3) describe the ways in which stress-conditioned soil biota could be deployed in order to assist ecological restoration; and (4) discuss the potential risks and outstanding questions associated with such an approach. If restoration practitioners are able to harness the soil microbiome to improve plant stress tolerance as is currently being explored in agriculture, this could revolutionize methods for the restoration of degraded lands under growing environmental change (United Nations, 2019).

1.1 | How do soil biota contribute to abiotic stress tolerance in plants?

Soil biota can contribute to plant stress tolerance in a number of ways, both directly (e.g. through physiological, molecular and biochemical effects) and indirectly through improved resource acquisition (Table 2). Mycorrhizal fungi improve plant performance under stressful conditions by enhancing nutrient (namely nitrogen and phosphorus but also micronutrients) and water availability, improving soil structure, promoting photosynthetic and water-use efficiency and contributing to

TABLE 2 Physiological impacts of abiotic stressors on plants and mechanisms by which soil biota may reduce such impacts and improve plant stress tolerance

Abiotic stress	Impact on plants	Microbially induced tolerance
Drought	Dehydration of cells and tissues; reduced stomatal conductance and photosynthesis; inhibition of water transport; oxidative stress	Enhanced uptake of water; production of microbial phytohormones (e.g. cytokinin which interferes with drought induced growth suppression); production of antioxidants; production of ACC deaminase; improved soil structure
Heat	Increased transpiration; elevated evaporation; water deficiency; protein inactivation, denaturation and degradation; increased membrane fluidity; cellular damage; oxidative stress	Reduced generation of reactive oxygen species thus reducing membrane injury; enhanced antioxidant enzyme activities; improved cellular metabolite production; activation of heat shock transcription factors
Salinity	Osmotic and ion homeostasis disruption; water uptake inhibition; decreased cellular metabolism; nutrient imbalance; membrane damage	Improved nutrition and plant-water relations; upregulation of ion transporters and channels; exclusion of salt ions in the soil; reduction of ethylene via ACC deaminase; production of phytohormones, exopolysaccharide (EPS), biofilms, antioxidants and osmolytes
Environmental pollution	Bioaccumulation of contaminants; inhibition of nutrient uptake; protein damage; disruption of metabolic function; oxidative stress; inhibition of root growth; chlorosis	Production of chelators and siderophores which bind heavy metals and reduce toxicity to plants; biodegradation and detoxification of pollutants; improved access to water and nutrients; enhanced volatilization of pollutants; alteration of phytohormones involved in plant stress response

osmotic adjustment (Begum et al., 2019; Ruiz-Lozano, Azcón, & Gomez, 1995). In addition to increasing N availability, N-fixing bacteria can also improve plant stress tolerance by contributing to soil aggregation or altering phytohormone levels (Alami, Achouak, Marol, & Heulin, 2000; Bhat, Ahmad, Ganai, & Khan, 2015). For example, Alami et al. (2000) found that an exopolysaccharide-producing strain of rhizobacterium improved plant growth and counteracted the negative effects of water stress in *Helianthus anuus* by improving rhizosphere soil aggregation. PGPR can mitigate the impacts of biotic and abiotic stress on plants through a variety of induced responses, including changes in gene expression, phytohormones, antioxidants, osmolytes (e.g. proline), heat shock proteins, dehydrins and volatile organic compounds (Balestrini, Chitarra, Fotopoulos, & Ruocco, 2017; Yang et al., 2009). Some PGPR strains produce cytokins, which promote stomatal opening and improve shoot growth under drought stress (Arkhipova et al., 2007). Bacterial production of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase increases the degradation of the ethylene precursor ACC, releasing plants from the effects of abiotic stress and maintaining plant growth (Glick et al., 2007). Soil bacteria can also contribute to plant nutrition through the solubilization of phosphorus and production of iron-chelating siderophores (Podile & Kishore, 2006). Finally, in addition to microorganisms found in the soil, microbial endophytes (i.e. bacteria, fungi, actinomycetes or viruses that live within plant tissues) are known to play an important role in plant stress tolerance (Lata, Chowdhury, Gond, & White, 2018; Rodriguez et al., 2008). Due to evolutionary, physiological and compositional changes in soil biota, microbial communities that have previously experienced a stressor could be especially effective at increasing stress tolerance in plants (Figure 2) and preserving ecological functioning of the soil under environmental stress (Andrade-Linares, Lehmann, & Rillig, 2016; Hawkes & Keitt, 2015; Millar & Bennett, 2016; Rodriguez et al., 2008).

1.2 | How does stress conditioning of soil microbial communities occur?

Conditioning of soil microbial communities could be accomplished in one of two ways: (1) making use of indigenous soil microbial communities that have been exposed to a stressor in situ (e.g. from soils at polluted sites, soils that have experienced climate-based stressors or soils from extreme environments) or (2) by artificially manipulating soil communities in the field, laboratory or glasshouse through the application of stress treatments. Successful conditioning (Figure 2) could manifest as the result of evolutionary changes in soil microorganisms, where stress events select for more stress-tolerant genotypes (Lau & Lennon, 2012; Torsvik & Øvreås, 2008). Soil biota could also become more stress tolerant through physiological acclimation, or stress priming, whereby mild previous stressors prepare microbes for future stress events (Andrade-Linares et al., 2016). Finally, soil microbial communities overall could undergo stress-induced shifts in community composition that favour more stress-tolerant taxa (Hawkes & Keitt, 2015). These shifts could be due to the direct effects of environmental conditions on soil biota, via plant-mediated changes (e.g. through root exudation), and feedbacks between these two processes over time (Kardol, De Deyn, Laliberté, Mariotte, & Hawkes, 2013).

1.3 | Evidence and implications for restoration

1.3.1 | Drought

Water availability is perhaps the most limiting factor for plant growth, especially in arid and semi-arid ecosystems. Periods of drought can reduce plant establishment and pose a major obstacle to ecological restoration in many terrestrial ecosystems, particularly as climate
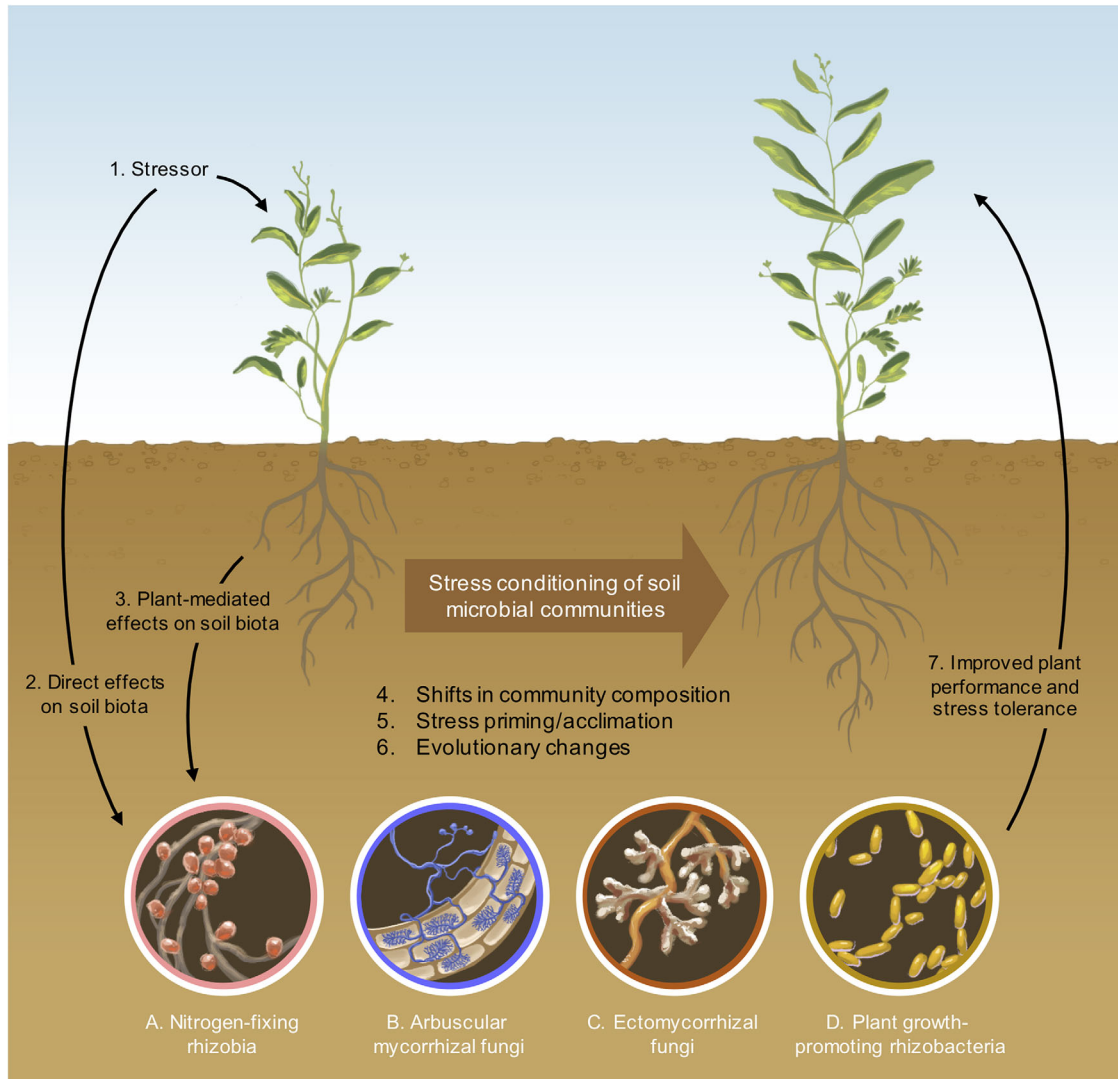
FIGURE 2 Abiotic stressors (1) can influence soil microbial communities directly (2) as well as through plant-mediated effects (3) such as changes in root exudation. Stress conditioning of soil microbial communities may occur through several mechanisms, including shifts in community composition (4), acclimation responses or 'stress priming' of microorganisms (5), and/or evolutionary changes over time (6). In some instances, stress-conditioned soil microbial communities will confer increased stress tolerance to plants, thereby improving plant performance (7). These responses may be due to symbiotic relationships with beneficial soil biota including rhizobial bacteria (A), arbuscular mycorrhizal fungi (B) or ectomycorrhizal fungi (C), as well as free-living plant growth-promoting rhizobacteria (D). Future research should further evaluate the physiological, evolutionary and community-level mechanisms involved in microbial stress conditioning, explore the development of best practices for artificially inducing such stress responses in soil microbial communities and aim to improve methods for the isolation, propagation and application of beneficial soil biota in a restoration context

predictions indicate global drying trends (Cook, Smerdon, Seager, & Coats, 2014). Many soil microorganisms can enhance plant drought tolerance through a variety of effects on plant physiology, biochemistry and gene expression, including mycorrhizal fungi and free-living and symbiotic bacteria (Kim, Glick, Bashan, & Ryu, 2012; Ruiz-Lozano et al., 1995).

Recent work has demonstrated that soil microbial communities conditioned by drought might be particularly useful in mitigating the impacts of water stress on plant performance (Lau & Lennon, 2012; Timmusk et al., 2014; Xu et al., 2018). Much of this work has been conducted in agricultural systems. For example, Timmusk et al. (2014)

demonstrated that rhizosphere bacteria from harsh environments enhanced drought tolerance in wheat. In another study, Vardharajula, Zulfikar Ali, Grover, Reddy, and Bandi (2011) used a laboratory screening procedure to identify drought tolerant *Bacillus* spp. from 25 semi-arid agricultural sites, and the isolated bacterial strains were shown to improve the drought tolerance of maize seedlings.

Relatively little work has been done to explore the effects of drought-tolerant or drought-conditioned soil biota on plants in natural systems, but if beneficial soil microorganisms that confer improved drought tolerance are identified, these could be useful targets for plant inoculation. Such a method could prove especially effective for

improving plant establishment in dryland ecosystems (Bashan & De-Bashan, 2010; Requena, Perez-Solis, Azcón-Aguilar, Jeffries, & Barea, 2001) and under continued climate change (van der Putten et al., 2013). For example, Marulanda, Porcel, Barea, and Azcón (2007) explored the use of drought-tolerant strains of arbuscular mycorrhizal fungi to promote the establishment of *Lavandula spica* for revegetation of dryland areas, finding that native strains isolated from dry sites were more effective at improving plant drought tolerance than those isolated from non-dry sites. Similar benefits were observed in a native shrub species, *Retama sphaerocarpa*, when inoculated with a drought-tolerant soil bacterium and arbuscular mycorrhizal fungi (Marulanda, Barea, & Azcón, 2006).

Interestingly, Lau and Lennon (2012) found that shifts in the soil microbial community due to multi-year manipulations of water availability were more important in driving native plant fitness than the adaptive responses of plants themselves. Specifically, they found that plants that were exposed to drought when grown in soils with a history of drought exhibited improved performance relative to plants grown in previously well-watered soils, and this improved fitness was associated with rapid responses in the soil microbial community (Lau & Lennon, 2012). In contrast, Kaisermann, de Vries, Griffiths, and Bardgett (2017) found that two plant species exhibited more negative plant–soil feedbacks in soils with a history of drought. Thus, it should not be assumed exposure to a stressor such as drought will yield a more stress tolerant or beneficial soil microbial community in all cases.

1.3.2 | Heat

Along with drought, rising global temperatures and increased frequency and severity of heatwaves (Meehl & Tebaldi, 2004) present an additional challenge for ecological restoration (Shriver et al., 2018). Elevated temperatures can inhibit photosynthesis and other physiological processes in plants, exacerbate water stress and lead to increased oxidative stress. Soil biota can ameliorate these negative effects through a variety of mechanisms, for example, by maintaining water uptake and plant gas exchange (thereby cooling leaves via transpiration), improving plant nutrition, altering phytohormone levels, reducing the accumulation of reactive oxygen species and the activation of heat shock proteins (Begum et al., 2019; El-Daim, Bejai, & Meijer, 2014; Sarkar, Chakraborty, & Chakraborty, 2018).

While there is growing interest in the application of microbial inoculants to improve crop production under rising temperatures (e.g. El-Daim et al., 2014, Sarkar et al., 2018), there are few examples from natural systems. One recent study by Rubin et al. (2018) explored whether or not soil microbial communities could be hardened against heat waves in order to develop 'climate-smart' restoration practices. The authors observed a marked shift in pre-heated rhizosphere bacterial communities, and inoculation with these soil communities resulted in reduced plant growth in a glasshouse trial. In the field, inoculation with pre-heated inoculum had no effect on plant survival during a simulated heat wave. Thus, in this case, heat conditioning appears to have shifted the soil microbial community in such a way that there were negative feedbacks on plant growth, perhaps through reductions in the abundance or activity of beneficial bacteria or increases in soil pathogens (Rubin et al., 2018). It therefore remains unclear if heat pre-conditioning of soil biota could aid restoration. In theory, heat-tolerant soil microbes could improve plant growth during restoration under a warming climate (Ali, Sandhya, Grover, Linga, & Bandi, 2011; Bunn, Lekberg, & Zabinski, 2009). For example, (Hashem et al., 1998) identified heat-tolerant Rhizobium strains capable of nodulating tree seedlings and fixing N under high temperatures. Further research on the topic will be useful in determining the potential benefits of such an approach, for example, through the use of simulated climate warming in the field and subsequent plant–soil feedback experiments.

1.3.4 | Salinity

Land degradation due to soil salinization is a growing problem worldwide that occurs as a consequence of inappropriate irrigation and drainage practices and land clearing, particularly in dryland ecosystems (Lambers, 2003; Shrivastava & Kumar, 2015). Methods that improve plant salinity tolerance are therefore highly desirable for both agricultural and ecological applications (Jesus, Danko, Fiúza, & Borges, 2015). Soil microbes can play a key role in promoting plant salt tolerance and improving plant growth in saline soils (Gamalero, Berta, & Glick, 2009; Porcel, Aroca, & Ruiz-Lozano, 2012). For example, infection by arbuscular mycorrhizal fungi can induce greater water-use efficiency, improve osmoprotection and upregulate genes involved in sodium and potassium ion transporters and channels (Evelin, Devi, Gupta, & Kapoor, 2019), while colonization by certain strains of ectomycorrhizal fungi has been shown to improve the ability of plants to exclude sodium ions in the soil (Chen, Hawighorst, Sun, & Polle, 2014). Soil bacteria can also improve plant salinity tolerance through a variety of mechanisms that enhance key physiological processes involved in proton transport, osmoregulation, salt compartmentalization and antioxidant activities (Ilangumaran & Smith, 2017).

Soil microbial communities that have been conditioned by high salinity may be especially effective at improving plant salt tolerance (Egamberdieva, Wirth, Bellingrath-Kimura, Mishra, & Arora, 2019). For example, Sharifi, Ghorbanli, and Ebrahimzadeh (2007) found that salt-conditioned arbuscular mycorrhizal fungi improved the growth of soybean in saline soils and resulted in greater root proline and plant K, P and Zn nutrition compared to plants inoculated with unconditioned fungi. Unfortunately, little work has been done to explore the microbially mediated revegetation of saline soils outside of agriculture (Grover et al., 2011) or with non-halophytic species (Estrada, Aroca, Azcón-Aguilar, Barea, & Ruiz-Lozano, 2013; Ruppel, Franken, & Witzel, 2013). However, the establishment of non-crop and non-halophytic plants, especially deep-rooted perennials, will be critical for rehabilitating sites impacted by anthropogenically induced soil salinity. In one such study, Zhang et al. (2011) found that arbuscular mycorrhizal fungi isolated from patches of vegetation growing on saline-alkaline soils improved the re-establishment of a native perennial grass in a degraded grassland impacted by salinity and low pH. Certain

salt-tolerant strains of ectomycorrhizal fungi that could improve tolerance in salt-sensitive tree species have also been identified, and inoculation with these fungi could improve plant establishment in saline soils (Bois & Coughlan, 2009; Chen et al., 2014). For example, Bois et al. (2006) found that inoculation with ectomycorrhizal fungi selected for in vitro tolerance to excess Na^+ and Cl^- improved growth and reduced salt stress in two conifer species exposed to a soil NaCl gradient.

Another possible solution is utilizing soil biota isolated from halophytic plant species to facilitate the establishment of non-halophytic species (Etesami & Beattie, 2018; Yuan et al., 2016). Yuan et al. (2016) demonstrated that the isolated belowground microbiome of the halophyte *Suaeda salsa* improved the growth and salt tolerance of two inoculated crop species, and if this method is successful in non-crop species it could greatly improve our ability to restore abandoned agricultural areas and drylands impacted by high salinity to native vegetation.

1.3.5 | Environmental contamination

Some of the strongest evidence demonstrating improved stress tolerance in plants driven by soil microbial conditioning is in response to environmental pollution. Soils contaminated by heavy metals, hydrocarbons and other toxic compounds represent a significant challenge for revegetation, as these pollutants can severely limit plant growth (Wong & Wong, 2013). While these pollutants may exert a strong negative effect on soil biota, belowground organisms may also play a key role in the restoration and phytoremediation of sites impacted by hazardous waste, mining, military activity and industrial pollution (Khan, 2005; Thijs, Sillen, Weyens, & Vangronsveld, 2017). Tolerant soil bacteria, mycorrhizal fungi and plant endophytes can facilitate plant establishment and growth in polluted sites and may also be involved in multiple processes that constitute phytoremediation including the extraction, degradation, immobilization and volatilization of contaminants (Khan, 2005; Thijs et al., 2017).

In some instances, it may be possible to isolate tolerant soil or plant-associated biota from polluted sites and inoculate target plant species to achieve restoration of otherwise inhospitable sites. Such an approach has been explored in ecosystems impacted by residues from military ordinances (Thijs et al., 2014), hydrocarbons (Gkorezis et al., 2016), mining (Babu & Reddy 2011; Jourand et al., 2014), heavy metals (Ruiz-Diez et al., 2012) and organic pesticides (McGuinness, Mazurkiewicz, Brennan, & Dowling, 2007). For example, a naturally occurring bacterial endophyte of poplar trees isolated from a site contaminated by trichloroethylene (TCE) was found to rapidly metabolize TCE, increase growth and reduce phytotoxic effects in trees grown at a TCE-contaminated site in Silicon Valley, California (Doty et al., 2017). Both arbuscular and ectomycorrhizal fungi have also been shown to improve plant growth and reduce accumulation of toxic metals in contaminated soils (Babu & Reddy, 2011, Jourand et al., 2014). Soil biota may also aid in the extraction (i.e. phytoaccumulation) and degradation of various pollutants. For example, a number of rhizosphere bacteria have been shown to successfully degrade persistent organic pollutants through plant–microbial partnerships (reviewed by Arslan

et al., 2017), and a recent meta-analysis by Wood, Tang, and Franks (2016) found strong support for the role of soil microbes in phytoextraction of soil contaminants. In addition to successful applications of microbially mediated phytoremediation for single soil contaminants, there is also evidence to suggest such an approach could be utilized for the restoration and detoxification of sites contaminated by mixtures of organic and inorganic pollutants (He, Megharaj, Wu, Subashchandrabose, & Dai, 2020).

2 | METHODS OF APPLICATION

If desirable soil biota are identified, there are several ways in which they could be deployed to aid in restoration. One approach is to use single strains of known beneficial microorganisms, which requires isolation and multiplication. The production of pure strains of soil microbes is in and of itself a significant challenge (Kaminsky, Trexler, Malik, Hockett, & Bell, 2018), with some taxa being more difficult than others (e.g. arbuscular mycorrhizal fungi are recalcitrant to in vitro culture and many soil bacteria are non-culturable). Practitioners could also make use of whole-soil inoculum, though this would likely include pathogenic constituents that could be counterproductive. However, there is evidence that in some cases introduction of the whole soil community is in fact more effective for promoting plant growth compared to individual strains (Hoeksema et al., 2010). Whole-soil communities can also be augmented through the use of 'trap cultures', where potted plants are used to amplify soil biota for later application (Koziol et al., 2018). While the use of whole-soil inoculation represents a 'black-box approach' where the identity of beneficial microbes and underlying mechanisms may be unknown, this could be the easiest and most cost-effective approach for restoration practitioners.

Inoculation of potted seedlings during nursery production has been employed for decades and allows targeted introduction of beneficial soil microbes (Corkidi, Evans, & Bohn, 2008; Trappe, 1977). This method could be used with pure microbial strains (or mixes of strains), whole-soil inoculum or a soil microbial sievate (i.e. a soil suspension sieved through a desired mesh size). Inoculum can also be applied directly in the field, either as a transplanted layer of soil (Wubs, van der Putten, Bosch, & Bezemer, 2016) or through the application of specialized 'biofertilizers' that contain specific microbial components (Vessey, 2003). Finally, the application of microbial inoculants directly to seeds through seed coating or pelleting could be a highly efficient method of delivery directly to establishing seedlings (O'Callaghan, 2016).

The method of delivery will also depend on the type of soil biota that is targeted for inoculation. For example, ectomycorrhizal fungi must be first isolated and cultivated in pure culture (e.g. in agar or liquid nutrient media) in the laboratory (Molina & Palmer, 1982). Once propagated, fungal inoculum can then be delivered to plant roots in liquid suspension, as a mixture of vermiculite and peat (or other soil substrate) into which the culture has been introduced, agar plugs colonized by mycelium or alginate-bead inoculum (Repáč, 2011). Crushed sporocarps or dry spores may also be used, either directly or in pelleted form (Repáč, 2011). Pure inoculum of arbuscular mycorrhizal fungi is

generally produced using pot cultures, where single spores are extracted from soil and used to inoculate plants grown in sterile soil or in aeroponics (Corkidi et al., 2008; Mohammad, Khan, & Kuek, 2000). Spores extracted from these plant cultures can then be used as inoculum for nursery stock or in the field. In some cases, infected root fragments may also be used (Klironomos & Hart, 2002). Cultured soil bacteria, such as rhizobia, can be applied either directly to seeds or to the soil during or after sowing. Seed inoculation techniques are varied and include dusting with dried peat-based cultures, treating seeds with a liquid slurry (often with an adhesive), pelleting seeds with inoculant and a coating (e.g. lime or rock phosphate) or seed impregnation where a vacuum is used to introduce bacteria into or under the seed coat (Deaker, Roughley, & Kennedy, 2004).

3 | LIMITATIONS, RISKS AND OUTSTANDING QUESTIONS

We have highlighted examples where soil microbial communities were successfully conditioned in ways that could facilitate ecological restoration in the face of human-caused environmental change (Table 1). However, as with any approach utilizing soil microbes, there are inherent limitations and risks (Hart, Antunes, Chaudhary, & Abbott, 2018; Kaminsky et al., 2018; Schwartz et al., 2006). First, the introduction of soil microbial communities, even indigenous ones, may not always achieve the desired outcome. For example, Meisner, De Deyn, de Boer, and van der Putten (2013) reported that drought-impacted soil communities promoted the growth of exotic species but not natives. Contaminated inoculum cultures could also inadvertently introduce unwanted pathogens or saprobes (Schwartz et al., 2006). In instances where local soil is not available, there is also the risk of introducing soil biota that will become invasive outside of the restoration site (Hart et al., 2018; Schwartz et al., 2006). It is also possible that stress-conditioned soil biota will exhibit trade-offs in other traits along with increased stress tolerance, which could be counterproductive. For example, rhizobia strains associated with multiple Australian *Acacia* species were found to exhibit a trade-off between growth rate and salinity tolerance (Thrall, Bever, & Slattery, 2008).

Stress events can exert a strong negative impact on soil biota, and it should not be assumed that subjecting soil microbial communities to a stressor will always result in increased resilience or improved plant performance (Millar & Bennett, 2016). In some instances, stress events could result in an inferior soil microbial community with detrimental impacts plant growth (Compant, Van Der Heijden, & Sessitsch, 2010; Rubin et al., 2018). For example, environmental stressors could reduce the abundance or activity of beneficial soil micro-organisms or increase plant susceptibility to soil pathogens. Furthermore, even if soil microbial communities are successfully conditioned to a given stressor, there is also a chance that this could increase susceptibility to other additional stressors. For example, Tobor-Kapłon, Bloem, Römkens, and Ruiter (2005) found that soil bacterial and fungal communities subjected to low pH and copper contamination were less resilient than unconditioned soil communities when exposed to a secondary stressor.

Conversely, multiple stressors could also steer the soil microbial community towards a similar 'stress microbiome; Timm et al. (2018) found that water limitation, shading and metal toxicity selected for a core set of bacterial genera that could buffer against multiple types of environmental stress. Some soil microbial communities exhibit high levels of resilience (Allison & Martiny, 2008). This resilience could contribute to improved plant performance under abiotic stress as functionality is preserved. However, such resilience could also make soil microbial communities resistant to change, thereby inhibiting their capacity to become conditioned to a particular stressor. Thus, the success (or failure) of stress conditioning of soil microbial communities is likely very context dependent and will be contingent upon the specific type, duration and severity of stress, the identity and composition of above- and belowground biota, and environmental conditions.

Plant responses to soil biota are often very species specific, and a key question is how compatible soil biota involved in plant stress tolerance will be across plant species and ecosystems (Marasco et al., 2013). This will depend on which plants and microbes are the targets for restoration and inoculation (Hoeksema et al., 2010). For example, some plant species require specific fungal or bacterial symbionts, whereas other free-living soil bacteria may provide more universal benefits across plant taxa by providing general 'soil health' benefits (Rosier, Medeiros, & Bais, 2018). The relative importance of cross compatibility will depend on restoration goals; if the restoration target is a diverse plant community, soil microbial communities that are able to confer greater stress tolerance to a variety of species will be more important than if a single plant species is being reintroduced to a site.

Another consideration is whether plants should be inoculated with single strains of biota, multiple strains or even mixtures of different types of microbes. For example, mixtures of multiple species of arbuscular mycorrhizal fungi may prove more beneficial for plants than single-species inoculants in some cases (Crossay et al., 2019). There may also be synergistic benefits of utilizing multiple types of soil biota simultaneously as inoculants. For example, Vivas, Biro, Ruiz-Lozano, Barea, and Azcon (2006) found that plants inoculated with arbuscular mycorrhizal fungi and two bacterial strains isolated from Zn-polluted soils exhibited enhanced growth under Zn toxicity, and plants dually inoculated with fungi and bacteria showed lower Zn levels than plants inoculated with single bacterial strains or fungi alone. The rhizosphere contains a diverse array of soil biota, and identifying the various members of the soil and root microbiome and their function may help unlock potential applications for ecological restoration. Such a microbiome-level approach may prove more successful than the use of individual species or strains as inoculants (Hartman et al. 2017).

If there are benefits to utilizing conditioned soil microbial communities, how long will they persist? The fate of introduced soil microbes depends on successful colonization of plant hosts (in symbiotic organisms) and their ability to compete with resident soil biota (Hart et al., 2018; van Veen, van Overbeek, & van Elsas, 1997). Few studies actually track the establishment and persistence of introduced microbial inoculants (Hart et al., 2018), so it is not well understood how persistent these introductions are even when positive plant responses are reported. The use of conditioned indigenous soil biota may be more

likely to persist than commercial inoculum sources given that they are better matched to edaphic, environmental and biotic conditions. However, it is possible that the conditioned state of these will wane over time due to evolutionary changes or shifts in abundance. In general, microbial inoculation techniques may be more successful in highly disturbed soils where competition from existing soil microbes is less intense (Hart et al., 2018), and these are precisely the types of sites where higher levels of intervention may be required to achieve restoration goals.

In order for soil microbial stress conditioning to be a viable tool for ecological restoration, it is important to be able to identify the specific soil biota involved in stress tolerance/resistance and characterize the interactions between plants and soil microbial communities. Recent advances in metagenomics and transcriptomics present an opportunity to improve our understanding of the benefits of soil biota to plants by revealing changes in the functional potential and gene transcription profiles of both microbes and plants under stress (Hartman & Tringe, 2019). For example, meta-transcriptomic sequencing of the rhizosphere of sorghum subjected to drought revealed changes in Actinobacteria-dominated soil communities that were correlated with changes in the root metabolomic profile (Xu et al., 2018). The authors suggested that the discovery of such exchanges between plants and microbes under drought could provide a blueprint for manipulating plant microbiomes to improve plant fitness (Xu et al., 2018). Recent development of in silico approaches has also facilitated taxonomic surveys by matching barcoding sequences to known genome sequences in a database. These approaches infer metagenomic function and can be used to identify genes that are part of soil biological processes (e.g. Mickan et al., 2018). Entire genome sequencing is the gold standard for understanding soil microbial community functioning and composition (Breitwieser, Lu, & Salzberg, 2017). However, this approach is still indirect, as the presence of a gene does not guarantee its organismal or ecosystem functional significance. In addition to identifying specific microbes involved in improved plant performance under environmental stress, these methods are also useful for tracking the persistence, abundance, activity and potential spread of microbial inoculants.

Finally, it is important to note that evidence from glasshouse and laboratory experiments may not indicate that microbial inoculations will be successful in the field (Heinze, Sitte, Schindhelm, Wright, & Joshi, 2016; Kaminsky et al., 2018). Controlled potted or laboratory experiments are undoubtedly important for demonstrating the potential benefits of soil biota for plant growth and stress tolerance, but similar results may not manifest under field conditions where there is more ecological complexity and environmental variability at play. Therefore, practitioners should interpret studies without field validation with caution, particularly where generalist plant growth benefits are claimed by manufacturers of commercial products.

4 | CONCLUSIONS

Soil biota are known to play a critical role in mediating plant response to environmental stress, and harnessing the ability of soil microbial communities to adapt and acclimate to different stressors could yield a novel strategy for ecological restoration in the Anthropocene. While there is growing interest in engineering the soil microbiome for improving plant stress tolerance in agriculture (Grover et al., 2011; Hussain, Mehnaz, & Siddique, 2018; Zachow et al., 2013), applications for restoration are still relatively unexplored. In light of ongoing environmental degradation and ever-improving methods for characterizing soil microbial communities, efforts to harness the soil microbiome for ecological restoration are likely to increase in the near future. The use of stress-conditioned soil microbial inoculations represents a significant challenge, but the existing evidence from both natural and managed systems highlights the potential benefits of such an approach for restoring native plant communities in a changing world. However, we recommend that researchers exploring this approach should carefully consider if methodologies being evaluated will be practical, feasible and cost-effective from the perspective of restoration practitioners.

AUTHORS' CONTRIBUTIONS

JV conceived of the manuscript idea. All authors contributed to writing and editing the paper.

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