Editor summary:

In this Perspective, the authors develop a risk assessment framework for forest microbiomes under climate change that unites microbial and forest ecology. They define processes that amplify or buffer microbial sensitivity and exposure risk and feedbacks that mediate impacts on microbial communities.

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Title: A Risk Assessment Framework for the Future of Forest Microbiomes in a Changing Climate

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Abstract: Microbes inhabiting the above and belowground tissues of forest trees and soils play a critical role in the response of forest ecosystems to global climate change. However, generalizations about the vulnerability of the forest microbiome to climate change have been challenging due to often context-dependent responses. Here we apply a risk assessment framework to evaluate microbial community vulnerability to climate change across forest ecosystems. We define factors that determine exposure risk and processes that amplify or buffer sensitivity to change and describe feedback mechanisms that will modulate this exposure and sensitivity as climatic change progresses. This risk assessment approach unites microbial ecology and forest ecology to develop a more comprehensive understanding of forest vulnerability in the 21st century.

Resumen (Español): Los microorganimos que habitan en los tejidos aéreos y subterráneos de los árboles y suelos forestales desempeñan un papel fundamental en la respuesta de los ecosistemas forestales al cambio climático. Sin embargo, las generalizaciones sobre la respuesta del microbioma forestal al cambio climático ha sido un reto debido a que las respuestas son contexto-dependientes. Aquí aplicamos un marco de evaluación de riesgos para evaluar la vulnerabilidad de la comunidad microbiana al cambio climático en los ecosistemas forestales. Definimos los factores que determinan el riesgo a la exposición y los procesos que amplifican o amortiguan la sensibilidad al cambio climático, y describimos los mecanismos de retroalimientación que modularán la exposición y sensibilidad a medida que avance el cambio climático. Esta aproximación de evaluación de riesgos une a la ecología microbiana y la ecología forestal para desarrollar una comprensión más completa de la vulnerabilidad de los bosques en el siglo XXI.

Resumo (Português): Os microrganismos que habitam o solo e os tecidos das árvores acima e abaixo do solo desempenham um papel crítico na resposta dos ecossistemas florestais às mudanças climáticas globais. No entanto, generalizações sobre a resposta do microbioma florestal às alterações climáticas têm sido um desafio devido às frequentes respostas dependentes do contexto. Aqui, nós aplicamos uma estrutura de avaliação de risco para avaliar a vulnerabilidade da comunidade microbiana às mudanças climáticas em ecossistemas florestais. Nós definimos os fatores que determinam o risco de exposição e os processos que amplificam ou atenuam a sensibilidade à mudança, e descrevemos os mecanismos de retroalimentação que modularão essa exposição e sensibilidade à medida que as alterações climáticas progridem. Essa abordagem de avaliação de risco une a ecologia microbiana e a ecologia florestal para desenvolver uma compreensão mais abrangente da vulnerabilidade das florestas no século XXI.

Introduction

Forest ecosystems cover approximately one-third of the Earth's land surface, harboring immense biodiversity[1] and supporting diverse human cultural needs and values[2]. Forests sequester over three-quarters of terrestrial carbon globally[3], however, due to climate change and land use practices in the "Capitalocene"[4], the functioning and persistence of forest ecosystems represents an area of critical scientific uncertainty[5,6]. Investigations of forest response to climate change have largely focused on tree demography and ecophysiology, satellite measurements, and restructuring of forest community structure and function. Collectively, these studies indicate that fire, drought, increasing CO_2 concentrations, and rising temperatures imperil the health and carbon sequestration potential of forest ecosystems[5,6]. Improving understanding of forest responses to climate change is critical for effective policy and climate adaptation initiatives.

The forest microbiome mediates forest responses to a number of climatic stressors including drought[7], rising temperatures[8], and elevated CO_2[9]. Microbiomes also play an important role in forest recovery from fire[10,11] and hurricanes[12], and microbes shape soil methane production and consumption[13], as well as the ability of soils to sequester CO_2[14]. There is now also unequivocal evidence that forest microbial communities are vulnerable to climate change[15–18], highlighting the need for their explicit consideration in efforts to predict the fate of forest ecosystems. Observational studies across local to global-scale environmental gradients document how microbial community composition and function are locally adapted, and highly sensitive to prevailing climatological conditions[17,19–22]. In addition to observational inferences, experimental studies of microbial communities across diverse forest environments demonstrate dynamic compositional and functional responses to climatic disturbances[18]. Because rates of microbial responses to disturbance may differ from forest trees, mismatches between plant communities, local-climates, and microbial communities can occur, with important implications for forest function[23,24].

Forest microbes often exhibit strong context- and scale-dependent responses to disturbance[25–27], challenging generalizations of microbiome response to climate change. Accordingly, these context dependencies have stymied the effective incorporation of microbial dynamics into predictive models and understanding of forest ecosystems[5,6,27,28]. To address this knowledge gap and better predict and integrate microbiomes into a more holistic understanding of forest response to climate change, we adapt a risk assessment framework for forest microbiomes in the Anthropocene.

Defining forests and their microbiomes

The Kyoto Protocol (1997) categorizes forests as areas greater than 0.5-1.0 hectares where the minimum "tree" crown cover ranges from 10-30%[29]. From the boreal to the Amazon, forest ecosystems span broad climatic regions[6]. Throughout these regions, trees scaffold and shape forest systems, giving rise to distinct habitats and microclimates for understory species[30]. Trees are generally defined as plants capable of growing at least two meters tall[29], though their stature and architecture varies greatly by species[31]. Lifespans of trees are also highly variable across taxa, ranging from 25 to over 5000 years[32]. The architectural, demographic, and ecophysiological characteristics of trees are predicted to play important roles in forest responses to climate change[5,6].

The forest microbiome – a rich diversity of bacteria, archaea, fungi, lichens, and viruses – supports plant productivity and forest function across the globe[33–35] (Fig. 1a). Forest ecosystems are among the most biodiverse microbial habitats on Earth. For example, individual leaves can host hundreds of bacterial and fungal taxa[36] and tens of thousands of microbial species inhabit forest soils[37]. Forest microbes span a range of interaction types, including pathogens and mutualists. These microbes cumulatively facilitate nutrient cycling[35,38] and impact plant community structure by mediating plant coexistence and diversity[39–41]. Key microbial groups in soil include saprotrophic fungi and bacteria, which drive decomposition and soil carbon accumulation[42]. Saprotrophic microbes mediate soil nutrient availability by mineralizing organic nitrogen into plant-available inorganic forms[42,43]. Other key groups include ancient interactions between tree roots and mutualistic mycorrhizal fungi, such as arbuscular (AMF) and ectomycorrhizal fungi (EMF), which shape host environmental tolerances[8] and represent an important component of nutrient acquisition strategies for trees[19] (Fig. 1c). Similarly, mutualistic relationships between roots of certain tree species and N-fixing bacteria influence biogeochemical cycling in forest systems[35]. Fungal and bacterial endophytes in roots and leaves can protect trees against pathogens[36], promote drought tolerance[44], influence host thermal tolerance[36], and contribute to host N supply through N-fixation[45] (Figure 1a). N-fixing bacteria have also been found in forest soils, leaves, and leaf litter, as well as in association with mosses and lichens, contributing to forest N-availability and biogeochemical cycling[46]. In this review, we especially focus on the bacterial and fungal components of the forest microbiome given available knowledge and their pivotal role in forest function[34].

A risk assessment framework for forest microbiomes

Risk assessments are used to predict and manage the vulnerability of diverse systems by providing insights into where exposure may be reduced or sensitivity might be mitigated[6,47]. Because risk frameworks have predominately been used in macroecological contexts[47], to utilize this framework, we first define microbially-relevant scales of exposure and attributes of microbial communities and individuals that govern their sensitivity to climatic disturbance (Fig. 2)[15,47,48]. Then, we define important feedbacks that can inform the trajectory of forest microbiome responses to ongoing climate change. This framework intends to synthesize forest microbiome response to climate change in order to unite forest microbial ecology with macroecological understanding of forest responses to climate change[6]. While we specifically apply the framework in a forest ecosystem context, the principles should also be broadly applicable, and the framework is intended for diverse terrestrial ecosystems.

Exposure

The effects of warming, drought, and other climatic disturbances vary across geographic and temporal scales[6]. We define exposure risk as the probability that climatic disturbance will extend beyond physical baseline conditions enough to impact forest microbiome community structure or function. Accordingly, quantifying climatic exposure risk for the forest microbiome depends on the integration of three different components of climatic disturbance: disturbance type, spatiotemporal scales of disturbance, and the capacity for physical buffering of disturbance across microbial habitats.

Categorizing climatic disturbances

The persistence of forest systems is threatened by the increasing frequency and severity of climatic disturbance[6]. Different types of perturbations associated with a changing climate can be categorized in a pulse-press framework to understand their potential impact across spatiotemporal scales and intensity of disturbance[15,49]. Disturbances like elevated CO_2 (eCO_2) and rising air temperatures represent press events, disturbances which are ongoing and relatively slow[49]. Press disturbances are predicted to select for microbial traits associated with greater physiological plasticity and niche breadth (tolerance), and strong acclimation or rapid adaptation will be required to maintain community composition as a result of continuing disturbance[15,16,50]. Conversely, pulse events are discrete disturbances, including droughts, hurricanes, floods, or wildfires[49]. Pulse disturbances tend to favor microbial community traits associated with rapid recovery (often referred to as resilience)[15]. Though pulse disturbances like forest fires can initially reduce soil fungal and bacterial biomass and diversity[51,52], pulse disturbances have a defined end period, in some cases allowing microbial communities to eventually recover parts of their original structure and function[15]. However, recovery of microbiome function following pulse events is variable and can take as long as several decades[10]. While the pulse-press framework is conceptually useful for comparing and synthesizing the physical impacts of diverse climatic stressors on organisms and communities, it is important to note that both press and pulse disturbances increasingly act in tandem[53].

Consideration of microbial lifespan and life-history strategies are essential to contextualizing exposure risk[15]. For instance, some long-lived soil fungi can persist for years to decades[54], whereas many co-occurring soil bacteria turnover on the order of hours or days in response to drought[55]. As a result, while a multi-month drought may represent a pulse disturbance for a tree or long-lived fungus, droughts typically impact many generations of more ephemeral fungi or bacteria[15]. Consequently, bacteria and some fungi may undergo rapid evolution in response to pulse disturbances, whereas evolution for some fungi may occur over longer timescales[56].

Climatic disturbances can act either directly on microbial cells, or through indirect pathways. For example, drought and rising temperatures can directly stress microbial cells[55,57]. In contrast, eCO_2 indirectly impacts soil communities, primarily via shifts in substrate-availability[58,59]. Greater C allocation of trees belowground in response to eCO_2 can increase colonization of roots by both EMF and AMF fungi, and result in greater rhizodeposition, increasing availability of carbon-substrates to microbes[60,61]. Tracing the various pathways whereby climatic stressors directly or indirectly impact microbial communities will be critical to accurately projecting the magnitude of community responses.

The spatial and temporal nature of climatic disturbances

The type, intensity, frequency, and timing of disturbances varies dramatically across forest biomes[6,18] (Fig. 3). Catastrophic droughts, flooding, and severe hurricanes affect tropical forests, while reduced snowpack and permafrost melt threaten boreal and high-elevation forest systems[62]. In many temperate forests, drought and rising temperatures compound with settler-colonial fire suppression to create fires of increasing frequency and intensity[63]. Increasing frequency and spatial extent of disturbance threaten the capacity of microbial communities to withstand and/or recover their pre-disturbance community structure[64] and shifts in pathogen ranges, including bark beetle and invasive microbial diseases, can result in mass tree mortality, jeapordizing forest persistence in some systems[7,65]. Importantly, the intensity of disturbance will also vary across forest biomes. The rate of warming, for instance, differs across the globe with boreal forest temperatures projected to increase at approximately twice the rate of other forests[66] (Fig. 3a-b). As a result, microbiome exposure to warming is likely greater in boreal compared to temperate and tropical forest systems[62].

For pulse-type disturbances, the timing of a disturbance also influences microbiome exposure risk, especially for forests with strong seasonality (Fig. 3c). For example, spring fires result in greater reductions in fungal saprotrophic diversity compared to fires of similar severity which occur in autumn[67]. One hypothesis is that spring fires are more damaging for microbial growth and reproduction than fires that occur during periods of higher microbial dormancy[67]. Climate change will continue to advance the onset of summer and spring, while autumn and winter seasons are expected to be shortened and delayed[68]. Thus, longer periods of microbial activity may increase the probability of greater impact of pulse disturbances on microbial community structure and function. Additionally, autumn is an especially critical ecological period, especially for many fungi, as this is when they transition from high periods of activity to reproduction[69]. Scarce datasets in Western science track long-term shifts in microbial reproduction, making generalizations about shifts in fruiting phenology associated with climate change challenging[70,71]. However, many Indigenous communities have been observing patterns and processes of fungal phenology for thousands of years[72]. For example, the Karuk tribe (Northern California, USA) has demonstrated how delays in autumn (warmer temperatures continuing into October/November and later rainfall) lead to declines in ectomycorrhizal fruiting, with important consequences for the communities and ecosystems these fungi help to sustain[73] (Box 1). Indigenous science has a critical lens into how climate change is shaping forest ecosystems as its period of observation extends back tens of thousands of years; the centering of Indigenous-led science will be critical in better understanding and managing forest systems in a changing climate[74].

Microclimates, microhabitats, and microbe-specific niches

The physical structure of forest ecosystems plays an underappreciated role in determining the exposure risk of different microbial communities to climatic disturbance (Fig. 3d). Due to their immense structural complexity relative to other terrestrial ecosystems, different locations in forests confer varying degrees of physical buffering from climatic disturbance[30]. Throughout the forest canopy, light, temperature, and moisture conditions vary dramatically[75,76]. Microbes associated with different forest compartments (e.g. leaves versus roots) experience varying degrees of physical buffering (Fig. 3d-e) and have different inherent exposure risks to climatic disturbances. To distinguish these from the physical structures that hosts can evolve to spatially separate symbionts (compartmentalization), herein, we refer to these different microbially habitats (leaves, roots, soil, etc.) as microbial-specific niches (MSNs)[34].

Plant hosts can also actively and passively modulate microbiome exposure. For example, bacterial communities associated with roots of *Sequoia sempervirens* are less sensitive to water-deficit relative to those in soil, potentially due to consistent water availability in roots[22]. In *Eucalyptus,* latent cooling through evapotranspiration reduced leaf temperatures by up to 7.5°C relative to air temperatures during a heatwave[77], helping to buffer heat exposure for phyllosphere and endophyte microbial communities. Active cooling via evapotranspiration may also help to explain how foliar endophyte communities associated with *Pinus ponderosa* can maintain community structure whereas root-associated microbial communities are reshaped by warmer temperatures[78]. The soil matrix can also buffer microbiome exposure. For example, the composition and diversity of bacterial and fungal communities in the soil surface (0-5 cm depth) are often strongly impacted by fire, but heat from surface fires attenuates rapidly with soil depth, suggesting that deeper soils may act as a potential refugia for microbial communities[79] (Fig. 3e).

Canopy gaps also create distinct microclimates (Fig. 3d). These gaps are relatively warmer and drier, and consequentially, distinct wood decay fungal communities inhabiting them exhibit reduced rates of decomposition[80]; similarly, canopy gaps may reduce the local diversity of EMF communities[81]. In xeric systems, removal and management of understory plants through practices such as cultural burning can increase soil water content and nutrient availability[82], providing important habitat for plant and microbial communities by reducing understory plant competition[83]. However, extensive habitat fragmentation (due to logging or large-scale climatic disturbances like stand-replacing fires or hurricanes) may exacerbate forest warming through reduced shading and evapotranspiration, further threatening forest communities. Altogether, the unique buffering capacity of distinct MSNs, suggests that microbiome community structure and function could shift at different rates across leaf, root, and soil communities potentially causing dysbiosis for tree hosts[84]. Exploring how different MSN combine to collectively influence plant health remains an intriguing area of future research.

Sensitivity

In the broadest terms, sensitivity describes the intrinsic factors that determine how a community, species, or individual is impacted by climatic disturbance[47]. At the community scale, sensitivity describes the degree to which microbial community composition or function responds to disturbance and their capacity to recover composition or function post-disturbance (Fig. 4a)[85]. At the species and individual scales, low sensitivity is the persistence of a taxon or individual or their capacity to recover physiological function following a short-term disturbance[85]. Here, we identify and describe evolutionary and ecological processes that modulate the sensitivity of microbial populations and communities.

Global variation in the sensitivity of microbial communities

Surveys across continental and global scales have identified strong biogeographic patterns in microbial communities, with high degrees of endemism (for some taxonomic groups) and unique functional trait profiles across the major tropical, temperate, and boreal forest biomes[21]. This suggests that climatic disturbances may result in divergent responses for microbial communities inhabiting different biomes or habitats. The biogeographic patterns in microbial communities result from prevailing climatic regimes (e.g. mean annual temperature; MAT)[21], geochemical attributes (e.g. parent material, pH, Ca)[86], different evolutionary origins of microbial taxa[87], and the composition of forest tree species[88,89]. Additionally, limitations to microbial dispersal can drive distinct community[90] and population structures[91].

In the face of climatic change, varying sensitivity of microbial communities can result in several response scenarios: tolerance (resistance to climate disturbance[92]), recovery (initial change followed by return to original abundance or community structure[93]), and transition (i.e. to an alternative state[15,50] (Fig 4a). There is growing consensus that communities which have experienced greater historical environmental fluctuations will be more likely to tolerate future disturbance[50,94]. For example, forest biomes in which temperature fluctuations are relatively large, such as in high-latitude forests, exhibit relatively small compositional changes when exposed to warming compared with lower latitude forests[95,96]. Similar patterns of tolerance have also been observed for short-lived disturbances like drought. In temperate forests, regions with lower historical precipitation select for microbial communities with higher tolerance to acute drought[92], including Actinobacteria, Firmicutes, and Thaumarchaeota[22,97]. Historical legacies of water-availability also correspond to drought tolerance for microbes in tropical forests; in forests where drought treatments had been experimentally imposed, tropical microbial communities experienced less pronounced shifts in community composition compared to the controls with no prior drought exposure[98].

Community recovery potential also appears to vary across biomes with different disturbance regimes. In forests where fire is historically common, microbial taxa and even whole microbial communities recover rapidly, even from severe disturbance[99–102]. Microbial community recovery is facilitated by an initial increase in fire-specialized taxa[51]. For example, spores of a root-associated EMF species (*Rhizopogon olivaceotinctus*), nearly double their colonization potential following heating[103], and soil-dwelling *Arthrobacter* bacteria experience post-fire population booms[51]. These pyrophilous microbes may facilitate recovery of the original community by breaking down hydrophobic or pyrolyzed organic matter[99]. Importantly, early successional microbes are generally poor competitors that do not appear to prevent re-establishment of the initial community[104]. In contrast, for forest ecosystems adapted to less frequent fire regimes and having fewer pyrophilous community members, populations of both saprotrophic and mutualistic microbes are heavily reduced after fire and appear less likely to recover their original state[52,100] (Fig. 4a).

The impacts of increasing frequency of disturbance and compounding disturbance types might be exceptionally stressful for microbial communities, potentially impeding community recovery and leading to a transition to alternative states[105]. More frequent disturbances are especially likely to result in functional collapse and transition in microbial ecosystems[64]. For example, while microbial recovery potential appears high in fire adapted landscapes, fire regimes are shifting rapidly[6]. In fire-adapted *Eucalyptus pilularis* forests of Australia and coniferous forests in Western USA, fire adapted microbial and lichen communities appear less likely to recover with increases in fire frequency[106], especially when combined with periods of intensifying drought stress[101] and emerging infectious disease[107]. Microbial community transitions are also predicted where disturbance results in novel environmental conditions. For example, rising temperatures decrease climatic controls on rates of decomposition, leading to predicated transitions from EMF to AMF-dominated forests, especially at boreal-temperate ecotones[19].

Studies documenting microbial community tolerance, recovery, or transition may not necessarily correspond with identical shifts in microbiome functioning. This decoupling could arise due to processes of microbial acclimation to warming via physiological shifts in cellular processes[108]. Similarly, high degrees of functional redundancy in microbial communities could result in modest or non-linear functional responses despite strong community shifts. Relative decoupling of composition-function relationships could also vary across forest biomes if historical environmental fluctuations exert a strong impact on community sensitivity and a more variable impact on functional sensitivity. Accordingly, in boreal forest soil communities, prolonged warming may trigger moderate community shifts (tolerance) and a temporarily increased but progressively weakening effect on soil respiration due to microbial acclimation[109]. This response contrasts with observations of accelerating community and respiration responses in experimentally warmed tropical forests[95]. Sufficient temporal inference is lacking to fully describe these relationships, and further work is required. We stress that community tolerance, recovery, and transitions represent operational definitions; the linkages between community composition and microbiome function remains one of the most critical areas of ongoing investigation[110].

Variation in sensitivity across microbe-specific niches

Microbes are adapted to distinct environmental fluctuations and resource availabilities across microbial-specific niches (MSNs) and therefore exhibit unique sensitivities among these habitats[34,111,112]. For example, wood decay fungi such as *Phlebiopsis* and *Phellinus* exhibit optimal growth temperatures that vary across biogeographic ranges but generally fall between 20-28°C, with growth declining rapidly above 30°C[113]. By contrast, the surface of sunlit leaves can frequently exceed 30°C[114] and leaf-inhabiting microbial endophytes are adapted to warmer temperatures; many of these endophytes, including *Burkholderia, Acinetobacter*, and yeasts such as *Rhodotorula*, are regularly cultured at 30°C[115]. For highly diverse MSNs such as soils, there is evidence that microbes found in these MSNs may be more tolerant as compared to leaf or root communities[116]. Accordingly, the potential for microbial communities to respond asymmetrically across MSNs, especially above and belowground, is an important area of future investigation[3]. Studies of potential dysbiosis among MSN and functional consequences for hosts are critical in elucidating forest sensitivity to climate change[117].

In addition to inhabiting unique physical niches in trees and forests (e.g. in roots versus leaves), microbial host-dependence is another important dimension of MSNs. While some microbes are free-living, others are facultatively or obligately host-associated and exhibit varying degrees of host specificity[34]. For obligately host-associated microbes or those with high host-specificity, the persistence of host plants is a minimum criterion for the presence of suitable MSNs[118,119]. For some obligate host associates, an effective tolerance strategy may be to improve host survival of the same disturbance[120]. By contrast, where microbial associations increase mortality risks of their hosts, a decline in available hosts to infect may render these microbes more sensitive to climate change. For example, white pine blister rust (*Cronatium ribicola*) increases host mortality at low elevations during drought, thereby decreasing the population of its available hosts (alongside rates of infection)[7].

Traits and tradeoffs that structure microbial sensitivity

Particular microbial traits predispose microbes to heightened climatic sensitivity because of how trait-tradeoffs interact with climatic perturbation[22,51,121,122]. Trait-tradeoffs have been observed for bacterial[48] and fungal taxa, such as EMF[123], as well as in response to diverse disturbances, including water deficit[22], warming[124] and fire[51,102]. For example, trade-offs in bacterial suitability to post-fire habitability and competitive abilities have been observed[102]. We expect that investigations exploring the identity and function of specific traits influencing microbial sensitivity at both the taxon and community scale will be an especially active area of future research.

Climatic disturbances could significantly impact microbial physiology, as well as community composition and function. Trait tradeoffs between microbial growth yield (Y), resource acquisition (A), and stress tolerance (S) broadly define microbial sensitivity to climatic perturbation (the Y-A-S framework; Fig. 4b)[48]. When climatic disturbance drives resource limitation, such as during drought, microbes exhibit tradeoffs between traits associated with microbial resource acquisition and growth yields[16,48]. This has been observed for soil bacteria across a natural gradient of water deficit, where filamentous *Streptomyces* bacteria associated with *Sequoia sempervirens* root communities dominate in dry soils but unicellular flagellate bacteria, such as *Bradyrhizobium,* are more dominant in wetter soils (Fig. 4b)[22]. Filamentous lifestyles excel at resource acquisition by scavenging a larger soil volume, whereas flagellate bacteria have higher growth yields, but are dependent on saturated soils for motility and access to soil resources[55].

Traits associated with stress tolerance are also important to microbial persistence during climatic perturbation[48,55,124]. For example, exposure to acute drought resulted in an upregulation of genes associated with cell wall and membrane maintenance, but an overall reduction in gene expression and resource acquisition in foraging hyphae for the EMF fungus, *Suillus pungens*[123], likely impacting the cellular tolerance of stress and resource-acquisition of this fungus. Similar cellular tradeoffs also appear to apply for rising temperatures. A study of long-term soil warming in the Alaskan boreal forest found that genes associated with cellular maintenance were upregulated compared to genes associated with microbial resource acquisition and growth[124]. Cellular dormancy is another important facet of microbial stress tolerance and could be a common strategy for members of the forest microbiome[51,125,126]. Due to larger intracellular investment costs, dormancy appears to have important tradeoffs with capacity for vegetative growth rates[48,51,102]. While little is known about cross forest biome variation in the distribution of cellular dormancy, dormancy and sporulation could be particularly common in forests which experience large seasonal climatic fluctuations or frequent pulse disturbances[15,94,125]. Soils experiencing frequent fire are enriched in endospore-forming Firmicute bacteria[10,102] and mycorrhizal fungi which form resistant spore banks may possess an early competitive advantage post-fire[126].

Feedback mechanisms that amplify or buffer vulnerability

Feedback processes can either amplify or buffer microbiome sensitivity and exposure to future climatic disturbance[47]. Feedbacks within forest systems play an underrecognized role in determining the vulnerability of the microbiome to future climate change. Here, we outline several pathways where biogeochemical, climatological, and biotic feedbacks could modify forest microbiome vulnerability to future climatic disturbance.

At the largest scales, shifts in forest microbiome structure and function will influence critical biogeochemical cycles. For example, trees that associate with N-fixing microbial symbionts are favored under increasingly dry forest conditions[127]. However, the dominance of N-fixation in arid soils has also been linked to the release of NO_x, a potent greenhouse gas[128]. As a result of NO_x release, warming and drying are likely to be amplified, increasing the exposure of forests and their microbiomes to further disturbance. Similarly, warming temperatures are poised to stimulate the decay of soil organic matter (SOM) by microbial communities, particularly in high-latitude soils[14]. The substantial release of CO_2 from increasing rates of microbial activity will result in a positive climate feedback loop, further exposing forest systems to higher temperatures in the future. Increased rainfall in certain tropical regions can also substantially shift biogeochemical cycles by stimulating microbial methane production, the release of which can further accelerate rising temperatures and other climatic disturbances; this is especially pronounced after deforestation has occurred[13]. Elevated CO_2 (eCO_2) has significantly increased the strength of the terrestrial C sink. This sink is contingent on the sustained nutrient-foraging attributes of mycorrhizal symbionts and their ability to stimulate plant growth[3,9]. However, for trees associated with EMF, enhanced plant investment in fungal mutualists under eCO_2 could reduce soil C stocks, with uncertain consequences on ecosystem C balance. Moreover, increased EMF foraging under eCO_2 could alter substrate quality for free-living bacteria and fungi[3], thereby influencing nutrient mobilization and potentially plant nutrition. Long-term observations of shifts in leaf and root-litter stoichiometry potentially support altered nutrient availability resultant from shifted microbial functioning[129]. In addition to eCO_2 effects, long-term shifts in soil substrate availability and quality could also occur due to drought stress or increased fire frequency[130], with similar consequences for microbial functioning, plant productivity and draw down of atmospheric CO_2.

Climatic disturbances that restructure plant communities or impact plant ecophysiology will also create feedbacks that impact future microbiome exposure and sensitivity. Warming, drying, and increased fire frequency and severity are hypothesized to increase the activity, abundance, and pathogenicity of certain bacteria and fungi[101,131]. Increased pathogenicity partially results from climatic release where higher winter temperatures increase winter survivorship for pathogens[132]. Increased pathogen abundance can hasten forest compositional turnover for trees already stressed due to changing climate. As climatic niches for EMF and AMF hosts shift with climate change, AMF-associated hosts are predicted to become more dominant in temperate systems[133]. Because EMF-associated trees are thought to have higher resistance to root pathogens due to physical protection conferred by hyphal mantles surrounding the host roots[39], increased root pathogen abundance may interact with other microbial guilds such as AMF or EMF, to generate plant compositional feedbacks[39]. The potential for transitions between plant communities dominated by different mycorrhizal associates will have consequences for nutrient cycling[19], soil water retention[134], and forest structure and diversity[135].

Finally, as microbial responses to climate change will influence plant community coexistence and competition dynamics[8,41], shifts in forest community structure may generate additional feedbacks for microbial communities. Similarly climatic processes which alter plant community diversity or function could have knock-on effects that mediate the vulnerability of the microbiome to future disturbance. For example, drought can destabilize plant community coexistence in forests through modification of plant-soil-feedbacks[136]. Drought or warming that result in reduced plant richness or plant trait diversity, could also reduce microbial network complexity[137], microbial multi-functionality, and potentially render communities less resilient to future disturbance[138]. As microbes play important roles in dynamics of plant coexistence and competition[8,41], investigating these relationships under different climatic conditions or with novel microbial consortia will be important in determining forest vulnerability to climate change.

Future Directions: Microbiome research in the Anthropocene

Synthesizing microbial responses to climatic change remains an ongoing challenge due to the context-dependency of these responses and lack of baseline measurements[18]. Moreover, there are relatively few studies which directly compare standardized microbial responses to climatic disturbance across biomes or MSNs. Large-scale manipulative experiments can provide standardized manipulations across a range of biomes (e.g. Free Air CO_2 Enrichment), and such initiatives provide important insights into the role of the microbiome in plant growth dynamics[3]. Similarly, sampling networks, such as the National Ecological Observatory Network (NEON), enable tracking microbiome and tree responses across natural gradients, over time, or across disturbance events[139,140]. Importantly, studies that standardize sequencing approaches[141], genetic markers[142,143], and downstream bioinformatic processing can ensure effective comparisons among studies[144].

Another important future direction for forest microbiome research is the incorporation of microbial processes into ecosystem and Earth system models[26]. One primary challenge involves modeling how rates of nutrient cycling, decomposition, pathogen spread, or tree health will be impacted by future microbiome responses to disturbance (Box 2). This is particularly complex as multiple types of climatic disturbance occur simultaneously, sometimes buffering and other times exacerbating the effects of these disturbances on one another[145]. Although microbial processes are often implicitly incorporated into models focusing on projecting future forest dynamics[6], a specific challenge revolves around understanding the contexts in which microbially-explicit models outperform traditional first-order process-based models[146]. Incorporating projections of microbiome functioning could potentially increase the uncertainty of some model projections[147], at least in the near term. Efforts to constrain the relative effect size of microbially-mediated processes in models remains a critical area of research[26]. Trait-based approaches, which delineate microbial communities based on gene or enzymatic traits, are a promising opportunity to integrate microbes into ecosystem models[148]. Additionally, properly measuring trait responses to climatic disturbances at model-relevant spatial and temporal scales will be essential to incorporating microbes into ecosystem models[147].

Last, there is bias towards North American and European authors cited in our literature, as well as in other recent reviews on the topic[18]; this stems in large part from our own language limitations as well as many structural and systemic biases in research and publication. Research investigating forest microbiome response to climate change and functional consequences for forest ecosystems is especially poorly represented for Latin America, Africa, and Southeast Asia. Decolonial approaches to research will be critical in better understanding and predicting a truly global response of forest microbiomes to climate change.

Conclusions

Forest microbiomes play a key role in the structure and function of global forests, but they are threatened by rapid and ongoing climate change. In this review, we adapt a risk assessment framework to identify the vulnerabilities of forest microbiomes to climate change, as well as contextualize potential impacts of microbiomes on forest function. Integrating the forest microbiome into conceptual and empirical models of forest functioning will advance understanding of forest health in the 21st century. There remains significant uncertainty in the cascade of microbiome-mediated feedbacks that will influence forest ecosystem function under climate change, and this represents an important area of future study. Overall, the forest microbiome remains an underappreciated target of conservation initiatives in Western science. We emphasize the importance of Indigenous science and sovereignty in managing Native ecosystems[73], as well as the need for more holistic studies linking macroecology with microbial ecology in determining responses of forests to climate change.

Box 1 | chí xáyviish nushtúkkareesh (Let's go pick mushrooms!)

Due to limitations in the extent of microbial natural history records in Western science, the study of microbial response to climate change presents many challenges. Consequently, studies of fungal fruiting phenology, for instance, have largely been restricted to temperate forests in Europe over the past several decades using herbaria collections[70,71]. By contrast, Indigenous communities, including the Karuk Tribe in Northern California, USA have been documenting patterns of fungal fruiting phenology for thousands of years . For example, *Tricholoma magnivelare*, known as matsutake or xáyviish in the Karuk language, is an important EMF species used not only as a food and medicine, but as an indicator species of forest health. Until recently, xáyviish has been accessible and abundant for the Karuk people. However, Karuk Cultural Practitioners describe how while substantial early rains in September stimulate xáyviish development, when seasonal rainfall is delayed as is happening more frequently with climate change (first substantial rain occurring in November), mushroom development ceases for the year.

While the impacts of a long-term decline in xáyviish fruiting are not fully known, declines in fungal fruiting may have consequences not just for the fungal taxa themselves, but also for the establishment of seedlings and persistence of forests and the many organisms which they support[40].

For instance, deer and elk rely on xáyviish in the fall, during their own reproductive periods[73]. For Karuk people, “Karuk traditional knowledge cannot be separated from either the practices that generated the knowledge, or the practices that emerge from it. These practices, known as ‘traditional management’ are, in turn, central to Karuk culture, identity, spirituality and mental and physical health”[73]. The centering of Indigenous voices and acknowledgement of Indigenous sovereignty will be critical towards a more in-depth understanding of forest (including forest microbiome) response to climate change.

Box 2 | Predicting the assembly of non-analog microbial communities

New methods in biodiversity modeling provide opportunities to forecast the composition and function of non-analog forest microbiome communities under future climates. Non-analog communities are comprised of new combinations of taxa with no contemporaneous parallels. Due to expectations of heterogeneous responses to climatic change (outlined above), non-analog communities are expected to proliferate. To predict the composition and function of these communities, species distribution models (SDMs), sometimes called ecological niche models, use contemporaneous geographic occurrence data along with local environmental variables to generate species range maps. SDMs can then be used with future climatic data to forecast shifts in single microbial taxa or functional groups[133]. However, concurrently modeling hundreds to thousands of species present in the forest microbiome is challenging using stacked SDM approaches. Joint Species Distribution Models (JSDMs), a relatively new class of statistical models, are well suited to the multivariate and sparse data structures generated by the molecular meta-barcoding studies used to study the forest microbiome[149]. These modeling approaches offer insight into the structure and potential function of non-analog communities by accounting for species tradeoffs and spatially explicit species-environment linkages[150]. JSDM provides opportunities for non-analog and shifting communities to be incorporated into temporal biogeochemical models seeking to predict forest soil respiration or CO_2 fertilization responses. One of the first studies to apply JSDM to the forest microbiome demonstrated that fungal saprotrophs with strong co-occurrence patterns were especially sensitive to forest management practices, indicating that biotic interactions can impact microbial community responses to disturbance and climate change more broadly[150].

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Figure captions

Figure 1 | The forest microbiome in a changing climate. **A** | The exceptionally diverse forest microbiome colonizes nearly every surface and plant tissue of the forest. Distinct microbial specific niches (MSN) occur throughout the forests, depicted with dashed yellow circles. Major microbial groups and associated MSN include: 1). Foliar endophytes and epiphytes (bacteria and fungi) within the 2). Forest Canopy. 3). Nitrogen fixing free-living bacteria occur in soil. 4). Forest gaps are unique microhabitats within forests. 5). Arbuscular mycorrhizal fungi (AMF); Ectomycorrhizal fungi (EMF), and the associated myco-rhizosphere dominate in soils; **B**| Heat stress and drying associated with climate change will shift the community structure and function of the forest microbiome. A reduction in available water is depicted by the reduction in the blue speckles throughout both panels 6). Wood and litter-decomposers in soil (bacteria, archaea, and fungi). Free-living soil microbes (bacteria, archaea, and fungi occur in soil and in decaying wood). 7). N-fixing bacteria may be free-living, root or leaf associated; 8). Forest canopy gaps can be particularly deleterious for microbial communities under climate change 9). Filamentous soil bacteria. 10). N-fixing bacterium associated with plant-roots. **C**| Distinct mycorrhizal symbioses are associated with major forest biomes where they influence biogeochemical cycles and forest responses to climate change. Boreal forest ecosystems are dominated by ectomycorrhizal fungi (EMF), some EMF may enzymatically degrade soil organic matter to obtain organic forms of nitrogen, which influences host nutrition. Contrastingly, in tropical forest ecosystems, the majority of plants are associated with arbuscular mycorrhizal fungi (AMF), which efficiently scavenge nitrate (NO_3^-) and ammonium (PO_4^{3-}) from soil solution. The relative abundance of AMF and EMF hosts is more variable in temperate forest ecosystems.

Figure 2 | An organizational framework for studying forest microbiomes in a changing climate. Together, the sensitivity and exposure risk of microbial communities determine their overall vulnerability to climatic disturbance. Subsequent feedbacks may exacerbate or buffer subsequent microbial responses to climate change. We define climatic exposure as the cumulative severity of disturbance. Microbial community exposure is broadly shaped by the disturbance type, spatiotemporal scale, and attributes of the microbial microhabitat. Microbial sensitivity describes the degree to which microbial fitness or community structure and function is impacted by climatic disturbance. Broadly, microbial traits, niche attributes, and the climatic history of a forest can impact the sensitivity of a taxon or community. Finally, climatic feedbacks represent an array of processes, spanning macro-scale biogeochemical processes, to plant soil feedbacks that modulate future microbial exposure and sensitivity (dashed arrows).

Figure 3 | Scales of forest microbiome exposure to climate change. A | Examples of three forest biomes (boreal, temperate broadleaf, and tropical) and the relative distributions of different forest types across the globe. Inset photos are representative examples of major forest biomes. **B** | Exposure risk varies across these three broad forest biomes. Here we compare the mean temperature in the warmest quarter from 1970-2000 to the values predicted for 2061-2080 based on the Coupled Model Intercomparison Projects 5 (CMIP5) from the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) in 2014. Three representative forest sites are reported. The predicted warming is based on the intermediate scenario where the concentrations of greenhouse gases (based on the Representative Concentration Pathways; RCP) assumes that emissions will peak in 2040 (RCP 4.5). Below, the line plot denotes the mean monthly temperature fluctuations throughout the year for these same plots from 1970-2000, indicating that microbes from these habitats are adapted to different temperature fluctuations and are liable to demonstrate varying sensitivity to climate change as a result. Data are taken from WorldClim 2 (Fick, S.E. and R.J. Hijmans, 2017). **C** | The deviation of monthly mean minimum and maximum temperatures (seasonality) across these three representative forest sites compared to the annual mean annual temperature. Data are taken from WorldClim 2 (Fick, S.E. and R.J. Hijmans, 2017). **D and E** | Temperature fluxes in microbial microhabitats (MSN) are poorly captured in measurements of air temperature. **D** |Temperatures across the different forest microclimates for a representative forest in a Costa Rican Lowland Tropical Forest. **E** | Soil temperatures across different depths for a hypothetical soil, indicating unique microclimates which influence microbiome exposure. Data for D | temperatures in different forest microhabitats, taken from Fetcher et al. (1985). Data for E | mean temperature of soil at different depths taken from Blume et al. (2016).

Figure 4 | Microbial sensitivity and underlying traits and tradeoffs. **A**| Microbial communities exhibit temporally variable responses to climatic disturbance (dashed white line in the grey bar), minimal shift in community structure (tolerance), recovery to pre-disturbance conditions after some recovery period (recovery), or a permanent shift in community structure (transition). Notably, these dynamics could vary across forest biomes (different colored lines). Underlying each response dynamic is a specific example shown below for different disturbance types and microbial communities. **B** | Trait-tradeoffs mediate microbial sensitivity to hypothetical drought stress for rhizosphere bacterial taxa (*Bradyrhizobium, Bacillus, Streptomyces*). Under ambient conditions, resource abundance may select for taxa with high growth yields (**Y**), and reduced investment in stress tolerance. In contrast, in periods of resource limitation, taxa that can rapidly acquire resources, using extracellular enzymes (**A**) may dominate. Under drought conditions (or other climatic disturbances), stress tolerance (**S**), or stress-tolerant-resource-acquisitive strategies may dominate (Adopted from Malik et al., 2020). We also display an example of how bacterial life-history trait trade-offs can be geographically structured. Trade-offs related to high-growth yield (orange) and resource acquisition (green) are expected to vary across a gradient of water availability; traits associated with resource acquisition may be favored in drier conditions. Hypothetical microbial communities are plotted across the coast redwood range of California, USA where the northern part of the redwood range receives twice as much annual rainfall as the southern extent (Johnson and Dawson, 2011). Consequently, microbes that tolerate water deficit are more abundant in the southern extent of the redwood range whereas microbes with high resource acquisition are more abundant at the wetter part of the range (Willing et al., 2020).

Photo associated with Box 1 | ***Tricholoma magnivelare*****, also known as matsutake, tanoak mushroom, or xáyviish in Karuk language.** Photo courtesy of Monika Fischer, University of California, Berkeley.

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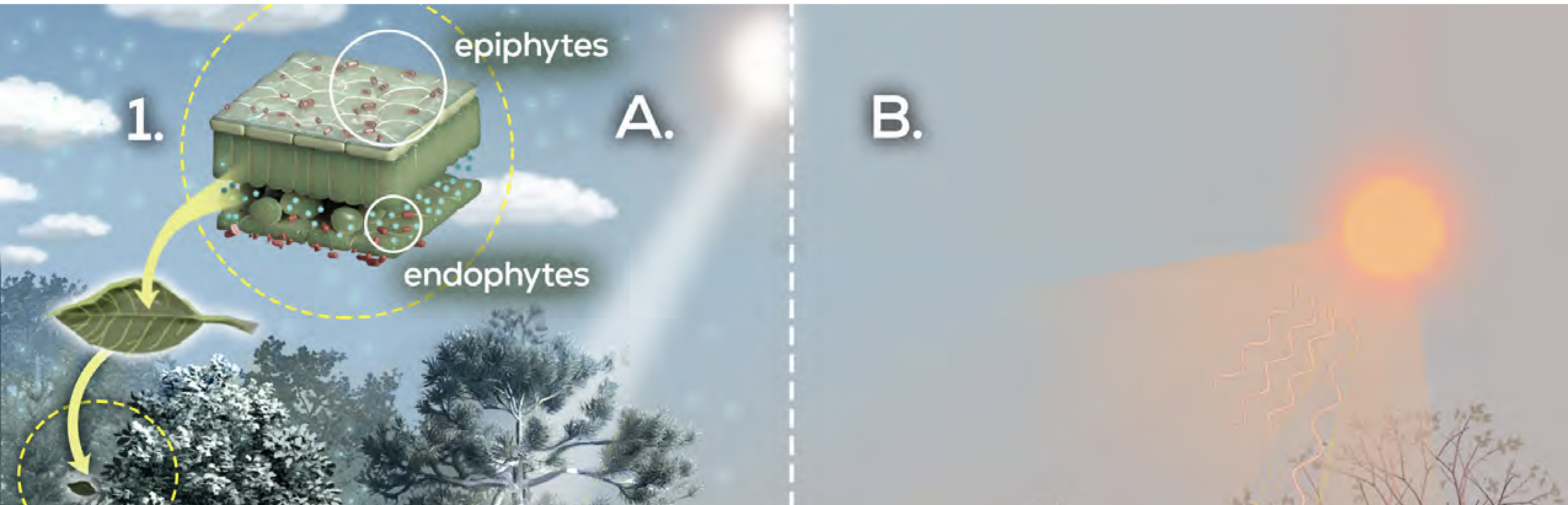
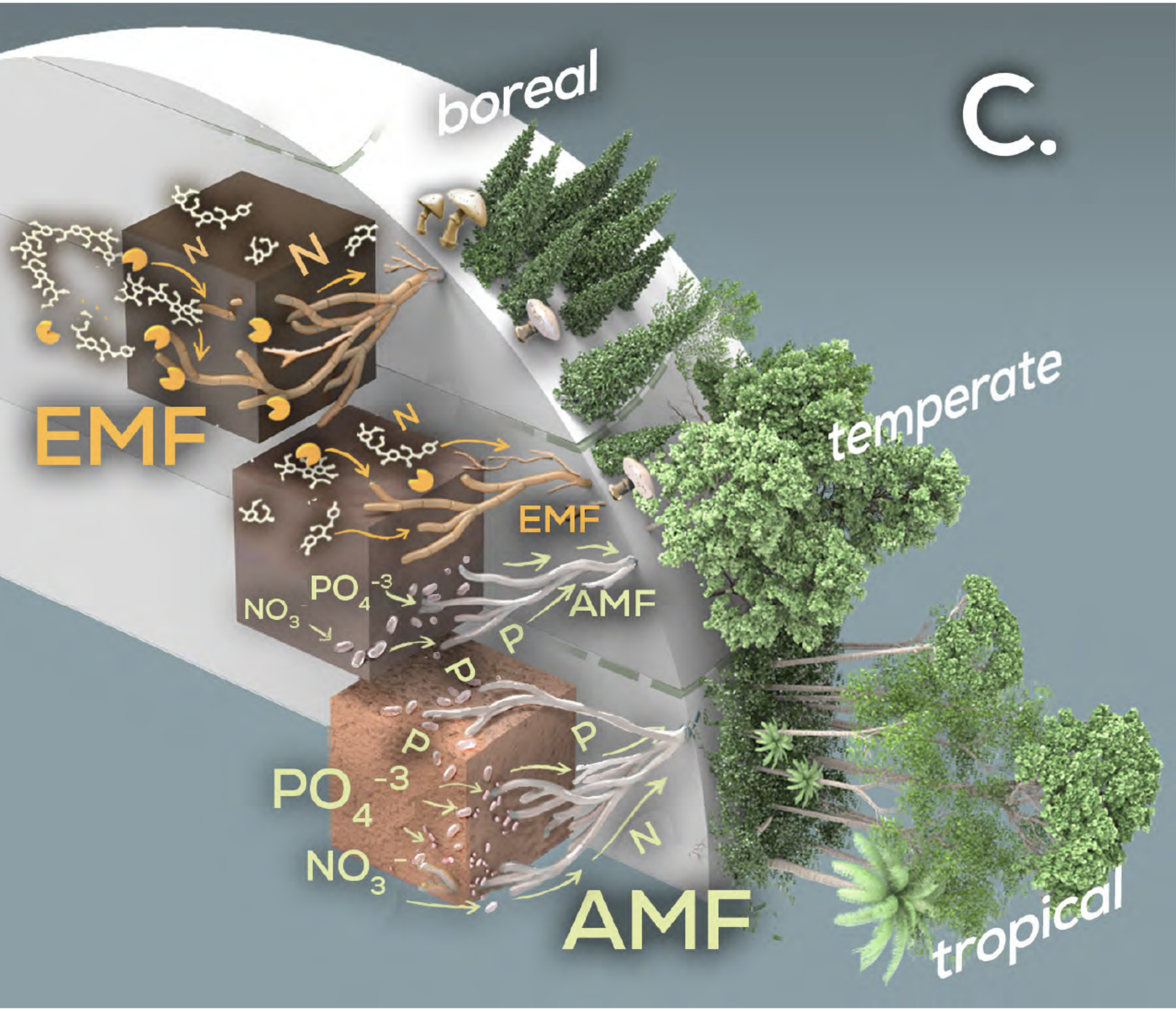
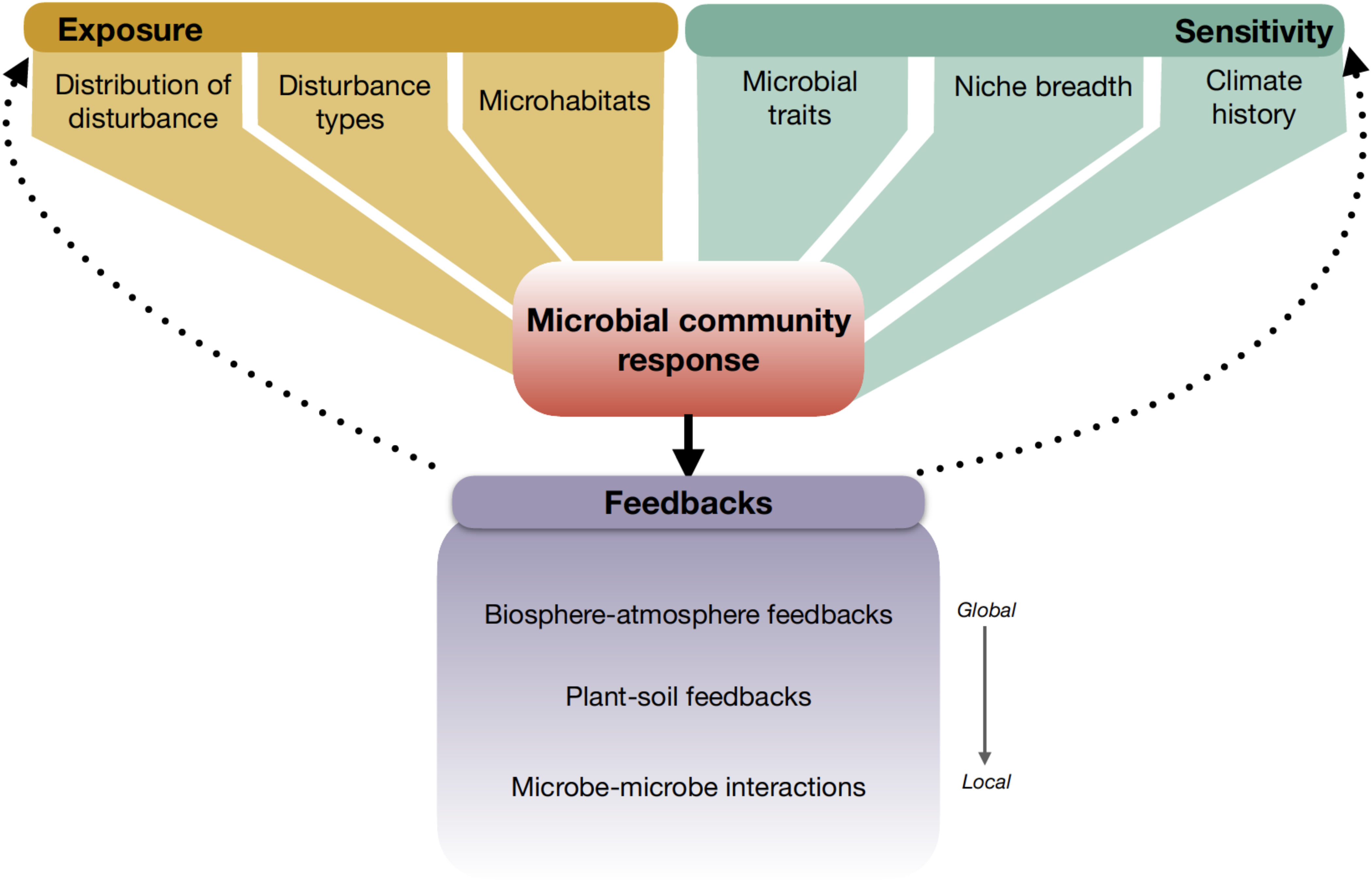
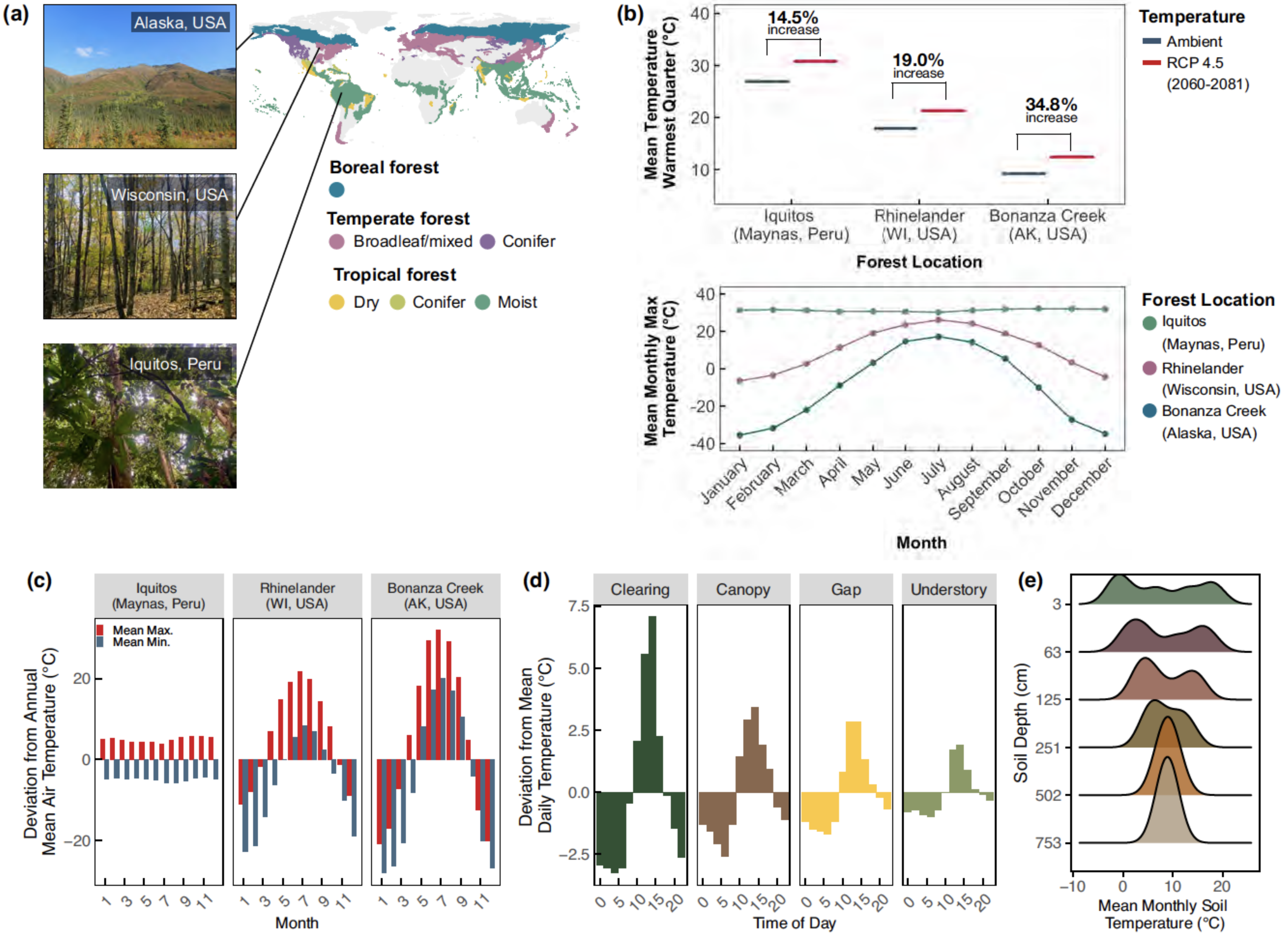
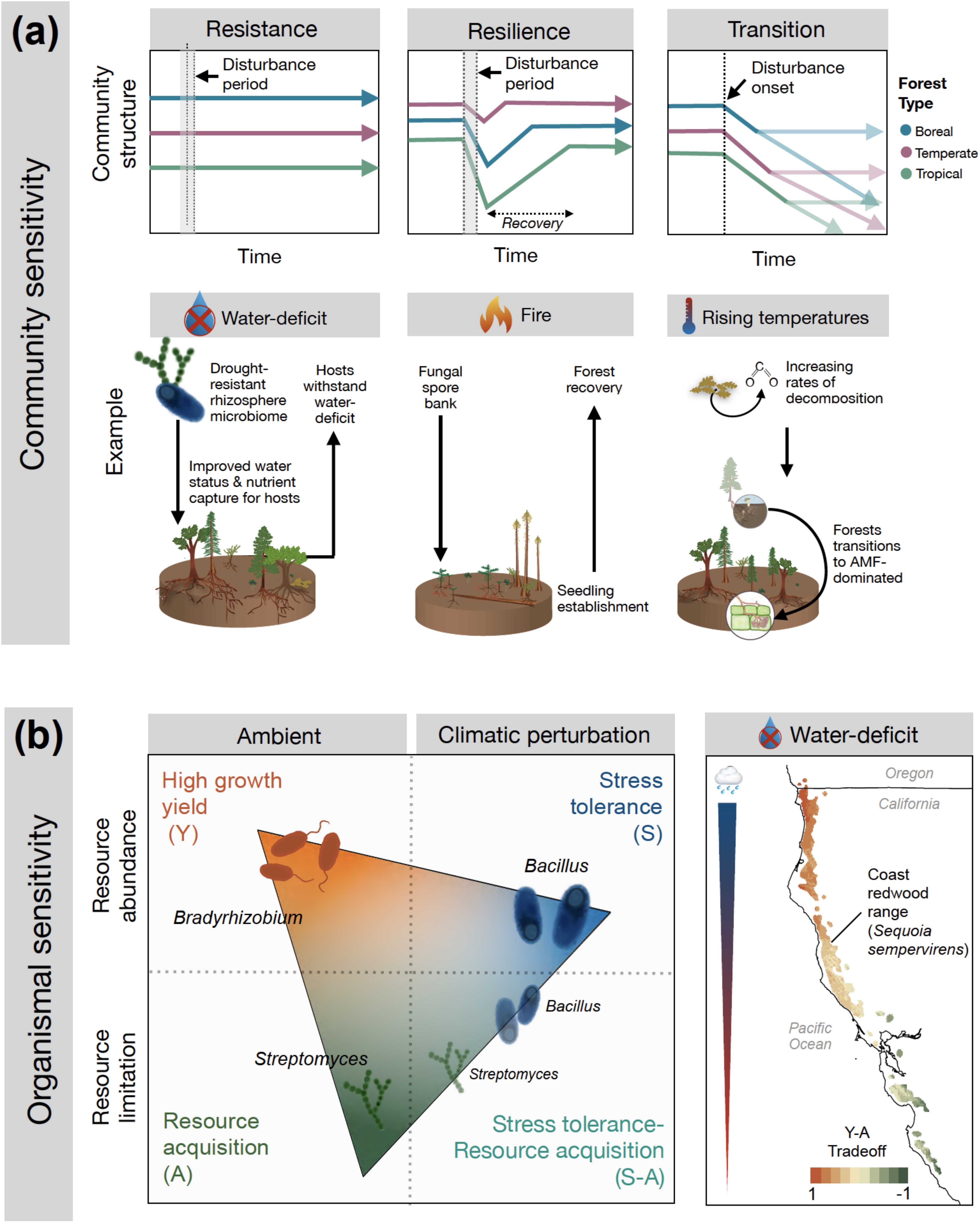

epiphytes
1.
A.
B.
endophytes
2.
N2
4.
6.
8.
N2
3.
N-fixers
AMF
EMF
5.
saprobes
7.
9.
10.


boreal
C.
N
N
EMF
N
temperate
EMF
PO_4^{-3}
NO_3^-
AMF
P
P
P
P
PO_4^{-3}
N
NO_3^-
AMF
tropical


Exposure
Distribution of disturbance
Disturbance types
Microhabitats
Sensitivity
Microbial traits
Niche breadth
Climate history
Microbial community response
Feedbacks
Biosphere-atmosphere feedbacks
Plant-soil feedbacks
Microbe-microbe interactions
Global
Local


(a)
Alaska, USA
Wisconsin, USA
Iquitos, Peru
Boreal forest
●
Temperate forest
● Broadleaf/mixed ● Conifer
Tropical forest
● Dry ● Conifer ● Moist
(b)
Mean Temperature Warmest Quarter (°C)
40
30
20
10
14.5% increase
19.0% increase
34.8% increase
Iquitos (Maynas, Peru)
Rhinelander (WI, USA)
Bonanza Creek (AK, USA)
Forest Location
Temperature
Ambient
RCP 4.5 (2060-2081)
Mean Monthly Max Temperature (°C)
40
20
0
-20
-40
January
February
March
April
May
June
July
August
September
October
November
December
Month
Forest Location
Iquitos (Maynas, Peru)
Rhinelander (Wisconsin, USA)
Bonanza Creek (Alaska, USA)
(c)
Iquitos (Maynas, Peru)
Rhinelander (WI, USA)
Bonanza Creek (AK, USA)
Mean Max.
Mean Min.
Deviation from Annual Mean Air Temperature (°C)
20
0
−20
1 3 5 7 9 11
Month
(d)
Clearing
Canopy
Gap
Understory
Deviation from Mean Daily Temperature (°C)
7.5
5.0
2.5
0.0
−2.5
0 5 10 15 20
Time of Day
(e)
Soil Depth (cm)
3
63
125
251
502
753
−10 0 10 20
Mean Monthly Soil Temperature (°C)


(a)
Community sensitivity
Resistance
Resilience
Transition
Community structure
Disturbance period
Disturbance period
Disturbance onset
Recovery
Time
Time
Time
Forest Type
Boreal
Temperate
Tropical
Example
Water-deficit
Fire
Rising temperatures
Drought-resistant rhizosphere microbiome
Hosts withstand water-deficit
Improved water status & nutrient capture for hosts
Fungal spore bank
Forest recovery
Seedling establishment
Increasing rates of decomposition
Forests transitions to AMF-dominated
(b)
Organismal sensitivity
Ambient
Climatic perturbation
Water-deficit
Resource abundance
Resource limitation
High growth yield (Y)
Stress tolerance (S)
Resource acquisition (A)
Stress tolerance-Resource acquisition (S-A)
Bradyrhizobium
Bacillus
Bacillus
Streptomyces
Streptomyces
Oregon
California
Pacific Ocean
Coast redwood range (Sequoia sempervirens)
Y-A Tradeoff
1
-1