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Review

Microbial regulation of feedbacks to ecosystem change

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Microbes are key biodiversity components of all ecosystems and control vital ecosystem functions. Although we have just begun to unravel the scales and factors that regulate microbial communities, their role in mediating ecosystem stability in response to disturbances remains underexplored. Here, we review evidence of how, when, and where microbes regulate or drive disturbance feedbacks. Negative feedbacks dampen the impacts of disturbance, which maintain ecosystem stability, whereas positive feedbacks instead erode stability by amplifying the disturbance. Here we describe the processes underlying the responses to disturbance using a hierarchy of functional traits, and we exemplify how these may drive biogeochemical feedbacks. We suggest that the feedback potential of functional traits at different hierarchical levels is contingent on the complexity and heterogeneity of the environment.

Highlights

Microbial functioning is intrinsically linked to the resistance and resilience of ecosystems.

Microbes drive and regulate disturbance feedbacks that impact ecosystem stability.

Functional traits from delineated genotypes to community-wide traits mediate the intensity and direction of feedbacks.

Feedbacks can be positive (amplifying) or negative (dampening) and emerge from altered biogeochemical cycling related to microbial disturbance responses.

Generalizable frameworks for how microbes adapt to disturbances in time and space are needed to increase the understanding and predictability of feedbacks and the temporal stability of ecosystems.

Microbes regulating disturbance feedbacks

Microorganisms such as archaea, bacteria, fungi, microplankton, and protists (hereafter microbes), play vital roles in driving ecosystem processes and in regulating community dynamics across terrestrial and aquatic food webs [1–4]. Microbes also continually respond and adapt to **disturbances** (see Glossary), through altered patterns of assembly and functioning, in ways that can cascade into the wider ecosystem and affect important ecosystem properties [5] (Box 1). In particular, feedbacks driven by altered microbial functioning may cause nonlinear dynamics that can affect the stability of ecosystems and trigger **regime shifts** between **stable states** [6]. For instance, recent evidence indicates that accelerated fluxes of N_2O, from the decomposition of nitrogen-rich organic matter in drought-impacted soils [7], are driven by altered functioning of nitrifying and denitrifying bacteria and archaea [8,9]. As N_2O is a powerful greenhouse gas, microbial disturbance responses that increase its production are a source of **positive feedbacks** that amplify the impacts of climate change through further warming and droughts [10]. At the same time, the direct impacts of drought on plant communities can be dampened by root-associated mycorrhizal fungi and rhizobacteria through **negative feedbacks** that alleviate heat stress impacts on their host plant communities, by, for example, distributing water between drought-stressed plants through common mycelial networks [11]. Although negative and positive feedbacks play a natural part in regulating disturbance impacts and underpin seasonal regime shifts in ecosystems at a local scale [12], climate change and anthropogenic activities are changing the frequency and intensity of disturbances, and there are growing concerns about how this could affect microbial functioning and the potential feedbacks induced [13–16]. Here we review the how, where, and when of microbially mediated feedbacks and their implications for **ecosystem stability** and regime shifts under climate-change disturbances. We conceptualize the mechanisms underpinning disturbance responses and functioning across a hierarchy of functional traits, and exemplify how these underpin feedbacks in the context of biogeochemical cycling.

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Box 1. Disturbance and ecosystem stability in the microbial world

What is a disturbance in the world of microbes? Disturbances can be defined as 'A discrete, unpredictable event that causes direct removal of living biomass, thereby altering community structure' [17] and conceptually distinguished from environmental stress, which is then taken as a chronic negative debilitating impact [18]. This definition emphasizes the transient and discrete nature of a disturbance, typically expressed as pulses, in contrast to the chronic nature of a stress. Biotic and abiotic stresses could also be seen as long-term or continuous press disturbances (sensu [19]) directly or indirectly altering community structure over time. As pointed out by Shade *et al*. [20], a tree falling in a forest may therefore constitute a pulse disturbance to the nearby understory vegetation while at the same time constituting a press disturbance to the underlying soil microbes. In line with this latter perspective, we here adopt the Shade *et al*. [20] definition of disturbances as 'causal events that either (1) alter the immediate environment and have possible repercussions for a community, or (2) directly alter a community', by which we also use the term 'stress' in the meaning of a press disturbance.

Ecosystem stability is a multifaceted concept encompassing related concepts such as resistance, resilience, stable states, and temporal stability, but also comprises the idea of a temporal continuity, as in the persistence of populations, diversity, or other ecological attributes through time [21]. In practice, ecosystem stability is often measured as the capacity of an ecosystem to absorb disturbance before undergoing a regime shift from one stable state to another [22], or by building on some measurement of the ecosystem's net primary productivity (NPP), as most aboveground and belowground life forms can be related back to this [23]. This latter notion of stability has the advantage that it is possible to evaluate before any regime shift occurs, by for example relating the mean annual NPP to its variation across a given time period, including disturbance events such as droughts, and relating this to microbial functioning or diversity [3]. Similarly, recent developments in the assessment of multiple ecosystem functions driven by soil microbes have opened a new avenue of inferring how disturbances affect the temporal stability of ecosystems [24]. Here, we define a stable ecosystem as one that, over a normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity, fertility, and rates of ecosystem functions.

Understanding feedbacks from functional traits

Historically, much focus in microbial ecology has been dedicated to assessing how disturbances impact on the taxonomic composition of populations or communities of microbes [20], and by inferring effects on ecosystem processes through putative links between taxonomy and functioning. However, more recently, research has shown various degrees of decoupling between taxonomy and functioning [25–27], and a growing focus among microbial ecologists is therefore to determine whether, and to what extent, disturbance responses can be deduced and predicted from **functional traits** [20,26,28]. At its core, a functional trait represents a single gene-encoded pathway that confers improved fitness to a given environmental stressor (**response trait**), or the capacity to produce enzymes that break down specific molecular compounds (**effect trait**) [29]. However, many aspects of functioning and disturbance response typically involve complex sets of interrelated response and effect traits [30] rather than single gene-encoded pathways. Indeed, evolutionary adaptations tend to blend genetic and phenotypic traits into sets of correlated traits that collectively govern how microbial communities respond to and function under disturbances [31]. Conceptually, disturbance responses can therefore be seen as operating across a hierarchy of levels, spanning from clearly delineated individual genes within individual microbes to the functioning of whole microbial communities or **microbiomes**, with the potential to drive and regulate feedbacks at every level. This implies the autonomy of microbiomes under disturbances, which can lead to their versatile mediating roles in feedback responses as discussed in the following text.

Predicting feedbacks from genotype traits

Under what circumstances could feedbacks be predicted by the quantification or expression of delineated genotype traits? A crucial issue relates to how measuring gene abundances can improve predictions of functioning and feedbacks under disturbances. For some genotype-level traits, direct linkages between metabolic pathways and functioning exist and can be used directly to inform altered biogeochemical cycling under perturbations, including feedback effects. For example, warming of coastal seawater increases the genetic pathways needed for degradation of complex biomolecules [32], which is likely to increase productivity and respiration at the expense of C-sequestration, and thereby contribute to a positive carbon feedback. Because environmental

Glossary

Carbon use efficiency (CUE): the ratio of organic carbon allocated for biomass growth to the organic carbon taken up.

Collective phenotype: population or community-level traits that emerge from the interaction of multiple individual organisms, and that typically enhance functioning compared to individual microbes.

Disturbance: a causal event that either (i) alters the immediate environment and has possible repercussions for a community, or (ii) directly alters a community.

Ecosystem stability: the capacity of an ecosystem to maintain its characteristic diversity of major functional groups, productivity, fertility, and rates of ecosystem functions over a normal cycle of disturbance events.

Effect traits: traits that determine the effect of organisms on the ecosystem processes (e.g., litter decomposition).

Functional trait: a measurable genotypic or phenotypic characteristic of microbes related to their fitness and functioning.

Hysteresis: the retardation of an effect when the forces acting upon a system are changed. Here we refer to hysteresis as the lag in response an ecosystem shows in response to environmental changes that can be attributed to soil microbial functioning.

Legacy effect: an indirect effect stemming from past microbial disturbance responses that impacts the current state of an ecosystem.

Microbiome: the sum of the microbes and their genomic elements in a particular environment. The microbiome can thus comprise one or several communities of microbes.

Negative feedback: feedback that reduces or counteracts the changes in conditions caused by a disturbance. These feedbacks provide resistance to natural or anthropogenic changes and maintain the ecosystem in a stable state.

Positive feedback: feedback that amplifies an initial change in conditions caused by a disturbance and may push the ecosystem towards a new state.

Regime shift: a sudden and often irreversible shift of an ecosystem from one stable state to another.

Response traits: traits delineating how a microbe responds to changing environments and perturbations (e.g., dormancy).

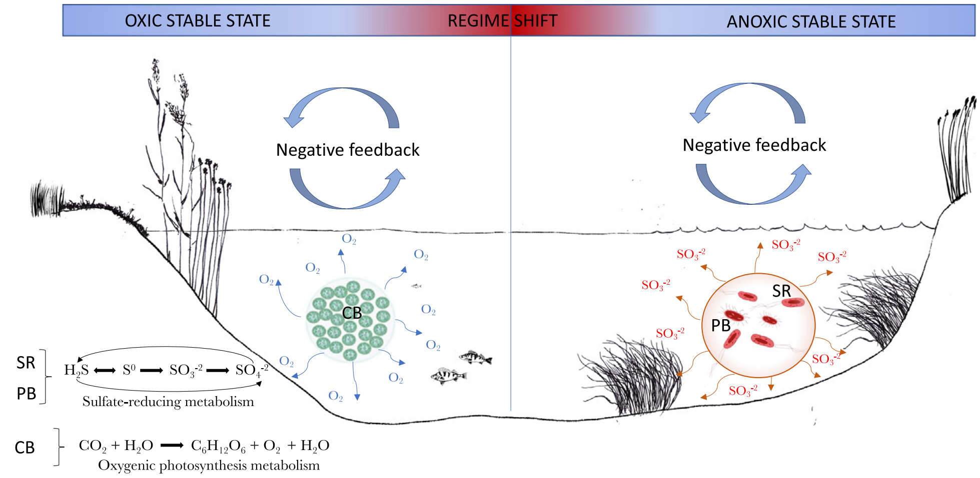


Figure 1. Example of negative feedbacks maintaining bistability patterns in a lake ecosystem. Microbial disturbance feedbacks can trigger regime shifts (i.e., large and persistent changes in the ecosystem structure) but also maintain stable states in ecosystems. In model and real lake ecosystems, the initial composition of three groups of bacteria with distinct redox-controlling metabolic pathways regulates the stability and shifts to oxic or anoxic states [35]. High densities of photosynthesizing cyanobacteria (CB) entail metabolic oxygenation of the lake despite gradual changes in the inflow of nutrients and oxygen diffusion, and thereby drive a negative disturbance feedback that maintains the lake in an oxic stable state. When the system reaches a critical level of disturbance and shifts into the anoxic stable state, a build-up of sulfate-reducing (SR) and phototrophic sulfur bacteria (PB) inhibit re-oxygenation by producing sulfites (SO_3^{-2}), and thereby driving a negative feedback that maintains the system in an anoxic state despite subsequent vertical mixing and oxygen diffusion. Disturbances such as rising temperatures and eutrophication, which affect the balance between photosynthesis and respiration and alter the rate of organic matter production and degradation, can lead to abrupt changes in the composition of SR, PB, and CB controlling the redox state of the lake's biogeochemical cycling (positive feedback), and push the ecosystem past a tipping point and into a new stable state [12,108].

Stable state: an ecosystem characterized by temporal stability, in which populations and ecosystem functions fluctuate around some trend or stable average (Box 1).

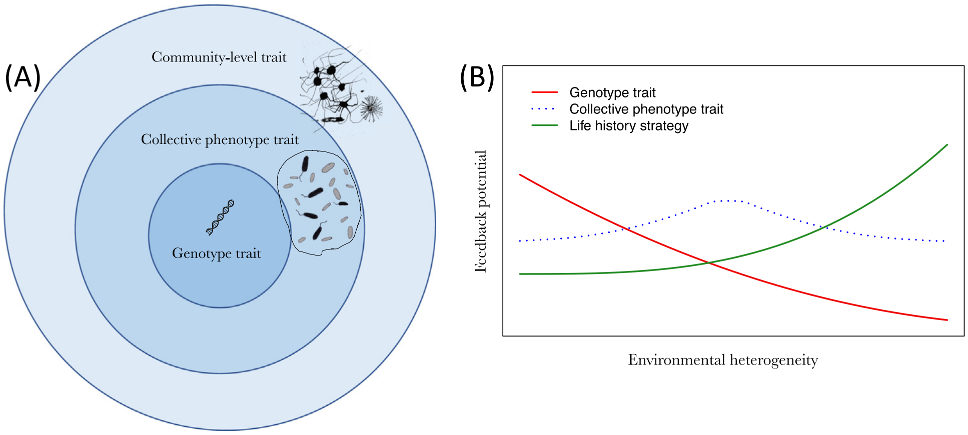
heterogeneity is a strong driver of both taxonomic and functional diversity of microbes [33,34], we can expect clearer signals of genotype-driven feedbacks in more secluded and well-structured ecosystems where biogeochemical cycling is driven by functionally differentiated pathways. Recent evidence from model and real freshwater ecosystems provides an elegant example of this. In a modeled lake ecosystem, Bush *et al*. [35] saw that shifts between stable states of the lake ecosystem were contingent on the composition of three dominant groups of bacteria exhibiting different metabolic pathways [35] (Figure 1). When they subsequently modeled the impact that gradual increases in stressors (oxygen influx, vertical stratification, and nutrient levels) had on the system, they found that a bistability pattern of either oxic or anoxic stable states bolstered by abrupt transitional shifts (i.e., regime shifts) governed the system. The main driving factor underpinning the bistability pattern was the buffering effect of the residing microbial communities and their differing metabolic pathways. In particular, high prevalence of photosynthesizing cyanobacteria effectively constituted a negative feedback that buffered the system through metabolically induced oxygenation, even at very low oxygen diffusion levels [35]. Conversely, when oxygen levels had reached a tipping point of critical depletion, and the lake abruptly shifted into an anoxic state, sulfate reduction replaced photosynthesis as the main metabolic pathway in the system and was accompanied by a shift to sulfur-reducing and phototrophic bacteria. Subsequent tests in a real-world lake ecosystem showed that the state of the system – that is, oxic or anoxic – was contingent on the initial densities of the differing metabolic pathways [35].

The example pinpoints how single microbial metabolic pathways, readily predicted from genotype traits, can underpin feedbacks that maintain spatially structured ecosystems in a stable state. The stability of the ecosystem in this example is thus contingent on negative feedbacks, independently of whether that state is oxic or anoxic. Studies of coastal shallow waters subjected to the same type of regime shifts [36,37] have also shown that experimental warming increases the expressed sulfate-reducing and methane-production pathways in sediment microbial communities, thus possibly extending and prolonging anoxic conditions in the way described by Bush *et al*. [35]. Moreover, the example also points to a more general function of negative feedbacks as a biotic component underpinning **hysteresis**, that is, the dependence of a system's current state that can be attributed to its history [38], as we discuss further. Naturally, genotype-based predictions could be equally valuable in predicting positive feedbacks in similarly secluded ecosystems. A recent study from globally distributed wetland sites found that the relative abundance of a single archaeal nitrification pathway (*amoA*) explained 62% of N_2O emissions [39] and is therefore most likely to be the single most important gene to quantify when assessing the feedback loop of increasing N_2O emissions from wetlands under warming [40]. Most biochemically underpinned feedbacks are nevertheless likely to play out at larger scales spanning more heterogeneous environments, involving domino effects and hidden feedbacks that work across ecosystems [41], which renders genotype-based predictions considerably more challenging. It is further difficult to link genotype traits and disturbance responses across multiple separate or compounded disturbances because they tend to vary according to the disturbance type and intensity. For example, linking microbially mediated shifts in nitrogen cycling from drought and rewetting disturbances is relatively straightforward because the gene-encoded pathways that correlate well with observed process rates of nitrification and denitrification are critically controlled by soil moisture [42]. Nevertheless, the same groups of bacteria show a highly varying response to nitrogen addition across environments [43], which indicates that a mixture of different effect and **response traits** determines the overall community response. Therefore, to understand the feedback potential of microbial functioning across larger spatiotemporal scales and more complex sets of disturbances, we need to broaden the perspective of functional traits to a population or community level.

Community-level functional traits

Expanding upon the view of functional traits as gene-encoded pathways, it is evident that many traits comprise multiple gene interactions that cannot be readily predicted from individual or even multiple gene expressions or quantifications alone [25]. At the organismal level, phenotype traits such as cell shape, pH tolerance, dispersal mode, and growth rate [44–46] constitute important effects and response traits that could potentially affect disturbance feedbacks. However, an array of traits exceed genotype and organism levels altogether and are instead located at population, community- or whole-microbiome level, operating as a **collective phenotype** [28]. It is likely that traits located at this super-organismal level would enhance a community's disturbance response compared to those of an individual microbe. For example, yeast populations can extend their heat tolerance through collective secretion and coating with the heat-damage-preventing antioxidant glutathione [47], despite exceeding critical heat levels for individual cells. As collective phenotypes are emergent traits resulting from the interaction of multiple individual microbes, they are also likely to show higher feedback potential compared to the aggregated sum of individual genotype responses in both well-structured and more heterogeneous environments (Figure 2).

The formation of relatively stationary but resilient aggregates (biofilms) is an example of a collective phenotype trait that has direct consequences for the turnover of marine organic matter, which constitutes the largest sink of carbon on the planet. Biofilms are formed as consortia of microbial cells attach to abiotic surfaces through a cohesive polymeric matrix that coats the residing community and reduces the individual cell's exposure to toxicity and stress. While biofilm formation provides enhanced protection from a range of disturbances – including physical stress, desiccation, toxic



Trends in Microbiology

Figure 2. The feedback potential of microbial functional traits related to environmental heterogeneity. Microbial traits can be situated in a framework (A) encompassing three hierarchical levels that all differ in their potential to regulate biogeochemical feedbacks depending on the heterogeneity of the surrounding environment (B). In well-structured habitats with low environmental heterogeneity and high filtering, specialized genotype traits needed for the breakdown of organic matter can drive much of the feedback potential in the system. For example, the bacterial *mcrA* and archaeal *amoA* genes that encode enzymes driving methanogenesis and nitrification respectively, can be used as proxies for methane and nitrous oxide emissions because of their strong correlations with these processes in secluded environments [39,109]. At microbial population level, collective phenotype traits, such as biofilm formation, can increase the feedback potential in environments characterized by relative spatial homogeneity but increasing resource complexity [32]. Environments characterized by high spatial and resource complexity also have higher functional diversity [52,53], and as a result the importance of genotype traits for predicting the system's feedback potential decreases due to multiple performance optima and asynchrony of species' intrinsic responses to environmental perturbation [105]. We therefore expect community-level traits such as life history strategies to become increasingly important to determine the feedback potential as the heterogeneity of the system increases.

compounds and grazing [48] – it can also enhance the breakdown of recalcitrant forms of organic matter through increased enzymatic concentrations in the boundary layer between the microbial aggregate and the substrate [49]. Recent experimental evidence from marine and model ecosystems shows that warming waters tend to increase biofilm formation and thereby also speed up rates of carbon degradation and respiration, as more bacterial cells gain surface access to the carbon compound [32,50]. In addition, marine biofilms formed between phytoplankton and bacteria increase the surface area and reduce the sinking velocity of biofilm particles [51], and are therefore likely to decrease the net export of carbon to the deeper oceanic layers, further exacerbating positive feedbacks related to marine carbon cycling with warming waters.

A framework relating community-wide functioning to disturbance feedbacks

Complex and heterogeneous environments are often characterized by higher levels of functional diversity than more well-structured and homogeneous environments because they typically constrain trophic interactions and increase microhabitat diversity [52,53]. As a consequence, individual- or population-level microbial disturbance responses are often masked or 'flattened' compared to community-level responses, as complex communities comprise an array of individual genotypes with multiple performance optima [54]. It is therefore plausible that the feedback potential of a given functional trait at a given hierarchical level is directly linked to the heterogeneity (complexity) of the ecosystem at hand (Figure 2), in ways that could facilitate predictions. At the higher levels of the trait hierarchy, correlated sets of traits that together define how a community or whole microbiome adapts to and functions can be classified into different life history strategies based on key variations in traits at cellular level [31]. Thus, in contrast to delineated metabolic pathways that are largely controlled by a single gene, or by a set of a few key genes, the cellular traits that underpin life history strategies typically involve multiple correlated genes with shallow phylogenetic conservation [25] that are aggregated to community level to infer community-wide functioning. Similar concepts of strategies underpinning community-wide niche differentiations and trade-offs in resource acquisition in relation to differing environmental pressures are key features of, for example, plant and animal ecology [55,56], and their recent adoption into microbial ecology has been greatly facilitated by advances in high-throughput molecular methods such as metagenomics. For example, the number of ribosomal RNA operon copies in bacterial genomes is intrinsically linked to two reproductive strategies, growth rate and growth efficiency [57]. Communities with higher weighted operon copy numbers are thought to reflect generalist bacteria with a high-yield strategy, which typically thrive in the early stages following recovery from severe disturbances [58] but are also susceptible to chronic stresses such as long-term warming [59]. Conversely, stress-tolerant communities resilient to extreme or compounded disturbances survive by allocating much of their consumed resources to maintaining cellular integrity and mechanisms that minimize or mitigate biomolecular damage [60]. Building on this, Malik *et al.* [60] recently developed the Yield-Acquisition-Stress (Y-A-S) framework on the basis of trade-offs between three well-known life history strategies and their implications for carbon cycling. Microbes with a high **carbon use efficiency (CUE)**, that is, the amount of biomass produced per unit of resource consumed, are thus characterized as growth-yield strategists (Y-strategists), whereas microbes with a resource acquisition strategy (A-strategists) invest more in enzyme production needed to break down complex substrates [60]. Lastly, stress-tolerant (S-strategist) microbes are characterized by a high allocation of resources for maintaining cellular integrity and osmotic balance. The Y-A-S framework could be seen as mirroring important biogeographical findings of disturbance-like thresholds in the distribution of important groups of microbial decomposers in relation to temperature [61], pH [62], and moisture [63], and provide a lens through which community-level functioning can be understood in more heterogeneous and complex environments.

In the following section, we build on the hierarchy of functional traits ranging from delineated genotype-level traits to the collective phenotypes and life history strategies which we have presented, to examine more closely where and when these traits could mediate climate feedbacks from warming in terrestrial and marine environments.

Where and when do microbial feedbacks regulate climate change?

By decomposing organic matter, microbes account for a major fraction of the thermal response of ecosystem-level respiration [64], and even relatively small changes in the thermal sensitivity of microbial community respiration may constitute powerful feedback mechanisms in the context of climate change [65]. A recent study examining changes in global soil respiration between 1987 and 2016 showed that, although overall soil respiration has remained stable during the last two decades, the heterotrophic respiration attributed to microbial decomposition of organic matter has increased in the same period [66]. If this trend remains intact, and rising temperatures indeed continue to increase soil microbial heterotrophic respiration, it will likely constitute one of the most important positive climate feedbacks in terms of sheer magnitude [67]. By contrast, the sequestration and long-term stabilization of carbon is also a function largely driven by microbes, and mechanisms that enhance sequestration are therefore increasingly advocated as key to climate-change mitigation strategies [68]. The direction and magnitude of the microbially mediated carbon feedback could ultimately be inferred from the net outcome of respiration and sequestration as microbes across the biosphere adapt their functioning to climate-change disturbances, but there are so far no encompassing ways of predicting the net outcome of various interrelated positive and negative feedbacks, and more research is needed to conceptually integrate local disturbances and altered functioning to planetary feedbacks, and vice versa.

Positive feedbacks amplifying climate change

In terrestrial environments, the CUE of microbial communities is likely to constitute a key mechanism that determines whether warming will increase heterotrophic respiration or not [69].

Microbes with high CUE are intrinsically linked to growth-yield strategy (Y) and thought to be important for soil organic matter production and persistence, while microbes with low CUE are typically either A- or S-strategists and more likely to be drivers of higher soil respiration because relatively fewer resources are allocated to biomass growth [70]. Globally, soil heterotrophic respiration has increased over the last three decades [66], despite concomitant increases in primary production stemming from CO_2 fertilization [67]. There is accumulating evidence that CUE is intrinsically linked to the levels and variability of soil moisture [71,72], and we could therefore expect that microbial adaptations to drought and precipitation variability through changes in life history strategy will be a main driver of positive feedbacks in increasingly drought-affected regions and ecosystems [73,74]. Recent findings from a tropical forest soil in Panama [75] provide fine-level details of this, in showing that warming lead to a decrease in bacterial diversity accompanied by a shift from *Bacteroidetes*, a phylum characterized by its capacity to degrade polysaccharides, to stress-tolerant *Firmicutes* and species of thermotolerant saprophytic fungi, coinciding with sharp increases in respiration and CO_2 emissions [75]. In high-latitude regions where warming proceeds twice as fast as the global average, a driving mechanism of positive feedbacks could be the introduction of more functionally versatile and specialized microbes into ecosystems where decomposition has been limited and large stocks of organic matter has accumulated. For example, permafrost and peatland soils each store more carbon than the atmosphere alone [76,77], and accelerated decomposition of these stocks would constitute major sources of positive feedbacks. Recent evidence from thawing permafrost soils show that freezing conditions and dispersal limitations over long timescales have exerted a strong filtering toward functionally limited microbial taxa, which alter the composition of the permafrost soil organic matter [78], and limit its decomposition [79]. As environmental filters collapse with thawing permafrost, more functionally versatile microbes gain access to exposed stocks of organic matter and rapidly increase decomposition rates [79]. Similar patterns of positive feedbacks from warming peatlands [80] could also be at least partially attributed to the establishment of novel groups of functionally specialized microbes [81].

Predicting feedbacks in aquatic ecosystems could be more straightforward than in terrestrial ecosystems because of the more homogeneous abiotic structuring and more size-structured food webs in these environments [82]. Moreover, as the link between microbial community composition and functioning appears to be relatively strong in marine environments [83], the feedback potential could be inferred directly from changes in community composition of key functional groups based on metabolism, or through genotype-based predictions [84]. At the base of the marine food web, unicellular eukaryotic phytoplankton produce around half of the biosphere's net primary productivity and play a fundamental role in setting the productivity of the entire marine ecosystem [85]. Several recent modeling studies project major reorganizations in the composition and distribution of phytoplankton communities with warming oceans, which are likely to amplify carbon-related feedbacks [86–88]. For example, rising ocean temperatures could entail a shift from larger to smaller warm-water diatoms in high-latitude oceans accompanied by decreased rates of carbon sequestration due to differences in their functional capacity to export carbon to the deep ocean layers [89]. Moreover, the interrelated processes of acidification, warming, stratification of density gradients, and deoxygenation are likely to constitute major disturbances driving altered redox pathways driving microbial metabolism. For instance, increased ocean acidification and stratification has an inhibitory effect on ammonia oxidation and could cause a net shift from oxidized to reduced forms of nitrogen [90], which in combination with deoxygenation drives powerful feedbacks that both reduce carbon sequestration to deeper ocean layers and emit N_2O [91].

Negative feedbacks dampening ecosystem change

As elevated temperature and CO_2 is expected to increase the primary productivity in both terrestrial and marine environments, negative climate-change feedbacks could be driven by the transformation of increased plant or algal residue into long-term buried or stable forms of organic carbon. In terrestrial environments, physical protection, chemical stabilization, and enzymatic processes contribute to the sequestration potential and the stabilization of soil organic matter, which are mainly mediated by microbes. Sequestration potential is jointly driven by increased sorption of root exudates and microbial necromass to mineral surfaces in the soil, where they remain physically protected from decomposition. A recent study by Witzgall *et al*. [92] – combining chemical profiling of particulate organic matter with electron microscopy techniques on the surface of decaying plant residues – shows how fungal hyphae operating in the plant–soil interface control the production of organic, long-term stable aggregates in the soil matrix from freshly translocated plant residues. As fresh litter input is typically accounted for as easily degradable compounds with short turnover times in most carbon cycling models [93], its transformation into stable forms with long turnover times could counterbalance some of the warming-induced increases in heterotrophic respiration. There is also increasing evidence that warming, particularly during winters in high-latitude regions, may increase carbon sequestration through both reduced heterotrophic respiration [94] and necromass accrual as bacterial growth outcompetes fungi across many ecosystems [95].

In aquatic ecosystems, the carbon sequestration potential is tightly connected to the redox cycle that regulates microbial metabolic pathways, as depicted in Figure 1. While climate change is rapidly reducing oxygen saturation in marine environments [96], complete deoxygenation entails a redox shift in microbial metabolism where sulfate or nitrate replaces oxygen as the electron acceptor for oxidative reactions. Isotopic evidence of anaerobic ammonia oxidizing bacteria (anammox) in marine sediments suggests that limited nitrogen availability triggered the proliferation of diatom–diazotroph symbiosis into fast-growing and rapidly sinking consortia, leading to greatly increased organic carbon burial fluxes [97]. Similarly, recent evidence from experiments in oxygen-depleted water columns shows a switch to sulfate-reduction pathways, resulting in the production of sulfide products that react with sinking organic detritus to forms of organic sulfur that are both resistant to further hydrolysis [98] and accumulate in the sediments [99]. However, although both the redox-shifting mechanisms described are likely to constitute powerful negative carbon feedbacks, they would also contribute to and sustain anoxic conditions that, over larger scales, would lead to mass extinctions [96].

Functional adaptations in an ecosystem's microbiome can also form **legacy effects** that buffer against climate-change disturbances and increase the overall stability of the ecosystem. Accumulating evidence shows that drought can change the life history strategies of microbial communities in ways that impact their functioning also to future drought events [100,101]. For example, by simulating physiological allocation mechanisms under ambient and different drought severity scenarios, Wang and Allison [101] found indications that both transient and persistent drought legacy effects on litter decomposition could be related back to trade-offs between enzyme production and stress tolerance, in line with the Y-A-S framework. Legacy effects of microbial functioning can be an important component of an ecosystem's resilience to change, and can provide a powerful biotic mechanism for the often observed hysteresis effect in disturbed or changing ecosystems [102]. However, it is not yet clear whether chronic stress disturbances related to climate change are enough to form legacy effects that buffer ecosystem stability (see Outstanding questions). A recent modeling study suggests that disturbance intensity rather than frequency is key to the creation of persistent legacy effects [103], but recurring low-intensity droughts have also been shown to create legacy effects in the soil microbiome that significantly reduced the overall multifunctionality of ecosystems to further drought events [100].

Feedbacks mediated by biotic interactions

We have here focused almost exclusively on microbe-mediated feedbacks related to altered biochemical cycling, as most literature examining microbial disturbance responses in the framework of traits is found in this area. However, this largely ignores the effects that biotic interactions, such as changing patterns of competition and facilitation under changing disturbances, will have on genotype and community traits that mediate feedbacks [104]. Interactions such as competition and asynchronous disturbance responses are intrinsically linked to ecosystem stability [105], and the ways in which altered microbial community dynamics under disturbances could generate positive or negative feedbacks merit further interest and conceptualization. Moreover, as climate change is rapidly altering symbioses between microbes and their hosts [106,107], we would expect this to lead to a range of feedbacks that should similarly be the scope of further investigations.

Concluding remarks

Microbial functioning is key to understanding the feedbacks that drive and restrict disturbances in general, and climate change in particular. Several lines of evidence point at the mediating roles of microbes in ecosystem-disturbance feedbacks; yet, there is a great variability in the direction and magnitude of effect and response of different microbial groups to disturbances, rendering negative, neutral, and positive feedbacks. What mechanisms underlie microbial mediated feedbacks remain to be established, but how microbes adapt to disturbances and their community functional traits could be a key regulating factor in this respect. Recent decades have seen intensive research studying microbial disturbance responses across spatiotemporal contexts, and how this in turn affects ecosystem functioning and stability. While we are still far away from a detailed knowledge of how, where, and when these feedbacks emerge, a hierarchical view of microbial functional traits ranging from genotype traits to collective phenotypes and life history strategies across gradients of environmental complexity could be a useful framework for building an understanding of their fundamental mechanisms. We envision that the accumulating data on microbiomes and advances in their functional assessments in the coming years, integrated with a trait-based framework, may allow us to better unravel the mechanisms and drivers of disturbance feedbacks both within and outside the context of climate change.

Outstanding questions

What factors define the direction and magnitude of microbially mediated disturbance feedbacks?

What is the relationship between the diversity of functional traits and disturbance feedbacks?

Do negative or positive feedbacks change over time in response to microbial community turnover?

Does environmental and biodiversity homogenization shift the feedback potential from community traits to genotype traits?

How do community dynamics such as competition and facilitation regulate disturbance feedbacks?

How are disturbance feedbacks affected by multiple compounded disturbances?

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Declaration of interests

There are no interests to declare.

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