

Connections and Feedback: Aquatic, Plant, and Soil Microbiomes in Heterogeneous and Changing Environments

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Plant, soil, and aquatic microbiomes interact, but scientists often study them independently. Integrating knowledge across these traditionally separate subdisciplines will generate better understanding of microbial ecological properties. Interactions among plant, soil, and aquatic microbiomes, as well as anthropogenic factors, influence important ecosystem processes, including greenhouse gas fluxes, crop production, nonnative species control, and nutrient flux from terrestrial to aquatic habitats. Terrestrial microbiomes influence nutrient retention and particle movement, thereby influencing the composition and functioning of aquatic microbiomes, which, themselves, govern water quality, and the potential for harmful algal blooms. Understanding how microbiomes drive links among terrestrial (plant and soil) and aquatic habitats will inform management decisions influencing ecosystem services. In the present article, we synthesize knowledge of microbiomes from traditionally disparate fields and how they mediate connections across physically separated systems. We identify knowledge gaps currently limiting our abilities to actualize microbiome management approaches for addressing environmental problems and optimize ecosystem services.

Keywords: microbiome, ecosystem services, productivity, water quality, terrestrial systems

Microbiomes, although they are hidden from our view, are global transformers, controllers, and mediators of many ecosystem processes. These microscopic communities of bacterial, archaeal, and eukaryotic microorganisms are complex and interactive, giving them the potential to affect their environment. The microbiome is defined in the present article as the full genomic content of a group of coexisting microorganisms, encompassing the functional potential and ecological roles of a taxonomically diverse community of bacteria, archaea, and fungi that mediate many ecosystem services on which we depend (e.g., Cavicchioli et al. 2019). These services include the diversity, productivity, and structure of plant communities (e.g., van der Heijden et al. 2008), as well as terrestrial and aquatic nutrient cycling, which affect, among other things, soil and water quality (e.g., Battin et al. 2016).

Many microbiome studies focus on isolated environments, such as the gut of a single animal or the roots of a particular plant. Several insightful and detailed reviews

have synthesized discipline-specific knowledge related to plant-associated (Chaudhary et al. 2017, Compant et al. 2019, Saleem et al. 2019), terrestrial (Wang and Li 2019), and aquatic (Battin et al. 2016, Zeglin 2015) microbiomes. Reviews have also focused on the response of system-specific microbiomes to environmental change (Hawkes and Keitt 2015, Dubey et al. 2019, Jansson and Hofmockel 2020).

Documenting the strength and direction of system-specific microbiome generated feedback is also an active and important area of research (Bever 2003, terHorst and Zee 2016, Crawford et al. 2019). Microbiomes link across environmental and physical boundaries (Baldrian 2017) so they have the potential to influence large-scale biodiversity and ecosystem function. In addition, connections mediated by microbes across systems may influence feedback both within and between these systems. Therefore, we need cross-system views of microbial community dynamics to better understand these microbial connections, their influence on ecosystem services, and microbial responses to human land use.

Recent advances suggest that weaving together disciplinary microbiome knowledge is increasingly feasible. Although the complexity of microbial communities makes their composition and function difficult to predict, recent research suggests that a predictive framework may be attainable. For example, coarse taxonomic structure and function of numerous synthetic microbiomes was predictable on the basis of resource availability even though fine scale taxonomy was not (Goldford et al. 2018). Our recently expanded capacity to sequence and identify a large portion of the microbial community allows us to begin the challenging task of linking microbiome identity with ecosystem function. Recent DNA sequencing data suggest that variations in microbiome composition and diversity can lead to differences in ecosystem function in numerous systems (Waldor et al. 2015). For example, some (though not all) mesocosm experiments indicate that microbial communities with contrasting diversity or composition can exhibit different integrated rates of respiration (Brophy et al. 2017), decomposition (Strickland et al. 2009), or denitrification (Philippot et al. 2013). Given the growing evidence that microbial community composition can control ecosystem functions, broader characterization of how microbiomes structure ecosystem feedback dynamics across systems represents a valuable next step for the microbiome research community.

In the present article, we draw attention to and demonstrate the microbiome's capacity to mediate connections across physically separated systems, and how that mediation may result in altered functions in one or more systems. We emphasize potential impacts from anthropogenic perturbations given that many microbially linked ecosystem functions provide important ecosystem services. Our goal is to examine the complex relationships between plant-associated, terrestrial, and aquatic systems and their importance to ecosystem function (figure 1). Importantly, this includes climate gradients that influence the ecological characteristics of terrestrial biomes, with cascading effects in aquatic systems (Dodds et al. 2019). These climatic gradients likely have concomitant influences on microbiome composition and function. This influence interacts with the anthropogenic activities that are radically changing these gradients and shifting the abiotic connections among broad microbial habitats. We focus on the microbiomes of plant, soil, and aquatic environments and their influential role in mediating and linking three vital ecosystem services: plant productivity and diversity, soil nutrient retention, and water quality (figure 2). Specifically, we consider how bulk soil and rhizosphere microbiomes can interact to influence plant productivity and diversity, how microbiomes mediate nutrient and carbon (C) retention and availability in terrestrial (plant and soil) environments, and how connections between microbiomes in terrestrial and aquatic habitats, as well as microbiome interactions within aquatic ecosystems influence water quality. We also describe the potential shifts in connections among these three relationships with anthropogenic climate and land-use change. Rather than

exhaustively reviewing information on every subhabitat, we highlight potential links and feedback.

Microbiomes influence plant productivity and diversity

Because plants and microbes have a long coevolutionary history (Delaux et al. 2015), understanding how microbiomes influence plant diversity and productivity may ultimately provide strategies to mitigate the negative impacts of human activity on both natural and agricultural plant systems. One view is that plants act as filters that shape the microbiome (e.g., Poudel et al. 2019). In this view, plants select subsets from the soil microbiome that are stimulated by the specific root exudates, or through physical effects at the soil–root interface. This filtering leads to increased beta diversity by creating specific niches adjacent to and within the roots. This view suggests it is important to delineate between soil and plant microbiomes. It also clearly indicates that strong feedback with soil microbes and plants is possible.

Because plants connect above and below ground systems, plant–microbiome interactions could have cascading effects for both soil and water systems. We therefore focus this section on how interactions between plants and their microbiomes directly influence plant productivity and diversity and the potential for humans to alter plant microbiomes in ways that positively influence the outcomes of these interactions.

Feedback between microbial communities and plant productivity and diversity.

Interactions among plants and their microbial partners can influence plant productivity in many ways. Traditionally, researchers viewed many of these interactions as competitive or pathogenic, but many positive forms of feedback exist as well. For instance, mycorrhizal fungi and nitrogen (N)–fixing bacteria enhance plant productivity by supplying nutrients that plants cannot easily acquire (e.g., van der Heijden et al. 2008). Partnerships with mycorrhizal and other root-associated fungi can also increase productivity by providing plants with additional resources to fight off infection, thus enhancing plant defenses against pathogens and increasing productivity. In addition, interactions among different soil microbial groups can protect plants from disease and promote their growth by inhibiting pathogens (Crawford et al. 1993, Vannier et al. 2019, Berg and Koskella 2018).

Interactions of plants with microbes and among microbes can also decrease plant productivity. Pathogens cause widespread disease and can significantly decrease plant productivity, especially when pathogen density is high and plant diversity is low (Bever et al. 2015). Nonbeneficial mycorrhizal fungi can function as conditional parasites that decrease plant host productivity. They can take more C than their beneficial counterparts but not supply benefits such as increasing P or water availability (Johnson et al. 1997). Competition between plants and nearby saprotrophic microbes can, especially in nutrient-limited systems, reduce nutrient availability to plants and thereby decrease plant

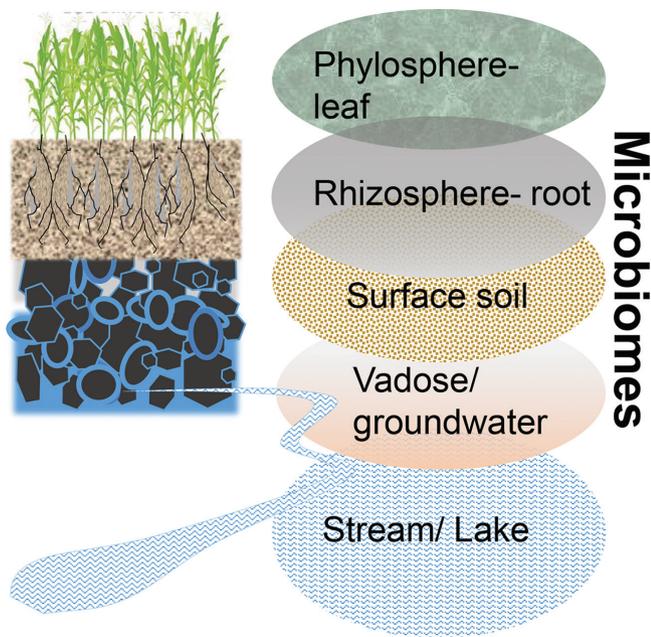


Figure 1. Linking more traditional subdisciplines is necessary to understand behaviors within and among habitats. Not all interactions are represented in the present article, for example leaves can fall directly into streams without passing through all the compartments.

productivity. For instance, in the Arctic, microbes strongly compete with plants for N, leading to a high proportion of N immobilized in microbial biomass and unavailable to plants (Jonasson 1997).

Plant–microbe interactions can have both positive and negative impacts on plant diversity. The mechanisms are similar to those driving changes in plant productivity. Differential effects of pathogens can generate negative feedback, thereby playing major roles in maintaining plant diversity (Bever et al. 2015) and plant successional trajectories (van der Putten et al. 1993). Differential associations with mutualists such as mycorrhizal fungi can generate positive feedback, which can lower plant diversity (Bever 2003), as with some invasive species (Wilson et al. 2012). N-fixing bacteria can facilitate the growth of nearby plants that do not host those bacteria, as is evidenced by N transfer from legumes to nonlegumes (Thilakarathna et al. 2016). N-fixing bacteria and mycorrhizal fungi can also influence plant diversity by promoting seedling establishment and the growth of specific species by enhancing the competitive abilities of their hosts (van der Heijden et al. 2008).

Soil microbes can facilitate the naturalization of nonnative species in addition to shaping the composition of native plant communities (Batten et al. 2008). Introduction of nonnative plants can shift microbial community structure and function (Kourtev et al. 2002). For example, plant invasion has altered soil N cycling (Hawkes et al. 2005) and native mycorrhizal fungal and N-fixing bacterial communities can

increase the competitive ability of the introduced plants (Pringle et al. 2009). A pathogen enemy-release process can occur where nonnative plants can evade the pathogens that limit their productivity in their native range (Liu and Stiling 2006) and contribute to successful naturalizations (Crawford et al. 2019).

Feedback between plant community composition and the plant and soil microbiome can influence terrestrial resource retention. For example, soil microbes can mediate ecosystem benefits derived from increasing plant diversity (Maron et al. 2011, Schnitzer et al. 2011, Wang et al. 2019). This mediation results from both pathogen build up and decreased efficiency of nutritional symbioses at low plant diversity reducing terrestrial resource acquisition. Microbial diversity can increase plant diversity and vice versa (van der Putten et al. 2016, Kowalchuk et al. 2002) and their interactions can positively influence resource retention (Thompson and Kao-Kniffin 2016), thereby reducing inputs into aquatic systems.

Human impacts and management of plants and their microbiomes. Human activity can alter each of the interactions mentioned above. The increased plant productivity generated by partnerships with microbial symbionts and microbiota-mediated disease protection is sensitive to disturbance, land use, and resource changes. Anthropogenic increases in soil resources through fertilization can change microbial community composition, and ultimately decrease efficiency of resource uptake in plants (Corkidi et al. 2002). This can lead to decreased plant growth efficiency. Similarly, urbanization can alter microbial community composition and microbiome richness, potentially resulting in compromised ecosystem services and poor host performance in urban areas (Hui et al. 2017). In contrast, increases in aboveground resources, such as atmospheric carbon dioxide (CO₂), can enhance the efficiency of mutualisms between plants and microbes (Corkidi et al. 2002, Bever 2015), generating the potential for increased plant productivity.

Anthropogenic disturbance including mechanical disruption or overgrazing can promote invasive plant species. Part of the promotion is related to homogenizing root microbiomes, including arbuscular mycorrhizal fungal communities. This homogenization can limit mycorrhizal benefit to plants (House and Bever 2018) and can also create opportunities for invasion by plants with reduced reliance on symbionts (Delavaux et al. 2019). Reintroduction of native symbionts in disturbed grassland sites can have strong, positive effects on native plant productivity, and counter plant invasions by aiding in native plant community recovery (Koziol et al. 2018).

Differential responses of plants and microbes to shifts in climate may decouple plant–soil microbiome interactions. For example, diversity-promoting negative plant–soil microbiome feedback was disrupted by cross-season climate variability (Duell et al. 2019), with implications for patterns of plant diversity. Climate-driven shifts in plant species distributions such as riparian species (Kominoski et al. 2013)

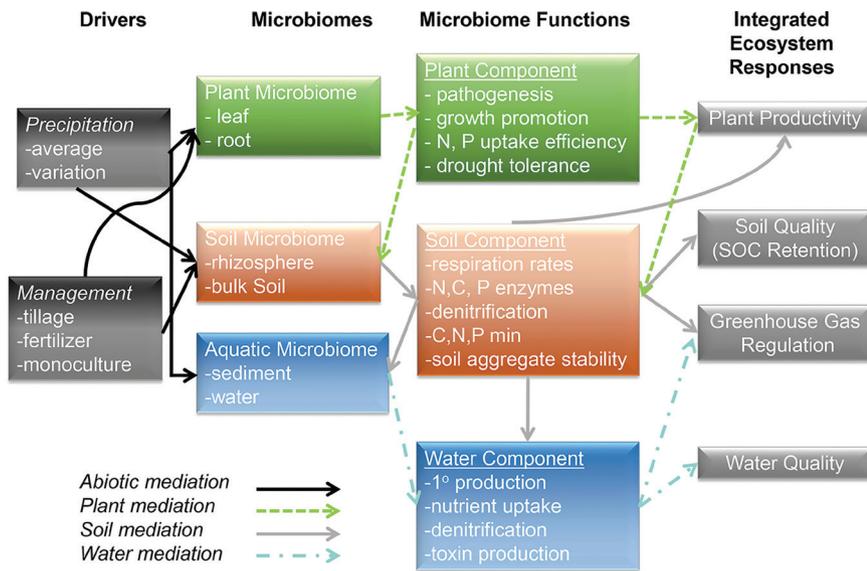


Figure 2. A conceptual view of how some environmental drivers and compartments could relate to microbiomes, their functions, links among compartments, and ecosystem services following the principles outlined in the present article.

could also alter the proportion of plants in a community with beneficial rhizosphere symbionts as well as the amount of resources allocated to mycorrhizae. These shifts could have high potential for feedback to ecosystem services. Moreover, microbes can mediate plant adaptation to changing climate by expanding the environmental envelope for plant survival and reproduction (Lankau and Keymer 2017) and may also limit or enhance plant establishment (Delavaux et al. 2019).

Therefore, microbial sensitivity to climate can mediate plant community response to climate change. For example, because climate controls on decomposition rates drive global patterns of mycorrhizal associations in trees (Steidinger et al. 2019), shifts away from historical climatic patterns may alter global distribution of those mycorrhizal associations. Warming-induced permafrost thaw can alter plant productivity and community composition because of high sensitivity of mycorrhizal fungi and saprotrophic microbes to thaw-induced changes in soil moisture (Schütte et al. 2019).

Climate change could decouple microbiome interactions and biogeochemical cycling because of differential responses from plants and microbes. For instance, Dijkstra and colleagues (2015) observed that microbial phosphorus (P) uptake is more sensitive to drought than plant P uptake, whereas plant N uptake is more sensitive to drought than microbial N uptake. This could create discrepancies in the relative nutrient needs of plants and microbes, disrupting their associations with one another, and shifting patterns of biogeochemical cycling.

Taken together, these examples illustrate the need for future studies to address the environmental dependence of both positive and negative plant–microbe feedback. Future research should characterize conditions under which

microbes have either positive or negative impacts on plant productivity and diversity to identify thresholds where plant–microbe feedback can transition from one interaction to another. Identification of such thresholds could illuminate how and when plant–microbial systems will decouple as environmental conditions change following anthropogenic perturbation. In addition, plant–microbe feedback at the local scale, such as the leaf or the rhizosphere, may influence soil nutrient and water retention, which, in turn, can affect ecosystem processes across systems, including the transport of materials such as water, nutrients, and microorganisms, to associated aquatic habitats. Therefore, investigating this intricate balance of plant–microbiome interactions is critical to understanding the processes that contribute to changes in agricultural and native plant productivity and diversity. This information has the potential to improve cropland

management, aid restoration efforts, combat invasion by nonnative plant species, and help conserve native lands and aquatic habitats across systems.

Soil microbiomes mediate ecosystem-scale retention and losses of materials

Soils and their microbiomes help control both local and landscape-scale ecosystem services because they are the medium in which plants grow and the source of much of the material that flows into aquatic systems. Resource retention and losses from soil profiles are a function of feedback among plant inputs, soil abiotic characteristics, as well as microbial diversity and physiology. The capacity of soil profiles and their microbiomes to retain or lose resources, whether in gaseous, dissolved, or solid form, depends strongly on both temperature and moisture (Davidson and Janssens 2006). Understanding resource retention and loss is central to predicting processes that link to downstream habitats, as well as understanding how soils influence global cycling, including the mediation of greenhouse gas fluxes. In the present article, we discuss the mechanisms by which soil microbiomes contribute to material fluxes through ecosystems, and the temperature, moisture, and anthropogenic drivers that alter their structure and function.

Material retention links to soil microbiomes. Physicochemical properties, climatic conditions, vegetation, and microbial dynamics govern soil resource retention. For example, loss of organic C as respired CO₂ depends on temperature and the physical and chemical accessibility of C-containing substrates and water to microbes. Microbial CO₂ release depends in part on microbial C use efficiency (the ratio of

the microbial production rate to the sum of production and respiration rates; Frey et al. 2013, Ballantyne and Billings 2018). Lower C use efficiency, all else equal, suggests that microbes mineralize a relatively greater fraction of soil organic C to CO₂ instead of transforming it into biomass. This phenomenon can shunt C losses to the atmosphere and away from dissolved organic compounds that either can undergo stabilization or leach into groundwater or streams (Sinsabaugh et al. 2013). Both soil and microbial attributes likewise dictate N release from soil; the ability of denitrifying bacteria to scavenge nitrate and nitrous oxide (N₂O) relies on limited diffusion of oxygen (O₂) to reaction sites. This limited diffusion then influences the fraction of soil inorganic N released as N₂O and N₂ (dinitrogen), as well as the genetic capacity of different microbial taxa to use N₂O or other forms of N as respiratory electron acceptors (Hallin et al. 2018). These complex suites of processes, in turn, govern C and N availability within the soil profile, as well as in ecosystems receiving soil system losses.

One key motivation to understanding how the soil microbiome influences organic matter release and retention is the importance of soil organic matter dynamics to the global C cycle. Therefore, much contemporary research focuses on microbial uptake and transformations of soil C and how biotic and abiotic environmental conditions influence microbial transformations of soil C (e.g., Sinsabaugh et al. 2016, Ballantyne and Billings 2018), how physical protection of organic matter by soil minerals and aggregate formation by microbes (e.g., Rillig and Mummey 2006, Logsdon 2013) can shield organic C from microbial processing over decadal time scales or more (Dungait et al. 2012), and processes such as macropore formation by roots that shunt organic C deeper in the subsurface where its probability of retention is greater (Banfield et al. 2018).

Although microbes may transform labile C to become part of the pool of persistent organic compounds (Cotrufo et al. 2013), they may also induce accelerated decomposition of diverse organic compounds (i.e., priming) when they encounter root exudates within the rhizosphere (Cheng et al. 2014) or labile substrates in deep, otherwise resource-poor environments (Hicks Pries et al. 2018). Furthermore, adding to these complex dynamics, microbes themselves contribute to soil organic C pools, with their necromass thought to contribute up to half of relatively persistent pools of soil organic C (Liang et al. 2019). Therefore, the extent to which microbes drive retention versus loss of materials in soil systems is context dependent.

The relative abundances of the functional groups that make up soil microbial communities are associated with patterns of soil organic matter decomposition (Gessner et al. 2010) and may therefore contribute to retention and loss in different ways. For example, soil fungi may physically disrupt organic particles, allowing bacteria to access them, and differential enzyme production by members within a bacterial community can allow the soil microbiome to break down a greater variety of organic compounds (Gessner et al.

2010, Sinsabaugh and Follstad-Shah 2012). Although microbially diverse soils maintain some functional redundancy among resident organisms, there is a positive association between soil microbial diversity and ecosystem multifunctionality (Delgado-Baquerizo et al. 2016). The degree to which these effects of microbial diversity matter for elemental retention depends on the relative dominance of abiotic factors as drivers of decomposition (i.e., redox potential, soil moisture content, or physical access to substrate). As such, soil microbiomes help maintain the soil metabolic activities that drive the retention or loss of C from terrestrial ecosystems as they interact with soil edaphic properties (Lehmann and Kleber 2015).

Microbial stoichiometry links elemental cycles and is an important driver of soil nutrient cycling and retention. Both empirical and modeled exoenzyme activities suggest that microbes attempt to acquire nutrients in generally consistent ratios relative to their needs (Sinsabaugh and Shah 2012). The degree to which soil microbes can exhibit plasticity in resource acquisition ultimately influences both the resources that remain outside of the microbial pool, as well as the elemental composition of microbial necromass. Therefore, the stoichiometry of microbial resource uptake can influence processes such as nitrate losses from soils to aquatic systems, and soil organic C retention or loss to the atmosphere as CO₂. However, microbial stoichiometric plasticity remains controversial. Microbial C:N ratios remain relatively constant, whereas C:P and N:P ratios exhibit higher plasticity, and shifts in the stoichiometry of microbial biomass might be more reflective of turnover in microbial community composition (Mooshammer et al. 2014). Overall, predicting nutrient retention in soil is difficult in part because of uncertain microbial responses to variations in temperature, moisture, and changes in land cover.

Human disturbance of soil and its microbiomes generates uncertainties about future ecosystem function: Temperature, moisture, and land use.

The response of soil microbiomes to anthropogenic perturbations is a key knowledge gap in projecting soil feedback to Earth's changing climate. We focus on soil C and N dynamics given the importance of these organically bound soil resources to microbes, but emphasize that soil retention of diverse elements, often in solute form, is changing in the Anthropocene (e.g., Li et al. 2018). One important feature of potentially altered microbial transformations of C and N, among other elements, is changing temperature regimes. Although mineral-associated soil organic matter can be protected from decay and subsequent mineralization and loss for millennia (Schmidt et al. 2011, Dungait et al. 2012, Cotrufo et al. 2013), temperature-sensitive microbial physiology plays an important role in determining the fate of materials in soils (Jilling et al. 2018). For example, C use efficiency appears to decrease in response to rising temperatures (Frey et al. 2013, Lehmeier et al. 2016). Enzymes themselves, the catalysts of organic matter decay, respond to temperature as well; the temperature response

Table 1. Prediction of some soil microbiome characteristics as a function of a gradient of soil moisture.

Dry	Moist	Saturated
Low oxic respiration	Maximum oxic respiration	Intermediate respiration
Low anoxic carbon cycling	Intermediate anoxic carbon cycling	Maximal anoxic carbon cycling
Lower biomass	Maximum biomass	Intermediate biomass
Low nitrous oxide and methane release	Intermediate nitrous oxide and methane release	Potentially high nitrous oxide and methane release
Low influence on carbon retention	Maximum influence on carbon retention	Modest influence on carbon retention (anoxia slows decomposition)
Slower decomposition rate	Maximum decomposition	Intermediate decomposition

can vary, however. Although many enzymes' responses to temperature are positive (Wallenstein et al. 2009, Lehmeier et al. 2013), a global meta-analysis suggests that soil peroxidase activity can decline with warming and that other enzymes may be less sensitive to warming (Xiao et al. 2018). Temperature sensitivity of some decay-inducing enzymes and CO₂ losses per unit biomass appears constant across time in some systems (Min et al. 2019), and some long-term soil warming studies indicate that increased soil respiration with warming can be ephemeral, with soil CO₂ efflux eventually returning to prewarming rates. These observations suggest that microbes can respond to warming over time in ways that conserve C (Allison et al. 2010), or at least exhibit predictable C losses (Min et al. 2019). Importantly, however, models based on global field experiments indicate that warming will stimulate soil C losses (Crowther et al. 2016), providing an important positive feedback to warming.

The influence of temperature on soil N dynamics is less well studied. Warming can increase the pool of soil inorganic N and stimulate rates of N mineralization and nitrification (Bai et al. 2013), which could increase N transport to streams and gaseous losses of soil N. However, as with the response of microbially mediated soil C dynamics, there is not a universal response of microbial transformations of N to temperature. For example, a meta-analysis of warming experiments indicates that the rate of soil N₂O production does not respond strongly to warming (Bai et al. 2013). In contrast, short-term (i.e., hourly) increases in temperature within a grassland prairie system showed declines in soil nitrate, shifting relative abundances of the genes responsible for driving N₂O production and consumption, and enhanced N₂O losses (Billings and Tiemann 2014). Within montane fen soils, short-term warming promoted net N₂O production (Wang et al. 2014), but long-term exposure of soils to a warmer mean annual temperature in boreal forest can result in an increase in the abundance of the bacterial gene linked to N₂O consumption (Buckeridge et al. 2019). It remains unclear to what extent these changes represent ecosystem-specific responses versus ubiquitous outcomes stemming from fundamental, bacterial responses to warming.

Given the dependency of the soil microbiome on soil moisture, it also important because precipitation patterns link to anthropogenic climate change. As with temperature perturbations, microbial responses to moisture regimes that control nutrient retention and loss are a function of microbial physiology (table 1). For example, precipitation patterns resulting in variable soil moisture tend to promote microbial communities that rely on osmolytes (compounds that provide protection against cellular water loss by altering a cell's osmotic potential, Schimel et al. 2007). In response to precipitation following drought, microbes release osmolytes to maintain water balance. Microbial production of these compounds, which can be rich in both C and N, can result in lower microbial C use efficiency because of the energy expended for their synthesis (Schimel et al. 2007, Tiemann and Billings 2011). The release of accumulated osmolytes provides a resource pulse for plants (N) and microbes (C, N) that can be substantial. Indeed, Schimel and colleagues (2007) estimated that the soil microbiome can transform 3%–6% of a grassland's annual net primary productivity into osmolytes during a single drought.

Soil moisture also governs organic substrate accessibility to exoenzymatic attack and therefore to microbial uptake and mineralization of diverse compounds. In an example of the direct, local feedback that microbes provide within their immediate surroundings, the sugars produced by soil microbes can enhance soil moisture retention (Rosenzweig et al. 2012); a C investment by soil microbes in sugars consequentially provides them with additional C substrates through moisture flow adjacent to their cell wall. Such feedback between soil moisture and the soil microbiome can further influence a soil microbiome's C use efficiency and nutrient dynamics (Xiao et al. 2018), even at levels meaningful in terms of a system's net primary productivity.

The responsiveness of microbiomes to changes in precipitation regime depends on the historical context of the ecosystem, demonstrating legacy effects in microbial functioning (e.g., Zeglin et al. 2013, Hawkes et al. 2017). The differences between xeric and relatively mesic soil systems likely relate to microbial community composition and life history strategies, substrate identity and soil structural landscape. Changes in the frequency of precipitation can control microbial community structure and life histories.

Table 2. Summary of predicted trends in microbiome activities and diversity comparing tilled and fertilized cropland to an undisturbed native habitat in the same region as an example of how common land-use changes can alter feedback and functions mediated by microbiomes.

Tilled and fertilized monoculture cropland	Native	Citation
Decreases soil organic C and N sequestration	Greater C and N sequestration	Cambardella and Elliot 1993
Smaller soil aggregates enhancing nutrient loss	Larger soil aggregates	Cambardella and Elliot 1993, Richter and Markewitz 2001
Decreased microbial respiration	Increased microbial respiration	Yamulki and Jarvis 2002
Increased gaseous N flux	Decreased gaseous N flux	Yamulki and Jarvis 2002
Lower bacterial diversity	Greater bacterial diversity	Szoboszlay et al. 2017
Introduced pathogens increase invasability by nonnative plants	Native symbionts decrease invasability by nonnatives by stimulating native productivity	Delavaux et al. 2019
Increase nutrient loading can alter microbiome decreasing efficiency of plant resource uptake	Greater proportional nutrient retention related to greater plant resource uptake	Corkidi et al. 2002
Decreased reliance on N-fixing bacteria and mycorrhizal fungi	Increased reliance on N-fixing bacteria and mycorrhizal fungi symbioses, decomposition, and deep soil respiration	

Note: We consider a mesic grassland as the native condition as many such grasslands have been tilled. See text for further explanation.

For example, a greater proportion of bacteria collected from soils with historically longer dry periods were more tolerant of experimental drying than bacteria collected from soils without long drying periods (Evans and Wallenstein 2012). Soil microbes that have survived more environmental variability also can show less sensitivity to environmental change (Tiemann and Billings 2011, Veach and Zeglin 2020). Therefore, genetic legacy (evolutionary or compositional) effects of environmental conditions exert influence on contemporary microbiome responses to changing moisture regimes. Therefore, the nature of global-scale perturbations in soil moisture regime means that legacy effects of current conditions will be difficult to project given a changing climate.

In conjunction with climate, land-use change (Setälä et al. 2017) adds yet another way in which soil environments undergo alteration in the Anthropocene. Changes in abiotic conditions due to land-use regimes influence the composition, activity, and function of soil microbial communities. For example, increases in soil N and P from fertilizers can reduce plant reliance on N-fixing bacteria and mycorrhizal fungi (Lambers et al. 2008). Nutrient additions also favor copiotrophic (i.e., high resource, particularly C, demand) bacteria and tend to decrease the abundance of mycorrhizal fungi (Leff et al. 2015). Fertilizers can also elicit changes in soil pH, which, in turn, have strong effects on soil microbes (Sinsabaugh et al. 2008, Geisseler and Scow 2014). These effects can last for years after fertilizer use ceases, such that agricultural activities may leave lasting legacies on microbial communities both in terms of structure and function (van der Putten et al. 2013).

Land use also changes physical soil structure with implications for its microbial inhabitants. Tillage (table 2), land clearing, and grazing typically disrupt macroaggregates, altering soil structural quality and enhancing rates of nutrient loss (Richter and Markewitz 2001). Such agricultural

practices also can result in the loss of organic matter via erosion, and enhance microbial use of extant organic matter (Kumar et al. 2018). Physical disruptions, whether from direct impacts of human activities or the loss of soil organic matter due to accelerated rates of microbially mediated decay, alter water and O₂ infiltration in soils, feeding back into soil chemical composition (Li et al. 2017). Urbanization, another major land-use change in the Anthropocene, can lead to enrichment of nutrients and heavy metals in urban-affected soils. Such enrichment can influence soil microbial community composition (Francini et al. 2018). Therefore, land-use impacts on physical and chemical soil factors alter microbial habitats in ways that will influence both the community composition of soil microbiomes and their metabolic capabilities.

We suggest some research needs related to the influence of temperature, moisture, and land cover change on microbially mediated soil nutrient retention. First, it is critical that we gain an understanding of the timescales over which microbial physiological responses to environmental change cede to changes in microbial community composition, or even to evolutionary adaptation of populations into new ecotypes. For example, plasticity in a microbial group's stoichiometry (Sinsabaugh et al. 2013) may not be a long-term option for survival, prompting shifts in microbial community composition over time. Addressing this question requires an understanding of the mechanisms and timescales of microbial evolution. Second, understanding how microbial community composition drives measurable physiological responses to temperature, moisture, and soil chemistry will facilitate future scientific progress. Currently, we know that functional redundancies across microbial groups obscure coupling between microbial identities and function (Delgado-Baquerizo et al. 2016, Hall et al. 2018). Finally, because changing temperature, moisture and land uses all promote changes in microbial substrate availabilities

(Sinsabaugh and Folstead-Shah 2012), it may be wise to focus on integrating microbial responses to substrate identities and abundances into otherwise soil-focused studies. For example, the idea that enhanced availability of labile C sources may counterintuitively result in greater rates of formation of persistent soil organic C stocks (Cotrufo et al. 2013), which tend to exhibit greater temperature sensitivities of decay (Davidson and Janssens 2006), highlights the importance of understanding microbial responses to substrate variability. Importantly, such research efforts will promote understanding of both resource release to the atmosphere (e.g., CO₂, N₂O) and release downstream (e.g., solute fluxes to aquatic systems).

Terrestrial microbiomes impose downstream influences, mediated by freshwater microbiomes

Microbes influence how materials move from terrestrial to aquatic habitats including nutrients and living cells. This transport can alter water quality, shift aquatic microbiomes, and enhance or inhibit harmful algal blooms. The factors discussed already for terrestrial microbiomes feed into this transport, but the aquatic microbiome potentially responds to terrestrial inputs in several ways.

Movement of microbes and nutrients from terrestrial habitats. Running waters capture nutrients and microorganisms throughout the watershed, linking terrestrial microbiomes and their habitats with downstream areas. Many aquatic habitats are net heterotrophic with food webs heavily dependent on input of terrestrial C (Dodds and Cole 2007). Therefore, movement of dissolved nutrients from terrestrial systems can influence basic aquatic ecosystem functions (e.g., Mulholland et al. 2008), selecting for or against particular microorganisms (Litchman 2010). Terrestrial ecosystems also deliver microbes to surface water, from both overland runoff (e.g., fungi in leaf litter washed to streams; Marks 2019) and through the soil profile (Crump et al. 2007). Microbial movement from the surface soils through groundwater must occur via flow pathways through deep soil and the vadose zone. This microbial highway can widen when the vadose zone of the soil profile is saturated. Chin (2010) found a strong link between the location and density of terrestrial fecal coliforms and stream water quality, where water quality was worst during high rainfall periods. Finally, changes in riparian vegetation can have particularly strong influence on aquatic microbiomes, and the structure of riparian plant communities is heavily influenced by land-use change, invasive species, flow alterations, and climate shifts (Kominoski et al. 2013, Gonzaléz et al. 2017), which can affect microbiome-mediated ecosystem functions (Kominoski et al. 2013, Keller and Phillips 2018, Marks 2019). Because terrestrial disturbances can cascade from riparian zones to stream microbiomes (Veach et al. 2015), land-use decisions can have substantial consequences for stream microbial community structure (Lear et al. 2011).

Once microbes enter the aquatic environment, microbiome composition in water shifts and becomes more suited to aquatic habitats. There are more terrestrial microbial inputs in smaller streams, and in-stream processes shift microbial communities toward dominance by those more suited to planktonic (water column) habitat in larger rivers, lakes, and reservoirs (Crump et al. 2007, Ruiz-González et al. 2015). Although microbes washed in from terrestrial habitats may be a minor portion of the metabolically active planktonic microbiome (Wisnoski et al. 2020), microbial transport through the water column also brings inocula to the benthic (streambed sediment) habitat, where biofilms perform essential water quality supporting functions (Battin et al. 2016). Some claim that terrestrial microbes can seed and make up a considerable portion of the downstream aquatic microbiome (Crump et al. 2012). Therefore, the links between terrestrial and aquatic microbial habitats are functions of the probability that microbes will move from terrestrial to aquatic habitats and the capacity of all microbes to survive, compete successfully, and contribute to ecosystem function in aquatic habitats.

Microbial traits and life histories can influence rates of microbial transfer from terrestrial habits. Sessile microbes that attach to particulate materials may be less likely than motile, free-swimming microbes to move through the soil, vadose zone, and groundwater into freshwater. However, these same microbes may be more likely to be transported with larger particles. Traits such as high growth rate, high genetic diversity, persistence, or a specific metabolic pathway (e.g., ability to cope with anoxia) may increase the likelihood of a group to proliferate after crossing a habitat boundary (Litchman 2010, Niño-García et al. 2016, Niederdorfer et al. 2017, Wisnoski et al. 2020).

Local environmental and community pressures in aquatic habitats influence the likelihood that microbes transported from soil into a stream will thrive, particularly in the benthic habitat (Zeglin 2015, Battin et al. 2016). Soil microbes may be better suited to a benthic sediment than a planktonic or epilithic (exposed biofilm) lifestyle (Griffin et al. 2017), because of their historically low exposure to a fluid hydraulic environment (Niederdorfer et al. 2016). In all aquatic habitats, factors such as nutrient availability constrain diversity (by limiting metabolic pathways) and abundance (by limiting resources) of microbial life.

Microbial activity occurring within stream channels has major consequences for the further downstream delivery of both nutrients and microbial cells (Battin et al. 2016). The importance of nutrient retention within streams for remediating water quality is well established (Mulholland et al. 2008), and microbial activity drives this function, but microbial diversity per se may (e.g., Tatariw et al. 2013), or may not (e.g., Veraart et al. 2017) promote nutrient removal. Terrestrial land-use changes could affect in-stream nutrient removal via impacts on the microbiota, through both nutrient and microbial inputs that influence in-stream microbial

community composition and gene function potential (Meziti et al. 2016, Hosen et al. 2017).

In addition to microbial transport through watershed infiltration, more rapid, direct inputs of cells are possible through storm events (Kan 2018). This transport could arise from surface runoff and erosion through riparian zones (Marks 2019), and mobilization of particles from impervious surfaces in urbanized areas (Hosen et al. 2017, Zhang et al. 2020). It will be important to learn more about the factors that support strong, predictable, links between terrestrial and aquatic microbiome structure and function in order to predict the cascading effects of terrestrial land-use change on aquatic ecosystem function.

A considerable body of literature exists on survival of pathogens that enter aquatic habitats and the use of microbial identity to track sources of microbial inputs to streams. Land use is a major determinant of pathogen occurrence in freshwaters (Bradshaw et al. 2016), and pathogen load can be reduced when movement of water from soil to stream is slowed (Wilkes et al. 2014). This literature offers further support for the concept that active microbes can enter aquatic microbiomes from terrestrial habitats and maintain their ability to influence other organisms.

Potential links with harmful algal blooms. Transport of nutrients can stimulate other undesirable conditions in freshwaters. Harmful algal blooms (HABs) are a worldwide problem occurring when one or more noxious or toxic cyanobacterial species dominate an environment. Toxic blooms are more probable with high nutrient (N, P) loading (Downing et al. 2001, Paerl et al. 2016). Cyanobacterial blooms in particular compromise many ecosystem services such as water quality, recreation uses, fish production, and property values (Dodds et al. 2009). Nutrient loading stimulating algal blooms is well studied, but the role of the aquatic microbiome in formation or collapse of blooms, and how such blooms influence other members of the microbiome could also be important. Facilitative or allelopathic interactions can occur with other microbiome constituents that affect cyanobacterial blooms. A wide variety of microbes have antagonistic effects on the common toxic cyanobacterium *Microcystis*, including viruses, other bacteria, and fungi (van Wichelen et al. 2016). In contrast, some types of heterotrophic bacteria can initiate *Microcystis* colony formation, possibly assisting in bloom formation (Wang et al. 2016). The interactome hypothesis (Garcia et al. 2015), which proposes that co-occurring microbial functional populations, such as those with essential vitamin biosynthesis pathways, are required for a toxic bloom to occur, has some global support (Cook et al. 2020). Still, we do not fully understand to what degree terrestrial microbes and remediation of nutrient loads in upstream waters influence probability of algal bloom formation and whether such blooms will be toxic.

Algal blooms can also alter microbiomes within freshwaters. HABs can dramatically alter bacterial diversity, but communities return to their initial state shortly following

the bloom in some systems (Berry et al. 2017). Therefore, certain aquatic microbiomes may be resilient to the environmental changes induced by HABs. Without further investigation into how terrestrial microbiomes influence these systems, the complex interactions that mediate HAB proliferation and frequency will remain unclear.

Future studies will need to examine the extent to which terrestrial microbial communities are transported to, and function in, aquatic systems. Studies tracing transfer and retention of microbial communities and the associated products, from land to water will help address questions regarding the link between plants, diversity, soils and water quality. Such studies might help us take advantage of plant diversity effects and soil processes for water quality improvement. In addition, quantifying the role of microbial diversity in nutrient transformations and fluxes as materials move downstream will be important to characterizing the extent to which terrestrial systems affect water quality at varying scales of space and time. Therefore, managing water quality will require understanding not only the microbiome in aquatic systems, but the links to upstream habitats, functions of upstream microbiomes, and their connections to downstream habitats.

Microbiome mediation: Linking systems to integrate dynamic landscapes and anthropogenic challenges

Researchers often treat the terrestrial–aquatic interface as a black box with respect to microbial-mediation of material transport. This reflects the challenge associated with characterizing the complexity of, and interactions between, terrestrial and aquatic microbiomes within a dynamic, integrated landscape (e.g., Triska et al. 1993). However, microbiome functions are a foundational component of ecological responses to abiotic gradients and connections among habitats, which will determine how ecosystems respond to anthropogenic pressures. The hypotheses explored in the present article (see below) demonstrate that the composition and function of microbial communities have important consequences for the movement of materials, including nutrients, contaminants and sediments, between terrestrial and aquatic systems, with important implications for downstream water quality. As such, assessing the impact of humans on the environment will require understanding how land-use changes influence microbiome structure and function.

We present a conceptual framework, which characterizes these relationships in figure 2, providing a springboard for future studies addressing microbially mediated links across systems. In the present article, specific feedback within terrestrial and aquatic systems and its influence on microbial activity (figure 2) inspire several hypotheses that we believe are worthy of further study. These include, first, microbiome community structure influences interactions among organisms more directly than overall ecosystem rates and a meaningful proportion of these entail positive feedback. Second, microbial diversity and processes in terrestrial and aquatic environments influence downstream water

Box 1. Conceptual model linking terrestrial and aquatic systems.

Nutrient pools influence the dynamics of both terrestrial and aquatic communities. For this reason, the transport of nutrients from terrestrial to aquatic systems is a key link between these systems. Soil nutrient pools are shaped by plants and microbes consuming and releasing nutrients into the soil (Lehmann and Kleber 2015). Terrestrial microbial processes can influence nutrient retention and availability and can affect nutrient transport to aquatic systems. The dynamics of freshwater aquatic systems are heavily influenced by P and N concentrations, and variation in inputs of these nutrients to aquatic systems has potential consequences for aquatic microbiomes and their associated ecosystem services. Of particular relevance to us and this illustrative model, the probability of cyanobacterial blooms increases dramatically with total phosphorus enrichment (Downing et al. 2001). To illustrate the potential value of research on the impact of terrestrial microbial processes on aquatic ecosystems and services, we develop a simplified conceptual model linking key terrestrial microbial processes that govern terrestrial P retention and the effect of variation in P loading on cyanobacterial dynamics. The model is based on the idea that mycorrhizae-mediated P retention will decrease movement of P to the aquatic environment, and that species interactions within the aquatic environment may exacerbate or mitigate this effect on harmful algal blooms.

In this model, we describe the simplified terrestrial dynamics of nutrient turnover, retention, and transport in terms of changes in plant biomass, plant detritus, the proportion of mutualistic arbuscular mycorrhizal fungi (AMF), the cost to plants of the AMF mutualism, the biomass of saprophytic soil microbes, and soil phosphorus levels (see the supplement and supplemental table S1). The efficiency of AMF facilitated P-uptake to plants is determined by the balance of plant preferential allocation and competition of beneficial and nonbeneficial AMF following Bever (2015). The terrestrial system is then expanded to incorporate dynamics in plant detritus, biomass of saprophytic soil microbes, and available soil phosphorus concentrations. We describe the simplified aquatic dynamics in terms of changes in green algae biomass, cyanobacterial biomass, aquatic phosphorus, and the biomass of one species of grazer of green algae and cyanobacteria (see the supplement and supplemental table S2).

The equilibrium soil phosphorus levels of a terrestrial system depend on the quality of the mycorrhizal mutualist measured by the rate of returned phosphorus per unit C allocated by the plant (figure 3a). Consequently, aquatic systems receiving soil phosphorus inputs from terrestrial systems with high mycorrhizal quality can have lower cyanobacterial biomass peaks than those receiving phosphorus inputs from terrestrial systems with low mycorrhizal quality (figure 3b). Parameter values used are listed in supplemental table S3.

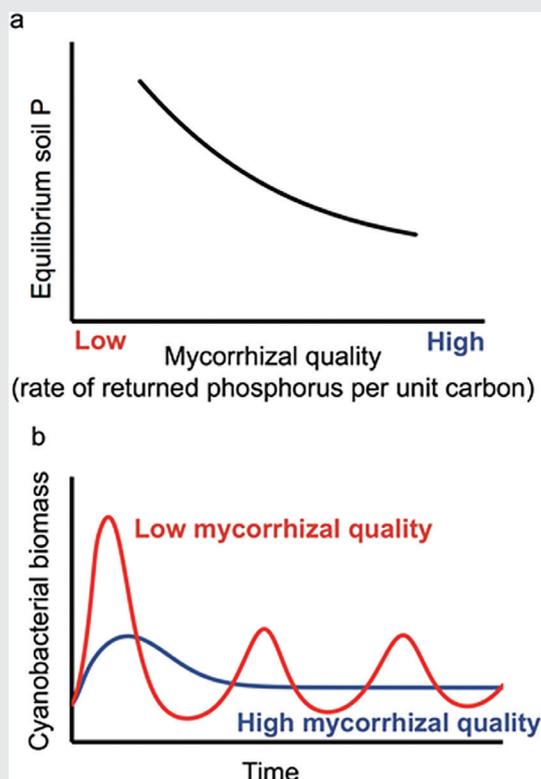


Figure 3. A conceptual model linking terrestrial and aquatic systems illustrates how terrestrial plant–microbe interactions can affect aquatic system dynamics because of consequences on phosphorus transport. Terrestrial systems with high quality mycorrhizal partners have lower equilibrium soil P than do terrestrial systems with lower quality mycorrhizal partners (a). As a consequence, aquatic systems receiving phosphorus inputs from terrestrial systems with lower quality mycorrhizal partners have larger and more cyanobacterial blooms than do aquatic systems with phosphorus loading from terrestrial systems with higher quality mycorrhizal partners (b). See box 1 and the supplemental materials for details on the model structure and parameter values used.

quality. Third, transport of terrestrial microbes can influence downstream aquatic microbiome composition and serve as a signal of material sources to freshwaters. And fourth, anthropogenic activities prompt shifts in microbiome composition and structure, and can be propagated via links across traditionally distinct systems. Although numerous studies examine how microbiomes function within bounded systems, these hypotheses emphasize investigations exploring the connections and feedback between terrestrial and aquatic systems. Because microbes are ubiquitous and facilitate a wide range of ecosystem services, it is necessary to integrate the study of the interactions of microbiomes across environments to capture the complex network of feedback occurring across plants, soils, and aquatic habitats.

Studies addressing such hypotheses may produce dynamic, context dependent results, given that microbiome-mediated ecosystem services are changing in response to anthropogenic climate and land-use change across multiple temporal and spatial scales. Changing environmental conditions and agricultural, silvicultural, and land-use conversion practices introduce changes in soil structure, chemical composition, and microbial community structure and function (e.g., Fischer et al. 2014, Liu et al. 2016, House and Bever 2018). The functional and compositional response of soil microbes to these increasing disturbances remains unclear and therefore currently limits our ability to predict and manage microbiomes across land-use types (e.g., Billings et al. 2018). Successful environmental restoration, as well as sustainable food production, following disturbance may require management of microbiome composition and functions (e.g., Koziol et al. 2018).

To provide an example of how one might approach examining these cross-system hypotheses with greater specificity, we provide a basic conceptual model to illustrate the potential links between terrestrial microbiomes and aquatic function (box 1). This model illustrates the principle of how connections between terrestrial and aquatic systems can influence cyanobacterial blooms by investigating the conditions under which variation in the efficiency of mycorrhizal mutualism will influence the downstream water quality. In so doing, the model provides testable hypotheses, although substantial resources will be required to test those hypotheses. A key feature of this example is that it links the impact of terrestrial microbially mediated nutrient dynamics to terrestrial P inputs into the aquatic habitats. The model makes predictions related to the impact of terrestrial dynamics on aquatic dynamics on the basis of empirical measurements of land use and how they relate to P loading into aquatic systems. The model does not mechanistically describe the complexities of nutrient transport itself, and consequently, a more complex model would be required to evaluate how different agricultural practices and their associated microbiome functions would alter P transport. We provide this example because it illustrates the benefits of future research establishing a mechanistic understanding of how

microbiome links across habitats influence ecosystem services valued by humans.

Ample evidence demonstrates that microbiomes influence ecosystem functions and services. By highlighting how microbiomes of plant and soil systems can govern elemental fluxes into aquatic systems, we illuminate how interactions among microbiomes and their habitats mediate many of the services that are essential to humans, including plant productivity and diversity as well as soil nutrient retention. Published data also support our hypothesis that microbial diversity and processes in terrestrial and aquatic environments influence downstream water quality, and that transport of terrestrial microbes can influence downstream microbiome functions. However, we make this statement realizing that much of the published research is on row-crop agriculture or natural systems. There is a significant need to research urban ecosystems, silviculture, grazing, and other industrial activities to increase understanding of the fundamental relationships between terrestrial and aquatic microbial communities in these systems, as well as their effects on water quality.

Conclusions

Despite the breadth of current knowledge within plant, soil, and aquatic microbiomes, studies directly linking these processes across habitats are scarce. Furthermore, anthropogenic activities shift microbiome composition and structure in ways that influence links across these systems. Because of the intimate link between these habitats, a change in any component of the microbiome can have profound effects on a variety of ecosystem services provided by these microbiomes. Motivated by the necessity of increasing our understanding of these effects, we provide a conceptual framework for future studies examining how climate and land-use change affects microbiomes, and therefore the influences on plant productivity and diversity, soil nutrient retention, and water quality. We emphasize that a future focus on the interactions within and among plant, soil and aquatic microbiomes is critical to predicting and managing the inevitable consequences of climate- and land-use-induced changes to our world to preserve ecosystem health and improve human welfare.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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