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Chapter 14.

Precipitation partitioning—Hydrologic highways between microbial communities of the plant microbiome?

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Abstract: There are multiple distinct habitats for microbiota inhabiting the plant microbiome (phyllosphere, endosphere, litter, rhizosphere) and habitats that act as additional sources (and sinks) of microbes and nutrients for the plant microbiome (atmosphere, pedosphere, bedrock, and fauna). These habitats harbor distinctive microbial communities that differ in structure, composition, function and spatiotemporal dynamics. Each habitat also differs in the mechanisms that provide "gateways" of exchange of microbes (and microbial products) between two communities, or in their access to "highways" that connect multiple communities. Of the environmental processes driving microbial community exchanges, precipitation events seem to represent the only one highway that can connect all the above-mentioned habitats—the "hydrologic highway." When precipitation contacts plants, it is partitioned into interception (water stored on, and evaporated from, plant surfaces), throughfall (water that drips from canopy surfaces and through gaps), and stemflow (water that is drained down the stem). This chapter describes the ways that precipitation partitioning in vegetated ecosystems (into interception, throughfall and stemflow) may connect microbial communities from the top (atmospheric boundary layer) to the bottom (bedrock face) of the critical zone via these hydrologic highways.

Keywords: throughfall, stemflow, ecohydrology, bacteria, fungi, archaea, plant microbiome.

14.1. Introduction.

The biogeochemical functioning of vegetated ecosystems depends on soil properties (i.e., mineral parental material, pH, and nutrient availability) and the activities of the biosphere, including plants, macro-(earthworms, insects) and microorganisms (protists, amoebae, fungi, bacteria and archaea). In recent decades, our ability to explore the abundance, composition, function, and dynamics of soil organisms has achieved an extraordinary level of detail. This is especially the case for microorganisms like bacteria, archaea and fungi, for which the development of high throughput sequencing methods was a real revolution. This has permitted and motivated research examining combined genomic information associated with all plant-related habitats, called the "plant microbiome" (Berg et al. 2014; Pérez-Jaramillo et al. 2018). Across vegetation-dominated ecosystems, there are multiple distinct habitats for microbiota that inhabit the plant microbiome (phyllosphere, endosphere, litter, rhizosphere) and that serve as sources of immigrants to the plant microbiome (atmosphere, pedosphere, bedrock, and fauna: Figure 14.1), all of which harbor taxonomically distinctive microbial communities that differ in abundance, function and spatiotemporal dynamics (Baldrian 2017; Turner et al. 2013). Each habitat also differs in environmental properties that influence the establishment and survival of microbial organisms, including: nutrient availability, radiation exposure, substrate texture, humidity, etc. Exchanges of microbes and microbial products may occur between two communities at physical or chemical "gateways"—e.g., effectors that mediate rhizo-endosphere interactions (Rovenich et al. 2014). Multiple environmental processes, however, can establish "highways" enabling interaction between multiple communities—e.g., aeolian action aerosolizing microorganisms from the phyllosphere to the atmosphere, which may then enter another habitat, like litter, via deposition (Morris et al. 2014b).

Few environmental processes can connect more than two or three habitats within a mature plant microbiome—as a seed more connections are possible (Nelson 2018). It may be that precipitation events represent the only one that can connect all habitats. Briefly, precipitation contains bioaerosols (Morris et al. 2014a), which interact with leaf and stem surfaces when draining to the litter (Chapters 4 and 5). Net precipitation fluxes are further partitioned in the litter, being stored, evaporated and elementally altered by litter decomposition (Chapter 11). Net precipitation then percolates through the pedosphere (Li et al. 2009) and rhizosphere (Johnson and Jost 2011), introducing suspended microbes, and their lysates and exudates, from every preceding habitat. Thus, this "hydrologic highway" may connect the atmospheric microbial community to the very bottom of the critical zone to the bedrock interface, via preferential flow paths through the soil matrix (Backnäs et al. 2012). All along the way, pathogenic and mutualistic microbes within net precipitation will pass gateways to the endosphere—like leaf stomata, stem lenticels, and root hairs. Few studies have examined how net precipitation, water storage and evaporative dynamics within and from vegetation elements relate to any aspect of microbiota throughout the plant microbiome. Insights from these few studies are further limited by "fingerprinting" methods that permit only coarse comparison of microbial communities, providing no taxonomic information (Moore et al. 2016; Rosier et al. 2016; Rosier et al. 2015); yet, more recent methods can yield detailed taxonomic data (Reuter et al. 2015). Therefore, we explicitly acknowledge this chapter's theoretical nature and hope it will inspire future research regarding the influence of precipitation partitioning on the plant microbiome. We begin with an introduction to the microbially-relevant aspects of precipitation partitioning, then the following sections describe major known and hypothetical effects of precipitation partitions on the habitat properties and processes of each sphere, including animal-associated microbiomes.

14.1.1. Microbially-relevant aspects of precipitation partitioning.

Precipitation interacts with plant canopies, where it is stored (Chapter 2), evaporated (Chapter 3), and redistributed to the surface in a spatially heterogeneous manner (Chapter 6). Precipitation reaches the surface as: (i) throughfall consisting of precipitation that falls through gaps and from canopy surfaces and (ii) stemflow consisting of precipitation that is entrained on branches and drained to the stem base (Chapter 4). Throughfall and stemflow are then stored, evaporated and chemically enriched in the litter layer (Chapter 11). The storage, evaporation and drainage of precipitation via throughfall and stemflow, despite being rarely considered in plant microbiome research, have clear relevance to microbial ecology. Most obviously, they represent a significant water supply to above-ground microbial communities, like water stored on or in foliage, bark, epiphytic vegetation, tree holes and litter. Subsurface microbial communities can exploit longer-lasting soilwater supplies; yet, throughfall and stemflow replenish soilwater resources (Guswa and Spence 2012; Návar 2011). Throughfall and stemflow provide water flows that may disrupt microbial communities by washing plant surfaces with hundreds of liters flowing rapidly through the canopy in <0.25 h (Keim and Link 2018; Keim and Skaugset 2004). Net precipitation and stored water contain dissolved nutrients and suspended particulate matter (Chapter 5) that, depending on concentration and chemical constituency, may nourish or stress microbes. Microbiota may rely on dissolved nutrients in net precipitation waters, having been found to consume ~90% of dissolved organic matter transported by throughfall and stemflow within 1-4 days, for example (Howard et al. 2018). Finally, evaporation from wet canopy and litter surfaces exerts a significant influence over humidity dynamics throughout the plant microbiome (Pypker et al. 2017; Van Stan et al. 2017b). Pathogenic disease susceptibility depends on a "triangular

interaction" between microbial pathogens, plants and environmental factors, called the "disease triangle" (Stevens et al. 1960), within which the role of humidity has been well researched (Colhoun 1973; Huber and Gillespie 1992). However, the importance of storms in pathogenic plant-microbe interactions beyond pathogen dispersal has only recently gained attention (Aung et al. 2018); which is surprising considering that conditions during precipitation partitioning may represent a triple-threat—open stomata, high humidity, and increased pathogen mobility along within-canopy flow paths (Davidson et al. 2008; Garbelotto et al. 2003). Thus, the following sections focus on water storage, evaporation, throughfall and stemflow as the relevant precipitation partitioning factors interacting to form hydrologic highways between the microbial communities of the plant microbiome.

14.2. Atmosphere

Precipitation connects the microorganisms of the atmosphere with the microbiomes of plants, soil and water. Given that it is difficult to identify clear distinctions between the component members of each of these different microbial communities, it would be more precise to state that precipitation transports microorganisms between the air, plant surfaces, soil, surface water and ground water. Precipitation that is partitioned as it falls through plant canopies concerns Earth's continental surfaces (rather than oceans). For the air over continents, the microorganisms that are aloft originate mostly from vegetation (Carotenuto et al. 2017; Fröhlich-Nowoisky et al. 2016; Lindemann et al. 1982). In urban centers, various anthropogenic features can also be important sources of air-borne microbial assemblages whose composition is subsequently influenced by the chemistry of the air and by extreme heat events typical of "urban heat islands" (Fang et al. 2018; Pyrri and Kapsanaki-Gotsi 2017). The various microorganisms that are aerosolized by active or passive mechanisms from land cover are readily lofted into the atmosphere, transported mostly by

turbulent wind (and other factors, see Edmonds 1979; Morris et al. 2014b). If microorganisms are lofted out of the planetary boundary layer and into the free atmosphere, they can travel very long distances and eventually mix with microorganisms such as viruses that more typically are emitted from ocean surfaces (Reche et al. 2018). Therefore, the tropospheric air column above any particular continental site will typically contain microorganisms in the boundary layer that are mostly of local origin overlaid with microorganisms that are moved with the air masses that transport clouds in the free atmosphere. For the return trip back to Earth's surface, deposition of these living particles occurs as gravitational settling, molecular diffusion, impacts onto surfaces (like vegetation), or by precipitation through rainout and washout (Edmonds 1979). For example, total "dry" deposition of viral particles has been observed on the order of 10^9 viruses m^{-2} day^{-1} (Reche et al. 2018). Although this quantity is impressive and greater than the number of bacteria dry-deposited under the same conditions (Reche et al. 2018), it is likely due to the immensely greater size of the total population of viruses on Earth and hence in the ensemble of its habitats compared to other microorganisms. The various forms of liquid or solid water in the atmosphere– rain, fog, or snow – are very effective downward highways for microorganisms in the atmosphere. The effectiveness of these atmospheric hydrologic highways depends on the capacity of the microorganisms to get on board.

14.2.1. Atmospheric "on-ramps" to the hydrologic highways

There are essentially two main "wet" deposition processes that allow air-borne microorganisms to get on board (or become "scavenged" by) the atmospheric hydrologic highways that will bring them downward: rainout and washout. Rainout is the incorporation of microorganisms into raindrops as they form in clouds. In temperate regions of the world, rain drops

form via the aggregation of super-cooled droplets on an ice crystal. Ice nucleation-active bacteria can catalyze the freezing of cloud water at temperatures warmer than most other atmospheric ice nuclei, thereby making initial ice crystals for rain drop formation, and can be considered to actively assure their integration into rain drops (Morris et al. 2013; Stopelli et al. 2017). As the droplets aggregate, any other microorganisms in the cloud water (Amato et al. 2017; Amato et al. 2007; Wei et al. 2017) will be assembled into the forming drops. The growing aggregates are initially solid, and their crystalline form is influenced by the conditions (temperature in particular) under which they form. As they fall, they can melt into rain drops depending on the temperature along the fall. Snow flakes and rain drops can bump into microorganisms in the dry air as they fall, allowing them to incorporate more particles in a second scavenging process called washout. The efficiency of washout in amassing microorganisms into falling precipitation depends on the probability for encounter between the hydrometeors (drops or flakes) and the air-borne microbial particles. Encounters with larger particles are more likely than with smaller particles (McDonald 1962) and especially when such particles are not rare in the trajectory of the falling hydrometeor. The importance of particle size is evident in the positive effect of rainfall on bacterial deposition; whereas, there is a lack of influence of rainfall on viral deposition (Reche et al. 2018). Although rain drops clearly scavenge microorganisms as they fall—as illustrated with simulated rainfall using water that was sterile at the beginning of the fall (Hanlon et al. 2017)—scavenging is likely to contribute more to the diversity than to the quantity of microbes in precipitation as direct counts of bacteria in cloud water and in rainfall across a range of studies reveal concentrations ranging from 10^3 to 10^5 cells mL^{-1} for both types of waters (Hu et al. 2018).

The combination of these two wet deposition processes for accessing downward hydrologic highways results in highly diverse mixtures of microorganisms that reflect the range of trajectories

and origins that contribute to the falling microbial assemblages. For example, in monsoon rains the relative abundance of *Pseudomonas* was highest during the south-west monsoon (75%) whereas *Pantoea* was abundant in the north-east monsoon (51.8%) (Akila et al. 2018). Likewise, for rain landing in high mountain "pristine" lakes in Austria, rain from events with Atlantic or continental origins were dominated by Betaproteobacteria, whereas those with Saharan dust storms were dominated by Gammaproteobacteria (Peter et al. 2014). It was shown that *Pseudomonas* is able to generate rain as a result of proteins that enable Gram-negative bacteria to promote nucleation of ice at relatively high temperatures, above -5 °C (Gurian-Sherman and Lindow 1993). These proteins are localized at the outer membrane surface and apparently play a role in the initiation of precipitation (Möhler et al. 2008) and can cause frost damage to many plants after deposition on the canopy. For fungi, for example, rainfall deposits classes that are not seen during dry deposition, like Agaricomycetes and Sordariomycetes (Woo et al. 2018). For specific microbial species such as *Pseudomonas syringae*, its presence in rain or snowfall collected in France was markedly enhanced by air masses from oceanic or Mediterranean origins that were not subjected to extreme negative temperatures; whereas, *Botrytis cinerea* in the same precipitation samples was not influenced by these parameters (Monteil et al. 2014). The composition of rain in terms of functional groups of microorganisms, and especially those that are ice nucleation active, can also be influenced by the physicochemical conditions of the hydrologic highway. The ice catalyzing bacteria that are active at the warmest temperatures will be the first to fall as rain forms in clouds (Pouzet et al. 2017; Stopelli et al. 2017; Stopelli et al. 2015) as long as their activity is not damaged by acidic conditions (Attard et al. 2012). Fog droplets also contain microorganisms whose composition is influenced by local sources (Evans et al. 2019). This reflects how fog forms – as condensation of water vapor in the planetary boundary layer. Fog capture and drainage by

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vegetation can represent a substantial water supply to the surface (Sampurno Bruijnzeel et al. 2006), transporting the microorganisms with them.

14.3. Phyllosphere

The "phyllosphere" refers to all above-ground surfaces of a plant (Ruinen 1956), such as flowers, fruits, branches, stems, epiphytic vegetation and leaves; however, most microbiological research has focused on leaves. The global leaf surface area alone has been estimated at ~1 billion km^2 and to host 10^{26} bacterial cells (Vorholt 2012). Global phyllosphere surface area and microbial abundance is likely larger as global bark surface area, estimated similarly to Vorholt's (2012) leaf area (sum of stem area from land surface model input data: e.g., Mendoza et al., 2015) is ~41 million km^2—or, nearly as large as the Asian continent! Epiphytic vegetation is ubiquitous across ecosystems, representing an additional 2-9,865 kg ha^{-1} of biomass (Zotz 2016). Moreover, some plant surfaces can pool and store precipitation, creating sub-habitats in the stem (called dendrotelmata) and on leaves (called phytotelmata).

14.3.1. Leaves

Plant leaves are covered by a cuticle, a polymer of long-chain aliphatic compounds that is embedded with (intracuticular) and overlaid by (epicuticular) soluble waxes (Zeisler-Diehl et al. 2018). Due to the hydrophobic (water repellent) nature of the cuticle, leaf surfaces are often self-cleaning, leading to aerial depositions being washed off during rainfalls (Barthlott and Neinhuis 1997; Neinhuis and Barthlott 1997). The cuticle serves as a barrier to limit loss of water and solutes from the apoplast to the leaf surface. Notably, the cuticle barrier is heterogeneous and different sites on the leaf surface are more or less susceptible to water and solute loss (Remus-Emsermann

et al. 2011; Schlegel et al. 2005). Leaf cuticle characteristics also, in large part, determine how precipitation will be partitioned into interception, throughfall and stemflow (Crockford and Richardson 2000; Holder and Gibbes 2017).

Another unique feature of the phyllosphere are the heavily fluctuating physical conditions: (i) The temperature on the same leaf may fluctuate more than 20 °C within a few hours (Yu et al. 2018). (ii) In temperate conditions, water availability is usually low on leaves due to their exposed nature and hydrophobic properties, even though it has been proposed that leaves may often retain microscopic amounts of water (Burkhardt and Hunsche 2013). However, during rain events, leaves will be flushed by ample amounts of water. (iii) Lastly, most trees and shrubs in temperate environments will shed their leaves once a year.

Physicochemical conditions strongly influence the microbial colonizers of the phyllosphere, which include oomycetes, fungi and bacteria (Agler et al. 2016). Bacteria dominate this environment and reach up to 10^8 colony forming units per gram of leaf material and cover about 5% of the leaf under temperate conditions (Remus-Emsermann et al. 2014). Microbial colonizers have different means of reaching the phyllosphere, depending on the plant species and the colonized organs. For annual plants that live close to the ground, such as the model plant *Arabidopsis thaliana*, initial colonizers are recruited during germination of the seed by the surrounding soil microbiota or the air (Bai et al. 2015; Maignien et al. 2014). During this stage, phyllosphere colonizers are selected by the leaf environment and dominate the phyllosphere microbiota thereafter (Maignien et al. 2014). Due to the yearly leaf fall on many plants, this cycle will re-occur every year when leaves re-emerge. This is why the species composition of plants' phyllosphere microbiota may differ from year-to-year, while it remains similar at lower phylogenetic resolutions (Vorholt 2012). The immigrants on freshly-emerged leaves either

originate from wind distributed soil particles or microbiota of surrounding vegetation where microorganisms were aerosolized (Lymperopoulou et al. 2016), or animal vectors such as foraging insects (Kovach et al. 2000). Once the first leaves are colonized, leaves that are emerging later are most likely colonized by microorganism from the same plant that are being dislodged by water and move via throughfall and stemflow or that are aerosolized and move with the air turbulences.

On a leaf scale, water droplets often adhere to trichomes, epidermal cell grooves and in the grooves along the nervature of leaves (Wang et al. 2015). On the micrometer scale, which is relevant to bacteria, water relationships are difficult to study and are not well understood (Beattie 2011). At an individual bacterium scale, it was found that bacterial bioreporters for water stress reported heterogeneous distributions of water stress conditions on bean leaves (Axtell and Beattie 2002). At the scale of an individual leaf, fungal infection (by *Erysiphe alphitoides*—the cause of powdery mildew) has been found to alter leaf water storage capacity, which may influence total rainfall interception (Klamerus-Iwan and Witek 2018). Fungal conidia from leaves (as well as bark and atmospheric sources) can be transported to other organs in the phyllosphere (and beyond) by throughfall and stemflow hydrologic highways (Gönczöl and Révay 2004; Magyar et al. 2016).

Phyllosphere microbiota thrive on soluble nutrients leached from the apoplast of leaves to the phyllosphere (Mercier and Lindow 2000; Remus-Emsermann et al. 2011; Ryffel et al. 2016; Shiraishi et al. 2015; Tukey and Mecklenburg 1964). Bacteria may increase the rate by which soluble compounds leach to the leaves by producing surfactants (Knoll and Schreiber 2000; Schreiber et al. 2005) and phytohormones (Ali et al. 2009; Dhandapani et al. 2016). Bacteria will also change the composition and reduce the concentration of nutrients in leachates (Mercier and Lindow 2000). However, thanks to the heterogeneous nature of leaves and the incomplete and segregated colonization by bacteria (Remus-Emsermann and Schlechter 2018) it is unlikely that

nutrients will be depleted completely. Leachates are redistributed via throughfall and stemflow within the phyllosphere and are lastly flushed into the litter layer and finally the pedosphere (Bittar et al. 2018).

14.3.2. Accumulation areas in the phyllosphere (bark, treeholes and epiphytes)

Little work focuses on microbiota on non-leaf elements of the phyllosphere; however, many of the particles travelling along canopy hydrologic highways do not reach the ground, but concentrates in canopy "accumulation areas," like bark fissures (Magyar 2008), tree hollows, or dendrotelmata when filled with water (Gonczol 1976; Gönczöl and Révay 2003; Magyar et al. 2017a; Sridhar et al. 2013), and epiphytes (Karamchand and Sridhar 2009; Sridhar et al. 2006). Much of the trapped organic matter is not microbiota, but leaf litter, twigs, anemochorous seeds and inflorescences (Chauvet et al. 2016) and microlitter (Carroll 1981) that is rich in various nutrients (Schroth et al. 2001), creating a crown humus deposit capable of higher fungal richness than forest floor soil (Cardelús et al. 2009). The accumulation areas store precipitation water for some hours or even weeks, creating aqueous microhabitats, particularly for dendrotelmata in tree holes (Magyar et al. 2017b). Water retention can also be substantial and longer-lived in epiphytes (Porada et al. 2018) and bark. Bark, for example, can store up to 700 L tree^{-1} (Van Stan et al. 2016) and experience evaporation rates typically lower, ~8-13%, than those experienced by leaves (Van Stan et al. 2017b). Particles transported by draining precipitation are consumed by saprotrophs, mostly by fungi and, thus, this subsection focuses on fungi; but bacteria, rotifera, amoebae, nematodes and insect larvae should also be mentioned as 'coworkers' in converting such debris into crown humus. In fact, mosquito larvae in stemflow-supplied tree holes (which are important vectors of human and animal pathogens) not only process canopy debris, but can alter the bacterial

and fungal community (Kaufman et al., 2008). From a mechanistic point of view, accumulation areas could be regarded as a sink of airborne particles trapped by plants where the stemflow hydrologic highway powers a self-cleaning system. Accumulation areas in plant canopies have surprisingly complex food webs (Figure 14.2) where the contribution of fungi is, again, important (Vass and Magyar 2013).

Only a few studies since the 1970s have examined the relationships of fungi with bark, epiphytes and tree holes, and the hydrologic highways connecting them (Gonczol 1976; Gönczöl and Révay 2003; Karamchand and Sridhar 2008; Kladwang et al. 2003). A recent long-term (5-year) observation of a tree hole in Budapest, Hungary found resident fungal species had various origins, but was dominated by spores known to be transported by stemflow and throughfall (Magyar et al. 2017b). Nevertheless, these transported fungi might have low competitive ability in aquatic habitats or serve as food for invertebrates such as insect larvae living in the tree hole (Vass and Magyar 2013). Tree hole fungal community composition varied significantly between years and interannually, likely as a result of changes in the frequency and stochasticity of stemflow and throughfall in tandem with variability in the quantity and quality of litter input, as the major energy source in such systems (Magyar et al. 2017b). The length of periods between stemflow events (i.e., age of stagnant water) may be an important factor on fungal species composition of tree hole ecosystems, which merits further studies (Vass and Magyar 2013). Also meritorious of future research is the potential for interactions between fungi, tree holes and storms to facilitate recolonization of organic matter in the forest floor. Studies of leaf litter in tree holes confirmed them to be permanent habitats of water-borne hyphomycetes (Gönczöl 1976; Gönczöl and Révay 2003). Such tree hole fungi may facilitate recolonization of organic matter when transported by hydrologic highways to the forest floor.

Hydrologic highways on the bark surface follow the bark topography, filling cavities and forming small temporary ponds (dendrotelma) where transported particles are accumulated. Considering large surface area of the bark of some tree species (especially those having complex, multilamellate structure), the number of accumulation areas in fissures and cracks enables storage of a vast number of spores (Magyar 2008). However, further studies are needed to calculate bark surface area of different tree species—see studies like Van Stan et al. (2010) or Sioma et al. (2018)—and its capacity to trap spores. Moreover, the bark itself is a substrate for many fungal species in stemflow. Large colonies of dematiaceous hyphomycetes often occupy deeper parts of bark fissures (Magyar 2008): *Bactrodesmium*, *Camposporium*, *Menispora*, and *Sporidesmium* are common there (Magyar, unpublished). Such large dematiaceous hyphomycete colonies seem to facilitate the deposition of waterborne particles. Waterborne spores of some apparently fungicolous species (*Spermosporella* sp., *Titaea complexa*, etc.) are often seen to anchor and develop on conidiophores and spores of these fungi (Magyar 2008).

Arboreal epiphytic and parasitic vegetation is ubiquitous across ecosystems and can accumulate higher quantities of litter and humus than those lacking such association, e.g., *Borassus* and *Cocos* accommodate orchids and ferns (Ghate and Sridhar 2015). Some epiphytic plants, like 'oak-leaf basket fern' (*Drynaria quercifolia*), a dominant fern in Western Ghats and west coast of India, access nutrients through accumulated materials from rainwater drainage along stems (Sridhar et al. 2006). "Tank" forming epiphytic plants (bromeliads) also form miniature detrital ecosystems that may host a variety of microbes transported by precipitation-related hydrologic highways through the canopy (Brouard et al. 2012; Kitching 1971). These reservoirs may also overflow and transport microbes to the litter layer below.

14.4. Detritusphere

The sphere that consists of dead litter on the soil surface and in soil depth (the "detritusphere") is one of the densest microbial habitats in terrestrial ecosystems, and this is especially pronounced in forest litter layers. The detritusphere in forests consists of litter at various decomposition stages, usually from 0 to ~5 years old, but also older tree twigs and stems can be present, especially in the bottom part. The detritusphere contains some 3-10 Mg C ha^{-1}, and has a very wide C:N:P ratio. The last fact results from (i) litter origin: the most limiting nutrients (including N, P and base cations) are resorbed to the plant from the leaves before dying (Aerts 1996), and (ii) the first step of its decomposition: intensive leaching of nutrients and base cations from the litter (Chapin et al. 2002). The wide range in C:N:P ratio shows not only a strong N and P limitation, but also reflects the high hydrophobicity of the detritusphere in forests. This hydrophobic, N and P limitation represents a direct connection between C and nutrient fluxes, specific microbial communities in the detritusphere, and water fluxes from throughfall and stemflow. In fact, the functioning of microbial communities in the detritusphere is completely dependent on moisture supplied from the plant canopy's redistribution of precipitation as canopies are the "functional interface" between the atmosphere and up to 90% of Earth's terrestrial biomass (Ozanne et al., 2003).

The first step of litter decomposition in the detritusphere is mainly mediated by insects grinding and chewing the cell walls. Therefore, this stage itself is not strongly dependent on throughfall and stemflow moistening the litter, because (i) fresh litter is partly moist (not completely dry), (ii) the litterfall occurs in autumn when precipitation and air moisture are typically high compared to other times of year, and (iii) insects are much less dependent on moisture compared to fungi and especially to bacteria. Because of cell wall destruction, the cytoplasmic

compounds—mainly proteinic compounds including various endoenzymes—will be fast leached from the detritusphere to the mineral soil surface. Here, on the soil surface, various pathways of these compounds are common. The low molecular weight organic compounds will be immediately trapped (Fischer et al. 2010) and utilized by microorganisms, mainly by bacteria (van Hees et al. 2005). An important part of released enzymes will be stabilized on mineral surfaces, where their functions for decomposition of organic substrates lasts for some weeks up to a few months (Schimel and Schaeffer 2012). Mineral N and P released by decomposition of organics will be intensively utilized in this and bottom soil layers. The cations (mainly K^+, Mg^{2+}, Ca^{2+}) released from cells will be leached into deeper soil layers, especially where TF drip points are temporally consistent in supplying substantial water fluxes (Keim et al. 2005) and close to any plant stems producing voluminous stemflow (Van Stan and Gordon 2018). Consequently, the C, nutrients, and enzymes released at the first stage of litter decomposition, and mobilized via throughfall and stemflow, will have strong impacts on the processes and microbial communities in the topsoil and partly in the subsoil.

The second step—decomposition of the remaining cell walls (mainly cellulose and lignified compounds)—is performed mainly by fungi. Fungi release not only hydrolytic enzymes (as bacteria do), but also oxidases and peroxidases. These enzyme groups are very efficient at decomposing high molecular-weight compounds under highly oxidative conditions, and this is another direct link to local moisture supply from net precipitation. Close to the stem, stemflow can preferentially infiltrate (Johnson and Lehmann 2006) and the water input can be higher, but the drainage is more intensive as this part of the soil and detritusphere litter is lifted by many roots. So, these areas of the detritusphere have large water inputs and well-oxidated conditions, leading to faster litter decomposition – on this stage – mainly by fungi. Another important advantage of

fungi decomposition, especially in the detritusphere, is that fungal hyphen can reach locations without water, like areas between non-densely packed litter. This is huge advantage of fungi compared to bacteria as it allows them to reach substrates even when disconnected from hydrologic highways (in this case, "bridges"), like throughfall and stemflow.

The vertical layering of the detritusphere corresponds not only to the well-known degradation state of the litter, but also to litter moisture patterns. Specifically, the water content of the detritusphere increases from top-to-bottom because of: (i) lower water permeability of the mineral topsoil compared to the detritusphere; (ii) decreasing hydrophobicity and increasing hydrophilic bonds (-C OOH, =CO) with the progression of litter decomposition by oxidative enzymes; and (iii) lower transpiration losses from the deeper part of detritusphere. Overall, the vertical (within detritusphere) and horizontal (within the distance from the main trunk) patterns of water flux to the detritusphere (due to the canopy's redistribution of precipitation into throughfall and stemflow) play significant roles in the decomposition rate of litter, to which insects, fungi and bacteria successively contribute.

14.5. Rhizosphere

The first few millimeters of soil surrounding roots host a unique microbiome compared to bulk soil (Prescott and Grayston 2013; Richter et al. 2007)—a microbiome that is made unique by plant selection from the more diverse microbial community in the bulk soil (Berendsen et al. 2018; Pieterse et al. 2016). The influx of moisture, nutrients and microbes from throughfall and stemflow hydrologic highways may influence the rhizosphere microbiome by (i) impacting the soil microbes available for selection by roots, (ii) providing nutrient subsidies in excess of root exudates, and (iii) engendering large spatiotemporal variability of edaphic conditions throughout the root system.

Fundamentally, rhizosphere development alters hydrologic processes during storms, compared to the bulk soil, as a result of autogenic environmental factors interacting with the above-ground partitioning of rainfall (Johnson and Jost 2011). Spaces in the soil surrounding roots are lined with root and microbial exudates that typically create hydrophobic margins around "rhizo-pathways" through the subsurface (Hinsinger et al. 2009; Jarvis 2007). During storms, net precipitation fluxes have been observed to enter and flow along these rhizo-pathways (Saffigna et al. 1976; Schwärzel et al. 2012; Spencer and van Meerveld 2016). As a result, the rhizosphere microbiome receives larger precipitation pulses and are bathed in the dissolved and particulate elements, including microbes, carried by throughfall and stemflow (Table 14.1). This is particularly true for the few voluminous stemflow generating trees (Van Stan and Gordon 2018), as they can concentrate substantial water flows at the base of the plant stem. Net precipitation effects on soil moisture and chemistry can influence microbial community structure in the bulk soil (Rosier et al. 2016; Rosier et al. 2015) and, therefore, may shape the rhizosphere at its beginnings—by shaping the microbial community from which plant roots select their microbial partners.

The greater microbial abundance and activity of the rhizosphere microbial community compared to those of the bulk soil is typically attributed to the abundance and diversity of C- and N-rich root exudates, like carbohydrates, amino acids and fatty acids (Baldrian 2017; Prescott and Grayston 2013). However, the dissolved organic matter in throughfall, stemflow and litter leachates is highly concentrated (see Chapter 8) and enhanced with carbohydrates and compounds with N-rich molecular formulae (Stubbins et al. 2017). Previous research on rhizosphere microbiota for model plants and crops indicates that many community members "cannot thrive on plant exudates alone" (Tkacz et al. 2015). So, perhaps the C- and N-rich supply of solutes from

net precipitation aid in supporting unique abundance and compositional aspects of the rhizosphere microbial community?

Spatial and temporal dynamics of rhizosphere microbiota are clearly connected with seasonal root dynamics (Shi et al. 2015), plant development (Chaparro et al. 2014), and soil disturbances (Tkacz et al. 2015). But, the amount and elemental composition of throughfall and stemflow also vary by orders of magnitude seasonally (Sadeghi et al. 2018; Van Stan et al. 2012), with plant development (Zheng et al. 2018) and with disturbances (Moore and Jackson 1989). Spatial dynamics in the rhizosphere may, therefore, be related to infiltration of net precipitation, as not all roots provide rhizo-pathways for throughfall and stemflow (Figure 14.3). Moreover, soils surrounding preferential subsurface flows of net precipitation are further enriched with nutrients as the organic acids carried by net precipitation fluxes can enhance weathering (Backnäs et al. 2012). Thus, soil conditions surrounding roots may vary according to variability in infiltrating net precipitation fluxes. As the amount and elemental composition of net precipitation can vary with storm conditions, most roots may, in reality, fall along a continuum of exposure to throughfall and stemflow—with some rhizo-pathways carrying net precipitation every storm and a few only during larger or more intense events.

14.6. Pedosphere: soils and bedrock

Hydrology is a major parameter in soil as it determines many biotic and abiotic processes and soil parameters. The quantities and frequencies of water input to the soil influence the soil solution, as well as its residence time with the different constituents and reactive interfaces existing within the soil (Van Breeman et al. 1982; Chang and Matzner 2000; Coenders-Gerrits et al. 2013). From the top-soil to the deep-soil, water is circulating, connecting different chemical gradients and

determining nutrient availability. Indeed, without water, most of the nutrients are immobile and unavailable for the biosphere. The physiological processes engaged by soil microorganisms are thus strongly affected by the water availability (Yan et al. 2015).

14.6.1. Hydrologic circulation conditions nutrient availability

The hydrologic circulation of chemical elements (protons, hydroxide, nutrients, cations, toxins) and complex molecules (sugars, amino acids, organic and inorganic acids, chelating compounds) through the critical zone directly affects the dissolution of soil minerals/rocks. When this circulation is perturbed, the dissolution rates are decreased. This is an important point to understand nutrient cycling into the soil. Without water, the quantities of exchangeable cations are limited, and the dissolution of minerals is stopped. When the soil is saturated in water, however, chemicals accumulate in the soil solution and the conditions tend to be anoxic. In other words, soil hydrologic processes, many of which are linked to the infiltration of precipitation via throughfall and stemflow, can condition mineral weathering and nutrient availability (including both organic nutrients and nutritive cations).

14.6.2. Soil properties and landcover determine the soil and plant microbiome

All mineral weathering and nutrient availability processes are, however, impacted by the action of the biosphere and especially of the plants, which modify hydrologic processes at local and regional scales. The presence of vegetation on a soil is known to modify the quantity of precipitation water coming from the atmosphere to the soil, its chemical composition, but also the quantity of water circulating into the soil due to the plant roots' water uptake and routing of throughfall and stemflow. Different plants in similar soils will differentially impact the soil

parameters including water, nutrient availability, pH and microbiome composition (Augusto et al. 2002; Uroz et al. 2016). A common point of these plants is the selection of a complex microbiota at the surface of its root system (rhizosphere microbiota) and inside their tissues (endophytic microbiota), which contribute to the development, health and nutrition of their host. As noted earlier, the rhizosphere was evidenced in several studies as a reactive interface where specific microorganisms carry out functions beneficial to the host plant. Among these functions, we can point out the mineral weathering ability (i.e., ability to dissolve minerals and rocks), an essential process in which microorganisms contribute to the release of nutritive cations and anions from insoluble forms (i.e., minerals and rocks) and transfer them to the plant. Among the main actors of these two processes are fungi and bacteria (Landweert et al. 2001; Uroz et al. 2009). Notably, mycorrhizal fungi, which form symbiotic association with the plant roots are able to provide water and nutritious elements (P, cations), due to their ability to forage large volumes of soil. A single symbiotic fungus associated to the tree root system can explore several square meters, representing in this sense a good insurance for the tree host. Regarding the bacteria, the effectiveness and frequency of mineral weathering bacteria in the rhizosphere was shown to vary according to the seasons, potentially in relation to the nutrition status of plants, but also potentially to seasonal hydrologic variability (Collignon et al. 2011). Such changes are not evident in the bulk soil, highlighting an important role of the plant and the environmental parameters (i.e., climate, phenology, hydrology) in modulating the distribution of soil bacterial communities. In the rhizosphere environment, variations in water availability may allow for the selection of adapted communities. For mycorrhizal fungi, drought periods will favor species such as *Cenococcum geophylum*, which is well known to increase in abundance in low water availability conditions and present functional traits adapted to recover water (Jany et al. 2003; Di Pietro and Garbaye 2007).

For bacteria, drought in soil is known to favor Actinobacteria and spore-forming bacteria such as *Firmicutes* and *Bacillus* (Fierer et al. 2003; Hueso et al. 2012; Naylor et al. 2017). Recent development using labeled water (^{18}O) and DNA stable isotope probing has clearly evidenced how bacterial and fungal communities respond to desiccation and rewetting events (Barnard et al. 2013; Engelhardt et al. 2018).

14.6.3. The mineralosphere microbiome: conditioned by soil moisture?

Nevertheless, while the tree root zone presents specific features, it is not disconnected from the rest of the soil matrix. Indeed, tree root and their associated microbiota are connected to the organic matter and the minerals and rocks present in the soil. In shallow soils the root system can be connected to the bedrock, while it depends on the plant species in deep soils. Notably effective mineral weathering bacteria have been reported at the interface between the bedrock and the roots, suggesting that they actively participate in the nutrition of plants. In the context of a nutrient-poor soil, the connection of the plant root to the soil minerals plays an important role, as minerals represent the main source of inorganic nutrients. Indeed, soil minerals and rocks are formed of insoluble forms of base cations (Ca, Mg, K), microelements (Fe, Al) and other nutrients such as phosphorous. Most of these chemicals are important elements in nutrient-limited soils for the biosphere, both for microorganisms and plants. Beside their nutritional role, minerals and rocks have themselves been shown to select different microbial communities according to their physico-chemical properties (Colin et al. 2016; Uroz et al 2015). Part of this selection is explained by the intrinsic properties of the minerals, which can contain nutritive or toxic elements in their crystalline structure. These chemicals can attract or repulse specific microbial communities. Another important driving factor of these communities is related to the weatherability of these minerals.

Indeed, recent studies found evidence that poorly weatherable minerals were colonized by effective mineral weathering bacterial communities compared to easily weatherable minerals, suggesting the selection of competitive microbes in nutrient-limited conditions (Uroz et al. 2009; Uroz et al. 2015; Wilson et al. 2008). However, all these selective events are determined by the environmental conditions (i.e., the extrinsic parameters) and notably by the hydrology. Indeed, in poor water availability conditions—like throughfall "dry" spots where localized precipitation interception is high (Keim et al. 2005), or near-stem soils where stemflow production is nearly non-existent (Van Stan and Gordon 2018)—microbial communities may be modified, allowing to the selection of a part of the microbiome capable of dealing with desiccation (Naylor et al. 2017). Consequently, we may expect a suite of cascade events, which will modulate both the chemistry of the soil solution and the microbial communities and their biotic and abiotic interactions. Investigating this cascade requires work at the frontiers of our current understanding and capabilities. For example, little is known about the water availability of rock-associated microbiota and observations of microbial interaction with rocks and minerals are difficult to distinguish from the rest of the soil interface.

14.7. The plant endosphere

The plant endosphere refers to the microbiota colonizing the inner parts of the plant. It has been known for decades that fungi forming arbuscular mycorrhiza can colonize the root cortical cells (e.g., Smith and Read 2010). However beside arbuscular mycorrhizal fungi, many other fungi can colonize the plant roots (Lê Van et al. 2017; Vandenkoornhuyse et al. 2002; Vannier et al. 2018) along with bacteria (Bulgarelli et al. 2012; Lundberg et al. 2012; Vannier et al. 2018), archaea (Vannier et al. 2018) and micro-eukaryotes (Sapp et al. 2018). These microorganisms

inhabiting plant tissues are called endophytes. All plants are colonized by a complex microbiota (Vandenkoornhuyse et al. 2015) which interact with its host and provide additive ecological functions (Bulgarelli et al. 2013). Because endophytes can play key roles in a plant's ability to quickly adapt to environmental changes, endophytic microbiota are regarded as fundamental to plant environmental responses over both short and longer time-scales (Vannier et al. 2016). The microbial endosphere is less complex than the microbial rhizosphere (e.g., Vandenkoornhuyse et al. 2015), although, for both, soil and litter microorganisms act as microbial "seed banks" from which a plant can actively or passively recruit symbionts to buffer an environmental stress (e.g., Vannier et al. 2016). Endophytes are transmitted horizontally or vertically (Frank et al. 2017). It seems that an ascending migration of endospheric microorganisms from roots to leaves is predominant (Chi et al. 2005) and that precipitation partitioning is considered one of the abiotic major factors facilitating the vertical dispersal of endophytic microbes (Frank et al. 2017). Uncovering the rules of community assembly in the endosphere is a current hot research topic in microbial ecology.

14.7.1. Precipitation partitioning and the endosphere "rules of assembly"

The endosphere symbiotic community composition and partnership stability is explained by different hypotheses—see Vandenkoornhuyse et al. (2015) for review. The 'partner choice' induces immediate fitness benefits for both the host and microbe (Sachs et al. 2004), but requires complex signaling (which is known for only a fraction of microbiota) and is a consequence of coevolution processes. Alternatively or complementarily, the hypothesis of 'forced cooperative behavior' by reward/sanction processes (Kiers et al. 2003) allows the filtering of endospheric microorganisms based on cooperation level (Werner et al. 2014) as demonstrated in the case of

arbuscular mycorrhiza symbiosis (Kiers et al. 2003). Beside these hypotheses developed to explain the forces at place to build up the plant endosphere composition, the conundrum of assembly rules of the plant microbiota has also been addressed under the biogeography framework, aiming to identify drivers of spatial microbial heterogeneity. In the biogeography framework, several biotic and abiotic factors, including insects, wind, and precipitation are identified as drivers of spatial heterogeneity. The storage and drainage of precipitation via throughfall and stemflow are quite heterogenous between different plant species co-existing in a single environment (e.g., Van Stan et al. 2015). In fact, the role of ecohydrologic processes (of which precipitation partitioning is a part) in the plant endosphere's rules of assembly has been recently identified as a promising research frontier (Krause et al. 2017).

14.7.2. Heterogeneity of endospheric microbiota

Published works that focus on the endospheric microbiota of plants, highlight the existence of heterogeneity in the composition of the microbiota between plants of different species co-existing in a given environment (e.g., Lê Van et al. 2017). This heterogeneity in the composition of symbiotic communities may be related to transient associations while other microorganisms may form long-lasting interactions with vertical transmission (Cankar et al. 2005; Vannier et al. 2018) or pseudo-vertical transmission (colonization of the immediate vicinity of the mother plant allowing access to a similar pool of microorganisms) (Wilkinson 1997). If this is true, heterogeneity in endospheric microbiota implies a heterogeneity in the reservoir of microorganisms near the host plant (Vandenkoornhuyse et al. 2015) available to be recruited passively (neutral process) or actively (selective process) by the plant. The part of the plant's selective process of acquisition and/or filtration of microorganisms from the available reservoir

can condition differences in spatial structures, while the share of neutral processes explains a stochastic heterogeneity which is however dependent on the available microbial reservoir. Thus, what controls the spatiotemporal heterogeneity of the microbial reservoir?

14.7.3. Water displacement as a possible driver of endospheric microbiota

Microbial reservoir heterogeneity through time and space is partly explained by biotic interactions, like the type of plants present and microbial predation (micro/mesofauna and microbial viruses), as well as abiotic factors including, wind, moisture, shading, patches of nutrients, and so on (Vandenkoornhuyse et al. 2015). Little attention has been paid so far to the possible effects of microbial dispersion, including dispersion by water. Water displacement can be seen as a driver (or helper) of microorganisms' migration through various types of soil macropores ('highways' of microbial dispersion, like earthworm burrows; Jarvis 2007) but also through all the other water movements in soils. During plant growth, with the help of their arbuscular mycorrhizal fungi, plants uptake water close to their roots. By doing so, a water depletion area close to the roots is produced inducing passive horizontal fluxes of water to the water depleted zone. Together with solutes, it can be hypothesized that this phenomenon allows the transfer of microorganisms close to the rhizosphere and allows the enrichment of the microbial reservoir from which the plant can recruit microorganisms. An additional hypothesis is an existing network of small galleries formed by fungal hypha grazers, like collembola. Because a dense mycorrhiza hyphal network linked to roots exists, it can be suggested that hyphal grazers might engineer an oriented network of little galleries replacing the former hypha, allowing an easier microbial dispersion together with water displacement to roots. Under this framework, microbial heterogeneity is expected since dispersion is expected to be stochastic and everything could not be everywhere.

Although these hypotheses sound possible, as far as we know there is no experimental evidence supporting the idea that the plant endosphere composition could be, at least in part, the consequence of microbial dispersion mediated by water displacements. If, similarly as solutes, this microbial dispersion by water movements is possible, so is dispersion of microbial viruses. The understanding of the impact of viruses in the control of soil microbial community composition is clearly hypothesized (Kimura et al. 2008; Williamson et al. 2017); however, their significance in the plant microbiota endosphere is unknown.

14.7.4. Pathogens and the endosphere: Storms as a triple-threat in the disease triangle

Processes in precipitation partitioning are considered one of the major factors facilitating the dispersal of endophytic microbes—although the exact terms for precipitation interception, throughfall and stemflow are rarely used in this literature. It has long been recognized that rain can disperse microbes from infected plants to surrounding plants (Walker and Patel 1964). Rain drops generate bioaerosols, which allow the spreading of microbes from soil to plants at distance (Joung et al. 2017). Moreover, heavy precipitation may damage plant surfaces (Baker and Hunt 1986), creating entry ways for phyllosphere and rhizosphere microbes to gain access into the apoplast. Together, precipitation partitioning not only facilitates the dispersal of endophytic microbes, but also create opportunities for microbes to enter new host plants. In addition, heavy precipitation may temporarily alter the microenvironment around plants and change endophytic community structure. Most endophytes are beneficial or harmless to plants; however, pathogenic microbes can also reside within host plants without causing disease (Bacon and White 2000; Strobel 2018). Environmental conditions are another set of major constraining factors for disease outbreaks—and water is a key trigger for pathogenic microbes to promptly proliferate in the apoplast. The interplay

between pathogen, host, and environment, known as the 'disease triangle,' has been long established as crucial for understanding disease outbreak (Stevens et al. 1960). For example, a field study identified more endophytic fungi during the rainy season, when these hydrologic highways are naturally more active, for two tree species, *Tectona grandis* and *Samanea sama* (Chareprasert et al. 2006). The study of the life cycle of *Pseudomonas savastanoi* pv. *phaseolicol*a, a causal agent of bean halo blight, showed that rain magnitude and intensity largely contribute to the proliferation of the bacteria and disease outbreak (Hollaway et al. 2007; Marques and Samson 2016). In a controlled environment, water availability in the atmosphere, and thus higher relative humidity, greatly facilitates the proliferation of a bacteria pathogen of tomato, *Pseudomonas syringae* strain DC3000, in a host plant *Arabidopsis* (Xin et al. 2016). In addition to a dispersal pathway, the resulting high humidity from rainwater storage and evaporation provide a more accessible water source for endophytic microbes to proliferate. High humidity from precipitation interception also suppresses the function and activity of resistance genes and downstream signaling events (Aung et al. 2018), which may allow opportunistic microbes to become pathogenic. As a result, conditions during precipitation partitioning represent an environmental "triple-threat" in the disease triangle: (i) throughfall and stemflow provide dispersal pathways while the high humidity from intercepted precipitation (ii) facilitates bacterial pathogen proliferation and (iii) can enable opportunistic microbes to become pathogenic. Together, the effects of precipitation partitioning can create drastic changes in the endophytic community and promote disease outbreak in plants.

14.8. Animal-associated microbiomes

The forest canopy is the habitat of multiple species of amphibians, reptiles, mammals and birds. This habitat accumulates organic matter derived mainly from leaf litter, feces, and other

faunal remains. These residues are in turn, the nutrient source of thousands of arthropod species that have also found a niche at the top of plant canopies (Nadkarni 1994). As all other animals, canopy animals harbor symbiotic communities in their guts and their skins, which play vital roles in their growth and health, including immune system development, gut nutrition, and pathogen defense (Hacquard et al. 2015; Hooper et al. 2012). In addition, when animals die, they become a nutrient source for a diverse array of heterotrophic microbes. Thus, the canopy is also the habitat of microorganisms that play a part in ecosystem nutrient cycling (Nadkarni 1994).

Most of the animal-associated microbiome studies in wildlife have focused on describing bacterial diversity and determining the abiotic and biotic factors that influence these symbiotic microbiomes (Hayakawa et al. 2018; Jiménez and Sommer 2017; Kohl et al. 2017). In many cases, the ultimate purpose of these studies relies on the need to integrate the role of symbiotic microbiomes to implement conservation strategies for threatened animals, such as primates and amphibians (McKenzie et al. 2018; West et al. 2019). However, to date, there has been no work aiming to evaluate how these animal-associated microbiomes contribute to other microbial communities in the ecosystem. Moreover, it is unknown how hydrologic highways like stemflow and throughfall contribute to the transfer or movement of animal-associated microbial communities to plant and soil microbiomes. Below we will exemplify how animal-associated microbes could contribute to microbial communities that are transferred through the various hydrologic highways to plant and soil microbiomes.

The amphibian skin microbiome is known to play an important defense role against pathogens, since many of its bacterial members are known to produce antifungal metabolites (Harris et al. 2009; Woodhams et al. 2015). Recent studies have shown that the composition of the skin microbiome of many amphibians is highly enriched in bacterial taxa that are not common in

their surrounding environments: e.g., leaves, soil, and leaf litter (Fitzpatrick and Allison 2014; Rebollar et al. 2016; Walke et al. 2014). However, environmental bacteria are of great importance since these serve as a reservoir to maintain skin bacterial diversity (Antwis et al. 2014; Loudon et al. 2014). In addition, changes in precipitation throughout the seasons have been associated with changes in the composition of skin microbial communities in frogs (Familiar López et al. 2017; Longo et al. 2015; Longo and Zamudio 2017). This leads to two hypotheses (non-mutually exclusive) on how changes in precipitation affect skin bacteria. Changes in precipitation regimes (which lead to changes in stemflow and throughfall volumes) could modify bacterial reservoirs by transferring (or isolating) microbial communities across canopy strata, in turn affecting the diversity and function of skin microbiomes. An alternative (perhaps complementary) mechanism is that skin bacteria are directly washed away from their hosts by rain. In this way skin bacteria would be transferred to new environments and hosts (i.e., plant surfaces, soil) through the hydrologic highways.

Although skin microbiomes might be important contributors of the bacterial pool in forests, these have a far lower bacterial density in contrast with gut microbiomes (Sender et al. 2016). Studies on gut microbiome of insects, birds, lizards and primates have shown that diet is one of the most important factors shaping these symbiotic communities (Clayton et al. 2018; Kohl et al. 2017; Lucas et al. 2017; Waite and Taylor 2015). This would mean there is a constant flow of bacteria from the environment (available food) to animal guts and vice versa (Colston 2017; Shukla et al. 2018; Trevelline et al. 2018). We could hypothesize that changes in stemflow and throughfall produce changes in environmental reservoirs, which would then be linked to changes in gut microbiomes. Likewise, feces can contribute to the bacterial pool present in the canopy, where stemflow and throughfall would transport gut bacteria through different strata and hosts.

Animal carcasses can serve as an additional source of bacteria, since they provide an important nutrient source for environmental bacteria and necrophagous insects (Shukla et al. 2018).

In summary, animal-associated microbiomes may be transferred from the canopy to other plant and soil habitats in the ecosystem by changes in net precipitation fluxes. However, it remains to be determined whether skin or gut bacteria, along with their associated functions (i.e., antifungal capacities), can be successfully transferred across habitats (i.e., colonize and proliferate). Many key questions about the role of precipitation partitioning in the microbial community dynamics need to be explored: i.e., What proportion of animal symbiotic bacteria is present in hydrologic highways? What ecological functions are these bacteria playing in different habitats or hosts?

14.9. Conclusions.

We note that every section discussing interactions between precipitation-related hydrologic highways (interception, throughfall and stemflow) and each habitat in, and surrounding, the plant microbiome found little-to-no research on the topic. However, current theory indicates that future research is merited throughout the critical zone. Most work on interception, throughfall and stemflow has been rooted in hydrologic (Newtonian) research traditions, which often contrasts with ecological (Darwinian) research traditions. Resolving differences between these scientific world views has been a challenge for many integrated research areas (Harte 2002) and has been particularly problematic for the subdiscipline within which most precipitation partitioning research is executed—ecohydrology (Harman and Troch 2014; Newman et al. 2006). A result of most work on throughfall, stemflow and interception being more hydrology-oriented is that few studies have included manipulation experiments. However, manipulation experiments involving the removal or relocation of throughfall and stemflow will be necessary to explicitly address most questions about

how net precipitation water and elemental fluxes connect and influence habitat properties and processes across the plant microbiome. Experiments based on the use of isotopically-labeled water as presented in the pedosphere section would also represent a way to bridge the different compartments connected by these hydrologic highways. Thus, we suggest future research design and deploy ways of removing and relocating hydrologic highways during storms (for example, see Figure 14.4). We again explicitly acknowledge the theoretical nature of this chapter and hope that this discussion will inspire future research regarding the influence of storms on the plant microbiome.

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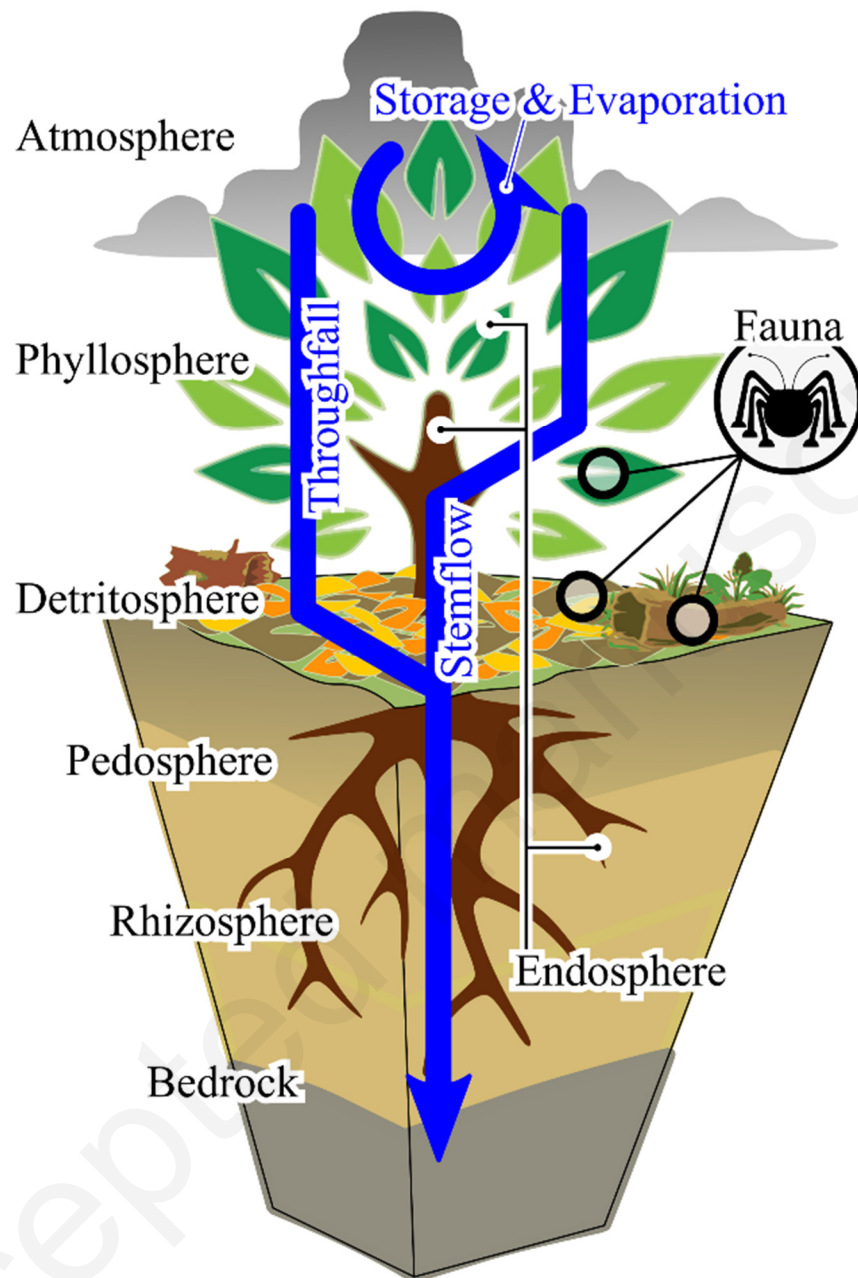
Figure 14.1. During storms, precipitation is stored or drained throughout the entire critical zone (from the atmospheric boundary layer to bedrock). Along the way, precipitation is partitioned while interacting across all habitats of the plant microbiome and those that serve as sources of immigrants to the plant microbiome.
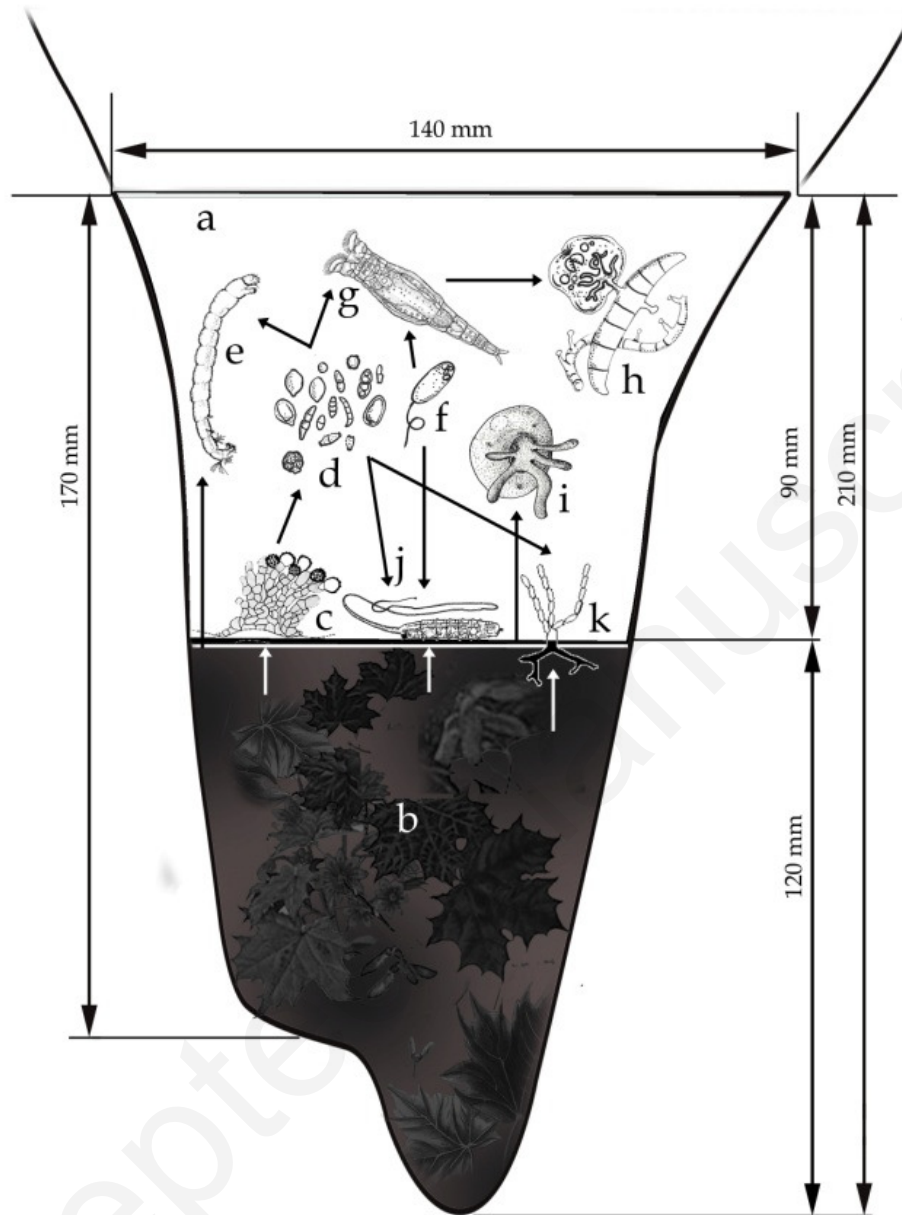
Figure 14.2. Water-filled tree holes in woody plants support a complex food web beneath (a) the water-level, which varies in response to precipitation dynamics. Hydrologic highways during precipitation not only supply moisture, but (b) detritus materials that support (c) saprophytic fungi, (d) fungal spores, (e) Chironomideae, (f) flagellates, (g) rotifera, (h) *Lecophagus muscicola* (a rotifer-capturing fungi), (i) testate amoebae, (j) larvae of *Eristalomya tenax*, and (k) actinobacteria.
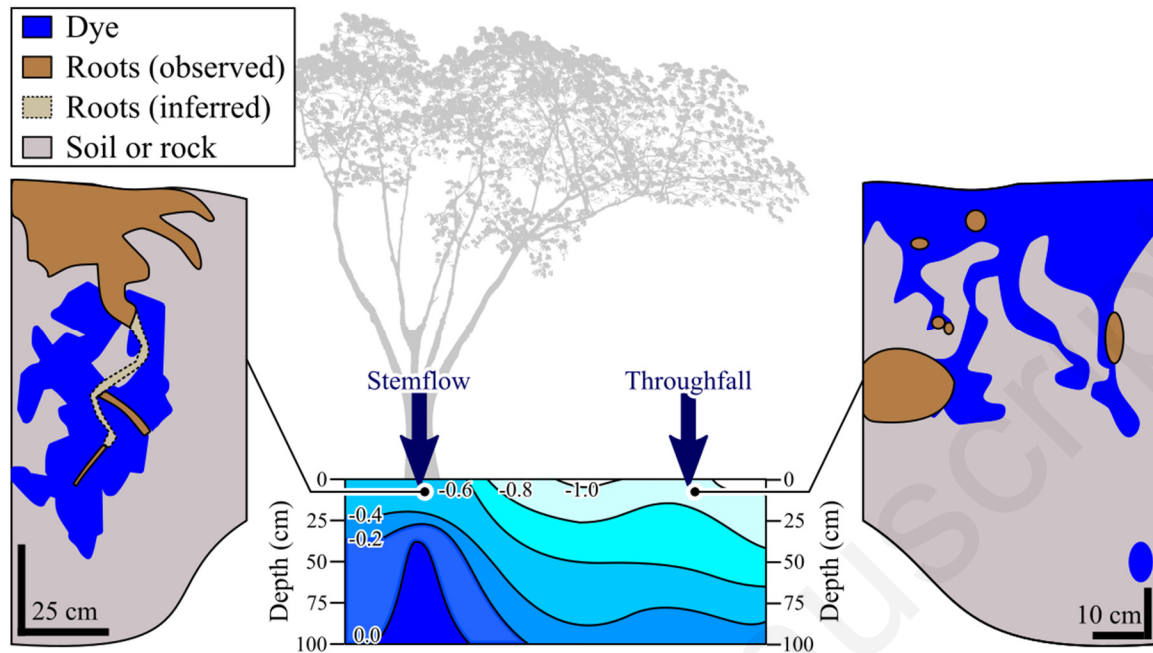
Figure 14.3. Soilwater potential monitoring and tracer dye mapping has identified spatially variable infiltration pathways linked to throughfall and stemflow. The center profile shows soil moisture patterns become concave beneath stemflow and throughfall drip areas; developed from data reported by Durocher (1990). Profiles on the sides, derived from data reported by Spencer and van Meerveld (2016), show some roots can channel net precipitation (those surrounded by blue dye), while others did not. Could this difference in moisture dynamics (and associated elements) drive significant spatial variability in the rhizosphere microbial community?

Figure 14.4. Manipulation experiments are needed to explicitly address research questions at the intersection of precipitation partitioning processes and the plant microbiome. This photo is an example stemflow collar outfitted to redirect flow to an area typically receiving throughfall (credit: John T. Van Stan, II). A video of SF redirection from this system is provided in the supplemental materials [https://youtu.be/AKhRV6Q7hGM].

Table 14.1. Materials suspended and transported by throughfall (TF) and stemflow (SF). Dashes indicate that the element was not measured.

Element	Concentration		Citation
	TF	SF	
Total dissolved solids (mg L^{-1})	2-102	38-334	(Mahendrappa 1974; Mosello et al. 2002)
Dissolved organic matter (mg-C L^{-1})	1-60	7-480	(Van Stan and Stubbins 2018)
C:N	9-57	10-37	(Van Stan II 2012)
C:S	73-136	29-55	(Goller et al. 2006; Schrumpf et al. 2006)
C:P	58-142	25-103	(Goller et al. 2006)
Total suspended solids (mg L^{-1})	5-99	8-140	(Muoghalu and Oakhuman 2000)
Particulate organic C	1-5	—	(le Mellec et al. 2010)
Particulate organic N	0.2-0.9	—	(le Mellec et al. 2010)
Bacteria (cells L^{-1})	2-4 x10^8	3-7 x10^8	(Bittar et al. 2018)
Fungi (conidia L^{-1})	10-16,000	10-13,800	(Sridhar and Karamchand 2009)
Macrofauna (individuals L^{-1})	—	0-1,170	(Ptatscheck et al. 2018)