

Chapter 2

Theories, Mechanisms and Patterns of Microbiome Species Coexistence in an Era of Climate Change

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2.1 Niche Theory and Microbial Diversity

Ecological diversity of microbes plays a major role in ecosystem functioning and services (Arshad et al. 2007; Saleem et al. 2007, 2008, 2015; Saleem 2012; Saleem and Moe 2014). Understanding the ecological mechanisms and processes that determine the coexistence of millions of microbial species from centimeter to continental scale in the earth's ecosystem represents a major challenge to microbial ecologists. The niche theory predicts the role of niche partitioning among species as a major factor structuring ecological communities, where niche is determined by locally sorting biotic and abiotic factors (e.g., pH, resources, temperature, competition, predation, etc.). The “niche” may be broadly defined as the biotic and abiotic environmental factors/conditions under which an organism can survive successfully in the absence of interspecies interactions, and its dimension may or may not be determined by a single ecological factor depending upon the preexisting environmental variables (Materna et al. 2012). Environmental factors favor the functional traits across different species that determine the niches or habitat specialization of species (Silvertown 2004; McGill et al. 2006). These traits are measurable evolutionary, biochemical, ecological, physiological, and morphological features of species that determine the fitness, survival, and coexistence of species in a community (Table 2.1). Though there is a known biogeographic pattern of functional traits of some globally

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Table 2.1 Some selected examples of evolutionary, ecological, morphological, and physiological microbiome functional traits

Trait	Proposed implications	Selected reference
Antibiotic compounds	Suppress enemies and competitors, microbe–microbe and host–microbe interactions, fitness	O’Sullivan and O’Gara 1992 ; Loper et al. 2012
Biofilm formation	Persistent against biotic and abiotic stressors, metabolically diverse, fix themselves in a niche	Davey and O’Toole 2000 ; Harrison and Buckling 2009
Cell or body side	Survival and functioning under changing environmental conditions	Giraud et al. 2001
Energy specific selection	Chemoautotrophs (carbon from CO ₂ , energy from light) Chemoheterotrophs (carbon and energy from organic molecules) Photoautotrophs (carbon from CO ₂ molecules, energy from light) Photoheterotrophs (carbon from organic molecules, energy from light)	www.uta.edu/.../Carbon%20and%20Ene... University of Texas at Arlington Brown 2014
Environmental condition	Psychrophile, mesophile, thermophile, pH conditions	Rinaldo et al. 2002
Evolution of resistant traits (antibiotic, viral, radiation, etc.)	Survival	Singer et al. 2006
Foraging	Generalist vs. specialist, determine niche breadth and host range	
Gene content	Carbon and energy metabolism, attachment and motility, gene mobility, host–viral interactions, community organization and functioning	DeLong et al. 2006
Genetic background	Determine several properties (e.g., virulence factors) to colonize and survive	Escobar-Páramo et al. 2004
Size of genome	Niche breadth, functioning and life history trajectories	Konstantinidis and Tiedje 2004
Growth rate	Determine the functioning, persistence, dispersal, competition for resources	Wallenstein and Hall 2012 ; Lennon et al. 2012
Habitat specialization	Freshwater, marine, soil, deep subsurface	–
Metabolite content	Survival and functioning under different environmental conditions	Rosselló-Mora et al. 2008
Mutation rate	Determine the capability to adapt to novel environmental conditions	Giraud et al. 2001
Public goods production	Production of a costly resource that benefits all the individuals in the mixture/ community. Determines species interactions, coexistence	Harrison and Buckling 2009 ; West et al. 2006
Rapid evolution	Survival and functioning under changing environmental conditions	Sabehi et al. 2007

Table 2.1 (continued)

Trait	Proposed implications	Selected reference
Ribosomal copy number	Determine the growth rate and responses to environmental conditions	Shrestha et al. 2007
Shape or size/phenotypic plasticity	Different shapes (rods, cocci, spirals, etc.) and sizes (smallest to biggest) to address biotic and abiotic stressors, capability to change morphology to survive in the ecosystem	Agrawal 2001; Matz and Kjelleberg 2005; Cohan and Koeppel 2008; Rinaldo et al. 2002
Transcript abundance	Survival and functioning under changing environmental conditions	Steunou et al. 2006

distributed species (e.g., *Arabidopsis thaliana*), little is known about the biogeographic patterns of microbial functional traits (Green et al. 2008) determining the microbial ecological niche across changing climatic regimes. Additionally, there is a great need for studies presenting broad trait-based biophysical, ecological, and evolutionary approaches to predict the role of functional trait differences across diverse microbial species for niche differentiation. Such knowledge is important to predicting the coexistence of species in species-rich communities typical for microbial communities (Curtis et al. 2002), and it will advance the field of microbiome community ecology on the basis of functional traits as it is suggested for other complex ecosystems (e.g., tropical and Amazonian forest, (McGill et al. 2006; Sterck et al. 2011). Similarly, evolutionary and ecological mechanisms (e.g., relaxed selection or strong selection pressure or balancing selection) and interactions that may lead to evolution and/or loss of functional traits (Ellers et al. 2012) in microbes need to be elucidated. Meanwhile, employing novel techniques such as genome wide association mapping may help us to identify the genetic basis of trade-offs, and the underlying genetic architectures of microbial functional traits. The following sections focus on different aspects of niche dimensions in microbiome ecology.

2.1.1 Temperature and the Metabolic Theory of Ecology

Temperature determines the ecology from an individual organism level (metabolic rate) to community level ecological processes (community-wide productivity, population growth, carbon flux, and patterns of diversity (Enquist et al. 2003; Allen et al. 2006; O'Connor et al. 2007). Microbiome species could be psychrophile, mesophile, and thermophile, where most of the bacteria and archaea in nature are mesophile and thermophile, respectively. Temperature influences several microbial mediated ecological processes such as nitrification (Myers 1975), denitrification (Stanford et al. 1975), ammonification (Stanford et al. 1975), mineralization (MacDonald et al. 1995), nitrogen fixation (Gundale et al. 2012), methanogenesis (Schmidt et al. 2014), biological and nonbiological interactions (Atlas and Bartha 1981; Elliot et al. 2002), and the biodegradation of contaminants (Paul 2006;

Hussain et al. 2007; Arshad et al. 2008; Hussain et al. 2009abc). It also indirectly influences microbial growth efficiency and community shifts in different ecosystems (e.g., phototransformations of dissolved organic matter versus microbial diversity in the marine ecosystem) (Abboudi et al. 2008).

Considering the vital importance of temperature in community ecology, there is a well-known theory, namely the “Metabolic Theory of Ecology (MTE)”, which links the metabolic rate of an organism to its mass and temperature (Clarke 2006). The MTE focuses on the metabolic rate of organisms, which determines the rates of resource uptake/utilization from the environment and thereby controls resource allocation for survival, growth, and reproduction. MTE may therefore explain patterns of ecological processes at all levels of organization from individuals to the biosphere (Brown et al. 2004). Though MTE possesses much broader implications in microbial ecology, it has not received much attention among microbial ecologists (Sinsabaugh et al. 2009). Presently, theory driven studies aiming at studying the “(1) life history attributes, including development rate, mortality rate, life span, and population growth rate; (2) population interactions (trophic and nontrophic interactions), including carrying capacity, rates of competition and predation, and patterns of species diversity, and (3) ecosystem processes, including rates of biomass production and respiration and patterns of trophic dynamics” (Brown et al. 2004) as a function of temperature are relatively less conducted in the field of microbiome ecology, especially in relation to the rising global temperature, greenhouse gas emissions, and accelerated microbial metabolisms in some ecosystems.

Moreover, whether and how seasonal alterations in temperature determine the functional ecology of the microbiome within the contexts of nutrient cycling, greenhouse gas emissions, oceanic acidifications, biological invasions/interactions (epidemiology, pathogenicity, etc.), turnover of communities and functional traits, resource turnover, habitat specific evolutionary adaptations, diversifications, divergence, and overall fitness under different temperature regimes and habitat type merit intensive future research. However, present research to some extent, has focused on either thermal niche specialization of different microbial functional groups and/or on the role of temperature as a source of ecological divergence, evolution, and speciation.

Thermal Niche Specialization Different temperature regimes act as major niche factors, and dramatically determine the microbiome species community composition, coexistence, diversity, and functioning. For instance, the *Synechococcus* A/B group of bacteria are ecological specialists across a wide range of temperature in terms of their productivity and activity (Miller and Castenholz 2000; Allewalt et al. 2006). These bacteria are also restricted *in situ* to different regions along hot spring thermal gradients (Ferris and Ward 1997). Likewise, thermal niche specialization is common for many functional groups of bacteria such as *Acidobacteria* (Miller et al. 2009). Recently, Weltzer and Miller (2013) showed that the different strains of the *Chloroflexus* Operational Taxonomic Unit (OTU) 10 exhibit ecological divergence in a range of temperature for their growth. They reported a positive correlation between thermal niche breadth and temperature optimum for one of their isolates namely “WC7” (C), as determined by the change in optical density at

660 nm (Weltzer and Miller 2013). Meyer et al. (2013) investigated the temperature (regimes) mediated niche differentiation in the Guaymas Basin benthic bacterial communities. They revealed that more than 80% of all observed OTUs were shared across different temperature realms and sediment depths (Meyer et al. 2013). Overall, they classified OTUs in relation to different temperature conditions such as cold ($T < 10^{\circ}\text{C}$), medium ($10^{\circ}\text{C} \leq T < 40^{\circ}\text{C}$) and/or hot ($T \geq 40^{\circ}\text{C}$). Meyer et al. (2013) interpreted their results within the framework of metacommunity ecology (Leibold et al. 2004), stating that the functional patterns of Guaymas bacterial communities were determined by a combination of local species sorting factors such as temperature (i.e., niche differentiation) and regional factors like species dispersal. Similarly, many other reports have also shown the role of temperature in structuring the microbial community composition and functioning of certain functional groups. For instance, incubating microcosms at varying temperatures markedly altered the microbial community composition, as described by 454 pyrosequencing (Wu et al. 2013). The microcosms were incubated for 8 weeks with [^{13}C] bicarbonate labeling of bacterial *amoA* genes that encode the ammonia monooxygenase subunit A. Wu et al. (2013) reported an increase in copy numbers, thus indicating enhanced activity and growth of ammonia-oxidizing bacteria in the microcosms (Wu et al. 2013). The microcosms were dominated by *Nitrosomonas* sp. strain Is79A3 and *Nitrosomonas communis* lineages in the heavy fraction of CsCl gradients at low and high temperatures respectively. The relative microbial dominance at different temperature regimes depicts the niche differentiation of active bacterial ammonia oxidizers across the temperature gradient (Wu et al. 2013). Overall, these examples predict the vital importance of different temperature regimes in structuring the ecological niche of microbiome communities, and call for theory driven research in microbiome community ecology in the time of climate change.

Temperature as a Driver of Ecological Divergence, Evolution, Speciation and Thermal Niche Evolution Trade-Offs As described before, temperature plays a pivotal role in the habitat specialization and functioning of microbiome species diversity and functioning. Several microbial functional groups and species are capable of evolving under a range of temperature regimes, which may ultimately lead to ecological divergence, specialization, and speciation in the microbial ecosystems (Miller and Castenholz 2000; Allewalt et al. 2006; Ferris and Ward 1997). Specialization under certain environmental conditions requires ecological fitness costs. There exist potential trade-offs in the sense that if some traits favor fitness in a specific environment, then these traits are not effective or costly in other environments (Weltzer and Miller 2013). In classical literature for instance, Darwin (1859) states that "... natural selection is continually trying to economize in every part of the organization. If under changed conditions of life a structure previously useful becomes less useful, any diminution however slight, in its development, will be seized on by natural selection, for it will profit the individual not to have its nutriment wasted in building up a useless structure (cited in (Bennett and Lenski 2007))." The assumption of ecological trade-offs remains a critical part of the ecological understanding of adaptive evolution (Bennett and Lenski 2007). General ecological and evolutionary theory also predicts the existence of such trade-offs. (Lynch and

Gabriel 1987; Huey and Kingsolver n. d.; Weltzer and Miller 2013) Elucidating trade-offs in microorganisms is highly challenging (Elena and Lenski 2003; Kassen and Rainey 2004; Bennett and Lenski 2007; Weltzer and Miller 2013). In this context, Levins (1968) view of resource allocation also considers fitness trade-offs in terms of evolving niche specialization in the environment. There is some empirical evidence indicating the role of temperature mediated ecological trades-offs in determining microbial ecological niches (Allewalt et al. 2006; Ferris and Ward 1997; Miller et al. 2009; Weltzer and Miller 2013) within the context of thermal niche specialization. Bennett and Lenski (2007) tested the hypothesis whether adaptation-driven fitness in a certain environment is accompanied by a trade-off, and whether a loss of fitness occurs in other environments. More specifically, they tested whether trade-offs at a relatively high temperature also accompany genetic adaptation to a relatively low temperature (Bennett and Lenski 2007). To test these hypotheses, they determined the relative fitness increment and decrement of 24 lineages of the bacterium *Escherichia coli* evolved for 2000 generations at 20 and 40 °C, respectively. Trade-offs at a higher temperature were tested for their universality, quantitative relationship, generality, and historical contingency (Bennett and Lenski 2007). Assuming all 24 lines as a group, they found a significant decline in fitness at 40 °C (mean decline = 9.4%), reflecting the generality of the trade-off effect. However, conducting a lineage-by-lineage analysis, only 15 out of 24 exhibited a significant trade-off while fitness of one lineage increased at a high temperature (Bennett and Lenski 2007), suggesting that trade-offs were not universal. They did not find a quantitative association between the magnitude of adaptive fitness increment and decrement at 20 and at 40 °C, respectively. Moreover, they also did not find the effect of the historical thermal environment of lineages on fitness increment and decrement at 20 and at 40 °C, respectively. They did not pinpoint the underlying mechanisms responsible for the trade-off, but suggested that the trade-offs are sufficiently prevalent to cause a general fitness effect (Bennett and Lenski 2007). However, they showed empirically that one-third of the experimental lineages attained low-temperature adaptation without obvious high-temperature trade-offs, suggesting that it might not be important that every change conferring benefit in cold environments might also cause a negative effect on function in warmer environments (Bennett and Lenski 2007). However, these trade-offs may differ from temperature-based adaptations to other environmental condition-based adaptations. For instance, Velicer and Lenski (1999) suggested that the adaptation to rich nutrient and energy resources caused a decrease in fitness under resource limited conditions. Later, Knight et al. (2010) studied the proteomic and genetic bases of temperature trade-offs in a saprophytic plant-colonizing bacterium *Pseudomonas fluorescens* SBW25. They reported proteins that were expressed differentially between 28 and 14 °C. Among different protein isoforms, 32 responded to a change in temperature. They selected seven of these proteins (*OmpR*, *MucD*, *GuaD*, *OsmY* and three of unknown function, *Tee1*, *Tee2* and *Tee3*) for genetic and ecological analyses. Moreover, temperature mediated changes in protein expression were linked also to parallel transcriptional changes (Knight et al. 2010). At genetic levels, they stated that the contribution of the genes encoding each of the seven proteins to the fitness was relatively greater at 14 °C than at 28 °C. Overall, they observed two cases of trade-

offs (increased fitness at one temperature and declined fitness at the other—*mucD* and *tee2* deletions). However, a variable relationship between the fitness effects of genes *in vitro* and *in vivo* was seen. But two temperature-responsive genes such as *osmY* and *mucD* contributed substantially to the capability of *P. fluorescens* to colonize the plant environment (Knight et al. 2010). Certainly, different microbial species exhibit temperature mediated fitness trade-offs to ensure their survival and functioning under different habitat conditions. However, it remains to elucidate the mechanisms of these trade-offs and their functional implications in determining the patterns of microbiome communities and functioning in present scenarios of changing microbial ecosystems and rising temperature regimes (i.e., climate warming).

2.1.2 Implication of Habitat Heterogeneity in Determining Ecological Niche

Habitat heterogeneity (spatial or temporal) is a very broad term, and it depends on several factors (e.g., topographies, climate types, resources, etc.). It is a measure of the number of available niches in an ecosystem (Bazzaz 1975). It also determines the dynamics and fluxes of organisms, materials, energy, and the way these are interlinked with each other (Hutchings et al. 2000) (Pickett and Cadenasso 1995). Some empirical evidence suggests that spatially structured habitats with varying physical and chemical gradients encourage ecological diversification rates (Doebeli and Dieckmann 2003) and tend to support greater diversity through the coexistence of multiple ecological specialists, which are locally adapted to different niches (Kassen and Rainey 2004; Weltzer and Miller 2013). The structurally complex and heterogeneous habitats may provide more ecological niches to different species and diverse ways of exploiting the available environmental resources. Consequently, these habitats increase and maintain species diversity (Bazzaz 1975; Kassen and Rainey 2004; Tews et al. 2004) through different eco-evolutionary processes such as drift, selection, mutations, and dispersal (Chap. 3). Habitat heterogeneity also enhances the strength of intra-specific competition as compared to that of inter-specific competition, and consequently promotes species coexistence and maintenance (Chesson 2000). Some evidence suggests that it may contribute to evolutionary divergence and speciation in microbes (Connor et al. 2010; Oakley et al. 2010). Furthermore, recent evidence also predicts that habitat heterogeneity favors the existence of the minor group of microbial functional groups like methane-oxidizing bacteria (MOB) in a riparian floodplain, for instance, and increases the role of these subgroups in methane consumption in riparian wetlands (Bodelier et al. 2013). Likewise, Porter and Rice (2013) stated that the fitness related trade-offs across heterogeneous ecosystems can enhance microbial diversity by checking competitive exclusion. However, the significance of these trade-offs in preserving diversity in natural microbial assemblages remains largely untested since it is hard to empirically test these trade-offs in artificial evolution experiments (Porter and Rice 2013). According to them, stressful ecosystems like heavy-metal contaminated serpentine soils are excellent model systems to investigate how do habitat heterogeneity increase genetic

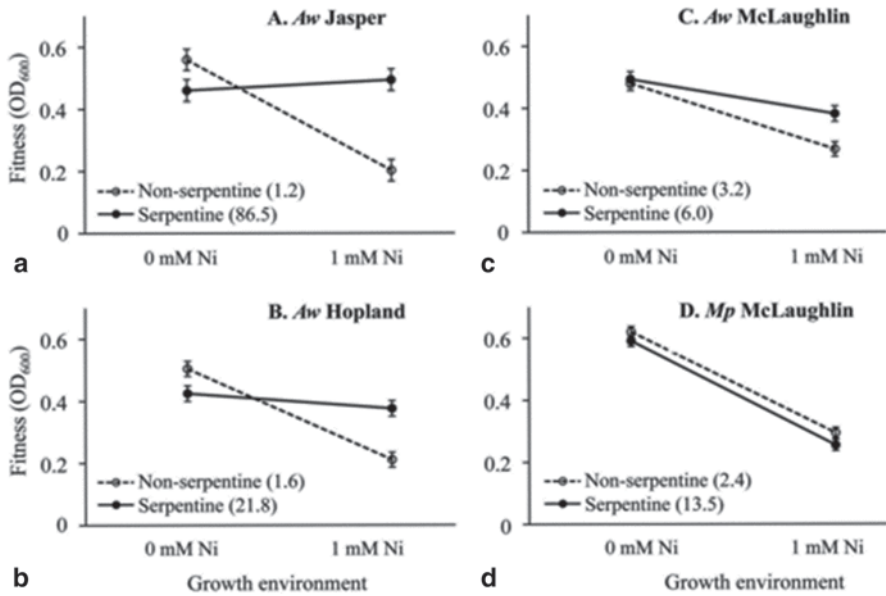


Fig. 2.1 Fitness of rhizobial strains isolated from non-serpentine (dashed line) and serpentine soils (solid line), which were grown with 1 mM or 0 mM nickel (with permission, Porter and Rice 2013)

diversity. Employing a spatially replicated experimental design, they showed that rhizobia symbiotic interactions with legumes inhabiting contrasting serpentine and non-serpentine soils demonstrated a trade-off between a genotype's nickel tolerance and its capability to replicate rapidly (Porter and Rice 2013). Fitness of rhizobial isolates was more pronounced in heterogonous serpentine soils (solid line) than in non-serpentine (dashed line) soil grown with 1 mM or 0 mM nickel (Fig. 2.1). Furthermore, they reported adaptive divergence in rhizobial assemblages at multiple sites across different soil-type heterogeneity, depicting that these trade-offs may enhance the coexistence of phenotypically distinct bacterial lineages (Porter and Rice 2013). Overall, their results greatly support the idea that habitat heterogeneity and associated habitat specific fitness trade-offs are important predictors of genetic diversity and evolution of bacterial assemblages. However, considering the potential role of climate and land-use changes in habitat alteration, destruction, and disturbance, forthcoming microbiome community ecology research must be an integral part of research and conservation strategies aiming at the conservation and preservation of natural ecosystems, habitats, and biodiversity. The following sections explain different dimensions of habitat heterogeneity and their role in shaping ecological diversity of microbiomes.

Resource Heterogeneity Resource heterogeneity promotes species diversity (Tilman and Pacala 1993) and species coexistence in the ecosystem (Tilman 1982a; Tilman and Pacala 1993). The heterogeneity of one or more limiting resources is thought to reduce competition among species and to sustain high species richness

Table 2.2 Different features of resource heterogeneity and their proposed role in general as well as microbiome ecology

Key features but not limited to these	Suggested effect on ecosystem properties but not limited to these	Selected references
Resource availability—net resource that results from the effects of both biotic and abiotic factors in a system including resource supply (per area or volume)	Fitness trade off, biogeochemical cycling, functional groups and traits, competition among species, species richness and coexistence, host colonization	Coley et al. 1985; Rasche et al. 2011; Delpin and Goodman 2009; Chesson 2000; Langenheder and Prosser 2008b; Tilman 1982
Resource complexity/diversity	Community composition, diversity-functioning relationships	Jousset et al. 2011; Langenheder et al. 2010
Resource opportunity—a high availability of resources on which a potential consumer depends	Competition among species, species richness and coexistence, host colonization	Shea and Chesson 2002
Resource quality—quality of the substrate/food in terms of nutrient composition	Diversity-functioning, species interactions, energy transfer in food web, foraging biology, food web stability, trophic and nontrophic interactions, biogeochemical cycling, promote key functional groups (e.g., oligotrophs favoured at low C/N quality)	Mayor et al. 2012; Bukovinszky et al. 2008; Fierer et al. 2007b)
Resource quantity—total amount of substrate in certain habitat	Maintain diversity, functional groups (e.g., copiotrophs), competition among species, species richness and coexistence, host colonization	Stevens and Carson 2002; Fierer et al. 2007b
Resource supply—net rate of resources entering into the system (amount per area or volume per time)	Community composition, diversity-productivity relationships, biogeochemical cycling, species interactions, supply of limiting resources remarkably influence different ecosystem properties	Tilman 1982b; Claire Horner-Devine et al. 2003; Chapin et al. 2000; Jardillier et al. 2005; Harpole and Tilman 2007

(Tilman 1982; Tilman and Pacala 1993). It tends to change the diversity and community structure of microbes (Nelson 2009). However in some cases, site specific conditions and shifts in community structure (random, ecosystem-specific and/or directional) may also determine the impact of a certain resource concentration on microorganisms (Vallino et al. 1996; Eiler et al. 2003). In general, resource heterogeneity is a complex variable as well as term, and its role in microbiome ecology may be explained in different ways (Table 2.2). Zhou et al. (2002) tested the hypothesis of whether carbon resource heterogeneity had an effect on microbial competition and diversity patterns. They hypothesized that if resources are present in several different forms, microbial populations can escape competition by specialization. Results obtained from their experiment suggested that carbon resource heterogeneity might be responsible for observed uniform diversity patterns in high-carbon samples even in the saturated zone (Zhou et al. 2002). Contemporary changes in

climate and land-use types may potentially alter the abundance and diversity of ecological resources by changing their dynamics and turnover rates, which might have pronounced effects on microbiome community composition, functioning, and stability in future.

Factors Determining Resource Heterogeneity Different factors determine resource heterogeneity in the ecosystems, and in-depth understanding of those is highly important to elucidate its role in structuring the ecological diversity of the microbiome. Resource heterogeneity is greatly influenced by the spatial location of the sites, which ultimately determines the occurrence and prevalence of the resources. For example, surface soils exhibit more resource diversity since these are subject to a variety of nutrient exposures from primary production and/or from surrounding environments (e.g., nutrient run off, etc.). Consequently, greater resource heterogeneity of these soils favors the maintenance of higher microbial diversity. Therefore, surface soils support much higher diversity than that of the corresponding subsurface soil surfaces (Zhou et al. 2004). The forest or other soil ecosystems that are heavily covered with diverse vegetation also display greater resource heterogeneity depending on type, intensity and diversity of the leaf litter, and plant diversity. Overall, plant diversity generates resource heterogeneity for soil microbial communities through different factors including but not limited to these: litter chemistry, quality, diversity, quantity, and root exudate chemistry (McIntosh et al. 2013). Therefore, higher plant diversity may lead to a greater diversity in soil microbial communities (Hooper et al. 2000; McIntosh et al. 2013). McIntosh et al. (2013) studied the relationship between the forest floor microbial communities and resource heterogeneity within the mature lodgepole pine forests. The results from this experiment predicted that the spatial partitioning of understory plant species and their rhizosphere resources (e.g., root exudates, nutrients) generated resource heterogeneity, which tended to reshape the patterns of variation in below-ground microbial communities in mature lodgepole pine forests (McIntosh et al. 2013). Moreover, anthropogenic activities including the release of nutrients and other organic contaminants from agricultural fields also increase the resource heterogeneity in the microbial habitats. Bengtsson et al. (2013) reported a positive covariation between microbial diversity, biomass, evenness, polycyclic aromatic hydrocarbons (PAHs) catabolic genes, and PAH concentrations, predicting that the creosote contamination enhanced the diversity and abundance of PAH degraders at this site. Furthermore, it was suggested that organic contaminants such as PAHs created a spatial resource heterogeneity, which promoted a greater variability in richness and diversity than was normally observed at similar scales in uncontaminated sites (Fig. 2.2) (Bengtsson et al. 2013). In another study, Vasileiadis et al. (2013) investigated the impact of land-use change on soil microbial communities and related diversity drivers as an effort to underpin the role of ecology theories with respect to the observed patterns. Microbial diversity was analyzed across a land-use transect using high-throughput partial 16 S rRNA gene sequencing. Land use seemed to greatly determine soil properties and microbial community compositions (Vasileiadis et al. 2013). The experimental results revealed a greater effect of soil total organic carbon and pH on the diversity of *bacteria* and *archaea*. Soil amendments were identified as potential drivers of the indigenous microbial communities,

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